The Transmission and Evolution of Human Culture

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of St. Andrews for the degree of Doctor of Philosophy

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Abstract

‘Culture’ is defined as information, such as knowledge, beliefs, skills, attitudes or values, that is passed from individual to individual via social (or cultural) transmission and expressed in behaviour or artifacts. ‘Cultural evolution’ holds that this cultural inheritance system is governed by the same Darwinian processes as gene-based biological evolution. In Part A of this thesis it is argued that as compelling a case can now be made for a Darwinian theory of cultural evolution as Darwin himself presented in *The Origin Of Species* for biological evolution. If culture does indeed evolve, then it follows that the structure of a science of cultural evolution should broadly resemble that of the science of biological evolution. Hence Part A concludes by outlining a unified science of cultural evolution based on the sub-disciplines of evolutionary biology.

Parts B and C comprise original empirical and theoretical work constituting two branches of this science of cultural evolution. Part B describes a series of experiments testing for a number of hypothesised biases in cultural transmission. Evidence was found for a ‘social bias’ that acts to promote information concerning third-party social relationships over equivalent non-social information, and a ‘hierarchical bias’ that acts to transform knowledge of everyday events from low-level actions into higher-level goals. Three other hypothesised biases concerning status, anthropomorphism and neoteny were not supported, although each gave rise to potential future work using this methodology. Part C presents a theoretical investigation into the coevolution of the genetic bases of human mating behaviour and culturally inherited folk beliefs regarding paternity. Gene-culture coevolution and agent-based models suggested that beliefs in ‘partible paternity’ (that more than one man can father a child) create a new more polygamous form of society compared with beliefs in singular paternity (that only one man can father a child).

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Introductory Remarks

CHAPTER 1 - INTRODUCTION

The core topic of this thesis is human culture, and in particular the study of culture and cultural transmission from an evolutionary perspective. Following Richerson and Boyd (2005), *culture* is defined as "information capable of affecting individuals' behavior that they acquire from other members of their species through teaching, imitation, and other forms of social transmission" (p.5). *Cultural* (or social) *transmission* hence describes the process by which this information is passed from individual to individual. Finally, *cultural evolution* concerns the application of Darwinian principles of evolutionary change to cultural phenomena.

Theories of 'cultural evolution' have had a somewhat troubled history in science. Early attempts to apply evolutionary theory to culture were deeply flawed, drawing more from Spencer than Darwin (Plotkin, 2004), resulting in the progressive and unilinear theories of Tylor (1871) and Morgan (1877). Hence human societies were seen as progressing inexorably through a fixed set of evolutionary stages, from 'savagery' through 'barbarism' and finally to 'civilisation' (Laland & Brown, 2002). Despite the notion of inevitable progress being antithetical to Darwinian evolution, these flaws persisted within anthropology until the mid-20th century (e.g. Sahlins & Service, 1960; Steward, 1955; White, 1959).

The application of a true Darwinian theory of evolution to culture remained rare and somewhat informal (e.g. Campbell, 1960; Dawkins, 1976b) until the seminal works of Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985), which applied rigorous population genetics methods to cultural phenomena. By this time, however, sociobiology (Wilson, 1975) had become the dominant school of evolutionary thought as applied to humans. Sociobiology, and its descendant evolutionary psychology (Barkow, Cosmides, & Tooby, 1992), have tended to ignore social influences on human behaviour in favour of explanations purely in terms of genetic fitness. And partly as a legacy of the early progressive theories of cultural 'evolution' and their association with eugenics and racism, social scientists within anthropology, psychology and sociology have tended to be hostile to any evolutionary approach to the cultural phenomena that they study (Laland & Brown, 2002). In the last few decades, then, any work that has sought to bridge the gap between the social and the biological sciences (e.g. Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Plotkin & Odling Smee, 1981) has been relatively neglected and unpopular. In essence, such work was deemed too social for evolutionary scientists, and too evolutionary for social scientists.

In recent years, however, there has been a growing interest in the topics of cultural transmission and cultural evolution amongst certain evolutionarily-minded psychologists, anthropologists, archaeologists, linguists and economists (e.g. Aunger, 2002; Aunger, 2000b; Blackmore, 1999; Boyd & Richerson, 2005; Mace & Holden, 2005; Mesoudi, Whiten, & Laland, 2004; Mufwene, 2001; O' Brien & Lyman, 2000, 2002; Pagel & Mace, 2004; Plotkin, 2002; Richerson & Boyd, 2005; Runciman, 2005; Schotter & Sopher, 2003; Shennan, 2002; Wheeler, Ziman, & Boden, 2002). There has also been a burgeoning interest in culture and social learning in non-human species (e.g. Avital & Jablonka, 2000; Byrne *et al.*, 2004; Fragaszy & Perry, 2003; Hurley & Chater, 2005; Laland & Hoppitt, 2003; van Schaik *et al.*, 2003; Whiten, 2000a; Whiten *et al.*, 1999, 2001; Whiten, Horner, & Marshall-Pescini, 2003).

This thesis represents an attempt to both integrate and contribute to this growing field of cultural evolution. Part A comprises two novel theoretical reviews concerning evolutionary approaches to human culture. The first of these (Chapter 2) argues that as compelling a case can now be made for a Darwinian theory of cultural evolution as Darwin himself presented in *The Origin Of Species* (1859) for biological evolution. The second (Chapter 3) takes this argument to its next logical step and contends that if a Darwinian theory of cultural evolution is accepted as valid, then the structure of a science of cultural evolution should resemble in key ways that of the science of biological evolution, i.e. evolutionary biology.

The following sections then present original empirical and theoretical work that represents two branches of this science of cultural evolution. Part B concerns the experimental study of human cultural transmission, comprising a literature review (Chapter 4) and five original experimental studies (Chapters 5-9). The literature review identifies Bartlett's (1932) 'transmission chain method' as a potentially valuable but underused means of investigating cultural transmission. In this method, material is passed along a chain of participants in a manner similar to the children's game 'Chinese Whispers' or 'Broken Telephone'. Measuring the changes that occur to the material as it is transmitted, and comparing the degradation rates of different types of material, can then reveal systematic biases in cultural transmission. The five subsequent chapters used this methodology to test for the presence of five such biases: Chapter 5 looked at whether human cultural transmission is biased towards social over equivalent non-social information; Chapter 6 studied how event knowledge is transformed according to a hierarchically structured 'action script'; Chapter 7 looked at the effect of the status of the source on transmission; Chapter 8 examined the effect of anthropomorphism on the transmission of descriptions of animal behaviour; and Chapter 9 tested whether a preference for neoteny affects the transmission of teddy bear faces.

Part C presents a mathematical model of gene-culture coevolution (Chapter 11). The 'gene-culture coevolution' approach (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Feldman & Cavalli-Sforza, 1976) uses a set of mathematical techniques drawn from population biology to explore the parallel transmission of both culture and genes, and the interaction between these two separate inheritance systems. An alternative agent-based modelling technique was also employed. The case investigated in Chapter 11 concerned the inheritance of cultural beliefs about paternity, specifically whether paternity is seen as 'singular' (only one male can father a child) or 'partible' (more than one male can father a child). The models explore the coevolution of these culturally transmitted beliefs with genes that influence mating behaviour. Finally, Chapter 12 draws general conclusions from the preceding chapters about cultural transmission and cultural evolution, and outlines how the studies presented in this thesis can guide future work in order to provide a fuller and richer understanding of human culture.

Part A - Cultural Evolution

CHAPTER 2 - IS HUMAN CULTURAL EVOLUTION DARWINIAN? EVIDENCE REVIEWED FROM THE PERSPECTIVE OF *THE ORIGIN OF SPECIES*[1]

2.1 ABSTRACT

The claim that human culture evolves through the differential adoption of cultural variants, in a manner analogous to the evolution of biological species, has been greeted with much resistance and confusion. Here it is argued that as compelling a case can now be made that cultural evolution has key Darwinian properties, as Darwin himself presented for biological evolution in *The Origin of Species*. Culture is shown to exhibit variation, competition, inheritance, and the accumulation of successive cultural modifications over time. Adaptation, convergence and the loss or change of function can also be identified in culture. Just as Darwin knew nothing of genes or particulate inheritance, a case for Darwinian cultural evolution can be made irrespective of whether unitary cultural replicators exist or whether cultural transmission mechanisms are well-understood.

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[1] Adapted with minor revisions from Mesoudi, A., Whiten, A. and Laland, K.N. (2004). Is human cultural evolution Darwinian? Evidence reviewed from the perspective of *The Origin Of Species*. *Evolution*, 58(1), 1-11.

2.2 INTRODUCTION

In *The Origin of Species* (1859), Darwin frequently used analogies with cultural change to illustrate his theory of biological evolution. More recently, arguments that insights into cultural evolution are to be gained by appreciating its Darwinian properties have been developed by eminent figures in fields ranging from biology to philosophy to psychology (e.g. Dawkins, 1976b; Dennett, 1995; Hull, 1982; Popper, 1979; Skinner, 1981). In the last few years such efforts have intensified, with an extensive literature proliferating on relationships between biological and cultural evolution (e.g. Aunger, 2002; Aunger, 2000b; Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Plotkin, 2002; Richerson & Boyd, 2005; Shennan, 2002; Wheeler *et al.*, 2002).

However, attempts to apply the theory of evolution by natural selection to the origins of the diverse range of beliefs, knowledge and artifacts that constitute human culture have met with great resistance in some quarters (e.g. Fracchia & Lewontin, 1999; Gould, 1991; Hallpike, 1986; Pinker, 1997), comparable to that which followed Darwin's insight. A prime focus of these debates (see Aunger, 2000b) is a preoccupation with the possibility of cultural 'units of inheritance', sometimes called ' memes'(Dawkins, 1976b), the delineation of which is often (erroneously) seen as a necessary prerequisite for Darwinian evolution. Darwinian models of cultural evolution have consequently been criticised (and are commonly being rejected) on the grounds that culture cannot be divided into discrete particles (e.g. Bloch, 2000; Kuper, 2000) or that to the extent that such particles exist, they do not faithfully replicate in the way genes do (Sperber, 2000). However, when he wrote *The Origin*, Darwin knew nothing of genes, and he had little understanding of Mendelian particulate inheritance. Many contemporary commentators therefore appear to be rejecting Darwinian cultural evolution on grounds that might have led them to reject the fundamental case made for evolution through natural selection in *The Origin*.

In this chapter it is argued that a clearer approach to these issues can be made by returning to the basic principles of the theory supported in *The Origin*, and testing these against the rich variety of empirical data concerning human culture that have been garnered in a diversity of human sciences since *The Origin* was written. Accordingly, we shall briefly reprise the key elements of the case for biological evolution through natural selection that were presented by Darwin in *The Origin of Species* and explore the extent to which a parallel case is justified for the evolution of culture. Just as *The Origin* forced biologists to take the theory of evolution seriously, it is hoped that a similar treatment for cultural evolution will force those in the social sciences to give the argument serious consideration, and provoke biologists into giving the matter more thought than they perhaps have done in the past.

The comparison with *The Origin* is more than just an intellectual exercise or historical curiosity. It is of considerable significance to biologists if the core evolutionary processes at the heart of their discipline govern an aspect of human life - culture - that is often contrasted with biology. This is not only because the theories, tools and findings of biological evolution may generalise to other disciplines, rendering the study of evolution far broader and more important than currently conceived, but also because biological evolution would have to be regarded as interwoven into a lattice of interacting evolutionary processes, for which hierarchical, multiple-level or multiple process models will be required (e.g. Hull, 2001; Laland, Odling Smee, & Feldman, 2000; Plotkin & Odling Smee, 1981).

A final justification for this comparison derives from a common criticism of the proliferating 'memetics' literature: its reliance on theory over data (Laland & Brown, 2002). In this field there is much armchair speculation and little attempt to integrate multiple sources of existing evidence to make a coherent case. By contrast, the integration of several disparate sources of evidence was instrumental to Darwin's argument (e.g. the fossil record, geographical distribution of species, taxonomy, morphological features, artificial breeding). A similar breadth of sources is drawn on below. If it is accepted that Darwin provided a robust case for biological evolution by natural selection, and an equivalent case can be made for the evolution of culture, then either Darwinian cultural evolution should be accepted as a valid theory in the domain of culture, or the burden of proof is being placed unfairly high. This position does not, of course, imply that a biological model is by itself expected to provide a complete theory of a phenomenon as complex as human culture, and this chapter concludes by highlighting some key points of departure of human cultural evolution from the principles of biological evolution.

2.3 PRELIMINARY DEFINITIONS

Darwin had the considerable luxury of not being required to define the phenomenon ('life') that he was trying to explain. However, a long history of confusion over how to define 'culture' (Kroeber & Kluckohn, 1952) suggests an explicit definition is needed here. Following Boyd and Richerson (1985), *culture* is defined as acquired information, such as knowledge, beliefs and values, that is inherited through social learning, and expressed in behaviour and artifacts. *Cultural evolution* is consequently the idea that the information in this cultural domain frequently changes according to a similar process by which species change, that is, through the selective retention of favourable cultural variants, as well as other non-selective processes such as drift. Forthwith, use of the term ‘cultural evolution’ will imply such a general Darwinian process. This should be distinguished from firstly non-evolutionary theories of cultural change, as exemplified in the cultural determinism of Boas (1940), Mead (1928) and Benedict (1934), the structuralism of Levi-Strauss (1963), or the semiotic theories of Geertz (1973), and secondly non-Darwinian theories of cultural evolution. This latter distinction is important, since distortions of Darwinian thinking have long been used to bolster erroneous, prejudicial, linear and progressive conceptions of cultural change (e.g. Morgan, 1877; Tylor, 1871).

The distinction between ‘cultural selection’ and ‘natural selection’ is also emphasised (Cavalli-Sforza & Feldman, 1981). For example, smoking may increase or decrease in frequency through the differential adoption of the habit (cultural selection) or through the differential survival of smokers (natural selection). Although both processes operate on human cultural variation, it is cultural selection that concerns us here.

2.4 THE EVIDENCE

In *The Origin*, Darwin set out his logical case, empirically backed at each step, by first establishing the extent of variation in characters, followed by analyses of the inevitable competitive struggle for existence, and its consequences, through inheritance, for the shaping of forms of life. Likewise we will consider in turn variation, competition and inheritance, followed by other major themes *The Origin* developed, namely the accumulation of modifications, adaptation, geographical distribution, convergence, and changes of function.

2.4.1 Variation

> …we have many slight differences which may be called individual differences…[which] are highly important for us, as they afford materials for natural selection to accumulate…(Darwin 1859, pp. 101-102)

Essential to Darwin's case was the need to demonstrate the existence of variation between individuals in a population. Without variation there can be no selection of favourable variants, and hence no accumulation of beneficial modifications. Does human culture meet this requirement?

That human culture displays great variation is obvious, but its extent is worth briefly documenting in comparative perspective, through illustrative statistics. A point of contrast is with our closest relatives. In the case of chimpanzees, 39 geographically variable behaviours have been distinguished, such as the use of different kinds of tools (Whiten *et al.*, 1999; 2001), which are thought to represent distinct cultural variants, with a comparable figure of 24 variants for orangutans (van Schaik *et al.*, 2003). In contrast, Basalla (1988) reports that 4.7 million patents had been issued in the U.S.A. alone since 1790, while the latest edition of the *Ethnologue* (Grimes, 2002) lists a total of 6,800 languages spoken world-wide. Steward (1955, p. 81) reports that an attempt to catalogue all 'culture elements' (e.g. pottery, the bow, shamanism, polyandry) in various groups of American Indians resulted in the identification of 3000-6000 elements, while the United States military force that landed in Casablanca during World War II was equipped with over 500,000 different material items. Finally, Basalla (1988) notes Karl Marx's surprise at learning that 500 different types of hammer were produced in Birmingham in 1867.

However, what is critically required for the Darwinian process is that variants are of a kind that will compete with each other for differential representation in the future. Thus, among any set of 500 different hammers, it will be important to distinguish between those which vary because they perform different functions, and those that represent alternative designs for the same purpose, for it is between the latter that the 'struggle for existence' is expected to be most acute. While certain cultural phenomena such as alternative religious beliefs would seem to be mutually incompatible and vying with each other, there appears to be surprisingly little systematic documentation of cultural variation that is in competition. One rather whimsical but significant example is provided by Hinde and Barden (1985), who measured the facial dimensions of teddy bears over an 80 year period and found a gradual enlargement of the forehead and shrinking of the snout, which they interpreted as reflecting a human preference for baby-like neonatal features. This was interpreted as the result of selection pressure from consumers of teddy bears, acting on the considerable variation on these dimensions that the authors measured at each point along the historical progression.

In general, we might expect that behavioural or technological innovations, such as those indicated in the patent statistic cited above, may be variations on existing patterns, and so provide the variation of interest. Competition between new and older variants would then ensue. According to an extensive analysis by Basalla (1988), technological change through gradual modifications of what went before is the rule rather than the exception. Amongst numerous examples cited by Basalla (1988) are Joseph Henry's 1831 electric motor, which borrowed many features from the steam engine, and Eli Whitney's 1793 cotton gin, designed to remove seeds from cotton plants, which was based on a long line of Indian devices. The new variations would be precisely the kind likely to compete with their more long-standing counterparts.

Evidence that two or more cultural variants are indeed competing comes from testing the prediction that over time one variant will increase in frequency while another shows a corresponding decrease. This has been demonstrated by archaeologists using the method of 'frequency seriation', in which the frequencies of excavated cultural artifacts are recorded at different time periods, thereby reconstructing lineages of competing artifacts (O' Brien & Lyman, 2000) For example, Kroeber (1916) reported that corrugated pottery found in New Mexico gradually decreased in frequency over time, while the frequency of painted pottery increased. More recently, O'Brien and Lyman (2000) have detailed how lineages of prehistoric projectile points from the south-western United States show an increase in functional efficiency over time, demonstrating competition of successive forms in one or more lineages, with each new, more efficient variant out-competing and replacing the older form. Section 2.4.4 below examines how other cultural traits, such as stone tools and mathematical systems, show a similar accumulation of successive forms over time, each the result of competition amongst similar variants.

What are the sources of cultural variation? Darwin had only the vaguest understanding of how the process of biological (sexual) reproduction could give rise to variation, noting only that: "..individual differences..are known frequently to appear in the offspring from the same parents.." (p. 102). At a similar level of analysis, cultural variation arises through errors or improvisation in learning and distortion in transmission. This distortion has been demonstrated by 'transmission chain studies', in which material is passed from person to person, in a manner similar to the children's game 'Chinese whispers'. For example, Bartlett (1932) found a tendency for British participants to distort material originating from a Native American culture according to their own cultural background, while Allport and Postman (1947) found that a description of a picture was distorted according to the subjects' racial prejudices. Reviewing the relevant literature, Campbell (1958) listed 21 different systematic biases in human social transmission that involve the loss of information, the distortion of existing information, or the introduction of novel information. Similarly, Buckhout (1974) detailed the selective and constructive nature of human memory in the context of eyewitness testimony research. Such studies show that the storage and transmission of cultural knowledge is far from perfect, and much variation is spontaneously introduced.

Darwin proposed that the presence of variation is required for there to be a response to selection pressures, a principle later formalised in Fisher's Fundamental Theorem (Fisher, 1930). A similar phenomenon is exemplified in the study of creativity. In a longitudinal study of teams of molecular biologists, Dunbar (1995; 1997) found that those teams composed of scientists with varied research backgrounds made more key discoveries and breakthroughs than otherwise equivalent teams composed of scientists with similar backgrounds and expertise. The implication here is that the more heterogeneous teams generated a richer variety of ideas upon which cultural selection could work than the more homogeneous teams. There was also a tendency for the successful teams to focus on unexpected findings, suggesting the benefit of introducing novel variation. These results echo more general findings in the human creativity literature (Simonton, 1999) that creative individuals tend to be more prolific in their output (irrespective of the quality of that output) and exhibit more divergent thinking compared with less creative individuals, both of which will increase the chances of encountering a successful variant. There is also widespread experimental evidence that groups, especially heterogeneous groups, outperform individuals in tasks of problem-solving or decision making (Garrod & Doherty, 1994; Moshman & Geil, 1998; Schulz Hardt, Frey, Luethgens, & Moscovici, 2000), again suggesting that more variation is generated on which selection can then act.

Darwin argued that biological variation is naturally produced without regard to its consequences (what we now think of as random mutation), with favourable variations being recognised through an independent selection process. In the case of human culture, however, we must contemplate the possibility that foresight may be applied to produce variation channelled towards a certain solution to a problem. This would constitute a departure from a Darwinian model of cultural change, raising the question of how much cultural evolution may be 'directed' in this way, rather than through the Darwinian algorithm of undirected variation coupled with selection.

In fact, the literature on human creativity indicates that much variation in culture is *not* directed in this sense. Simonton (1995) has shown that innovation or discovery is often the result of trial and error, such as when Watson and Crick painstakingly tried to fit molecular models together until they hit on the double helix. Although their intention was to solve this specific problem, intention itself was not sufficient to reach that solution. Other cases demonstrate that intention to solve is also not a necessary condition, such as when William Roentgen, winner of the first ever Nobel Prize for physics, accidentally and unwittingly discovered x-rays in 1895 whilst studying how cathode rays penetrate different materials. Other serendipitous or accidental discoveries and inventions listed by Simonton (1995) include animal electricity, laughing gas anaesthesia, electromagnetism, ozone, photography, dynamite, the gramophone, vaccination, saccharin, radioactivity, classical conditioning, penicillin, Teflon and Velcro.

In other cases, however, cultural variation may not be independent of selection, representing what Laland, Odling-Smee and Feldman (2000) have termed 'smart variants'. Biologically evolved biases in cognition and other cultural traits may guide behaviour in a non-random direction. What remains to be clearly determined is the relative importance of directed and non-directed variation in actual cultural evolution.

Viewing the comparison between biological and cultural evolution from the reverse perspective, it is also important to note that biological variation is also to a degree directed, insofar as any potential variation is heavily constrained by an organism's present form, which is in turn determined by the species' history of selection. Variation is only random within such boundaries. Indeed, Hull, Langman and Glenn (2001), in a general account of Darwinian selection processes, have argued that

> ..statements about the sorts of variation that function in selection processes need not include any reference to their being blind, random, or what have you. All of the terms that have been used to modify variation are extremely misleading. Hence, we see no reason to put any adjective before variation in our definition of selection. (Hull *et al.*, 2001, p. 514)

In conclusion, human culture has been shown to exhibit extensive variation that is both necessary and conducive to cultural evolution. Although this variation may not be entirely random with respect to selection, ultimately it matters less to the Darwinian process how variation arises, than that variation exists and is exposed to selection.

2.4.2 Competition

> A struggle for existence follows from the high rate at which all organic beings tend to increase. (Darwin 1859, p. 116)

Inspired by Malthus' *Essay on the Principle of Population* (1798), which showed how a geometric increase in the world's population will lead to rapid overcrowding and a shortage of key resources, Darwin realised that a similar shortage of resources in nature will lead to *competition* between variants, and hence the selection of favourable variants. Similarly, no individual person can adopt and express all of the immense cultural variability indicated above, so competition for expression in human brains, behavioural repertoires and material products will occur. Darwin (1871) himself argued that such competition occurs amongst words:

> A struggle for life is constantly going on amongst the words and grammatical forms in each language. The better, the shorter, the easier forms are constantly gaining the upper hand, and they owe their success to their own inherent virtue. (Darwin 1871, p. 91)

Clearly, the 'struggle' Darwin was alluding to here cannot be directly compared to the competition over finite physical resources alluded to by the reference to Malthus. Rather, we have to think in more general terms, of a competition for limited 'slots' or functionally equivalent 'solutions' to specific 'problems'. In the case of Malthusian overcrowding the available slots are limited by the carrying capacity of the environment. In Darwin's linguistic example, the slots may instead be semantic categories, which alternative terms compete to label, an example of which would be the successive replacement over recent years in youth culture of the adjectival synonyms 'neat', 'fab' and 'cool'.

One way to conceptualise what any set of cultural variations are in general competing over is in terms of functional categories. Thus, synonyms will be in competition for describing the same semantic category; different hammers will be in competition with respect to effective hammering; and different gestures may be in competition to fulfil the same social function. This is analogous to the biological case, for although variations such as those in foraging strategies and territorial defence may indeed sub-serve competition for limited resources in the narrow Malthusian sense, 'competition' considered more broadly is focused on relative functionality, thus extending to characters such as predator defence strategies, which are not directly concerned with competition for resources.

Competition between functionally equivalent variants is predicted to lead to the eventual extinction of less favourable forms. Darwin argued against the permanence of species by pointing to fossils of extinct species:

> ..each new variety, and ultimately each new species, is produced and maintained by having some advantage over those with which it comes into competition; and the consequent extinction of less favoured forms almost inevitably follows. (Darwin 1859, p. 323)

The typically faster rate of cultural change compared with biological change potentially makes cultural extinctions much easier to observe. For example, Rivers (1926) detailed how the canoe, pottery, the bow and arrow and circumcision disappeared from various islands of Oceania. Some cases, such as the canoe, were attributed to the death of all members of the society who had the requisite skills to manufacture the artifact, but some, like circumcision, died out despite the continued survival of its former practitioners. Similar extinction of technology has been documented in Japan, with the loss of the gun and of domesticated animals and wheeled vehicles (MacFarlane & Harrison, 2000; Perrin, 1979), and in Tasmania, where cultural artifacts such as bone tools and cultural practices such as fishing were lost following isolation from mainland Australian populations (Diamond, 1978). There is also at present a very high extinction rate of languages, with Krauss (1992) estimating that half of the 6,800 languages world-wide will be extinct within a century if the present rate continues, although estimates as high as 90% are plausible (compared to just 7.4% of mammalian and 2.7% of avian species that are listed as endangered: Krauss 1992).

The latter data illustrate the important point that, as in biological evolution, the scale of competition can vary considerably. At one extreme, whole languages may be in competition, with one replacing the other; at the other end of the scale, individual synonyms for denoting 'the same thing' may compete; and in between, as the Darwin quotation above illustrated, there could be competition over the grammar that a linguistic community must share.

Cultural variants are commonly conceived as being passed from brain to brain, in which case the 'struggle for existence' can also be construed as over representation in the brain. In one sense this is simply a reference to the neural counterpart of the functional categories outlined above: it is brains that make the selections between competing cultural variants. However, the properties of the human mind/brain impose additional competitive pressures on available variants. 'Interference effects' on memory indicate competition for finite 'brain space'. Interference occurs when recall of previously learned information is disrupted by the learning of new information, with the new information displacing the old. This phenomenon has been shown in countless studies (for a review see Baddeley, 1990), although is best illustrated by McGeoch and MacDonald's (1931) original demonstration. These authors found that recall of a list of previously learned adjectives was greatest when no task was performed during the interval between learning and recall, and decreased when the subjects were given a second list to remember in the interval. Notably, greater interference occurred for synonymous adjectives than for unrelated or nonsense words, suggesting that, as Darwin observed, competition is greatest between similar kinds:

> ..it is the most closely-allied forms, – varieties of the same species, and species of the same genus or of related genera, – which, from having nearly the same structure, constitution, and habits, generally come into the severest competition with each other. (Darwin 1859, p. 154)

2.4.3 Inheritance

Essential to Darwin's case was that the favourable variation is preserved along successive generations, or that it is *heritable*: "Any variation which is not inherited is unimportant for us" (p. 75). At the same time, however, he admitted that "[t]he laws governing inheritance are quite unknown" (p. 76).

Darwin's focus on inheritance reflects the fact that biological characters are constrained to being transmitted from parent to offspring, a constraint which does not apply to cultural transmission. Hence, a more appropriate focus for cultural evolution would be between-individual 'transmission' or 'replication', rather than 'inheritance'.

Cavalli-Sforza and Feldman (1981) adopted the terms ‘vertical’ to describe transmission of cultural traits from biological parents to their offspring (paralleling biological inheritance), and ‘horizontal’ to describe transmission of traits within a single biological generation (resembling the transmission of pathogens as studied by epidemiologists). Cavalli-Sforza, Feldman, Chen and Dornbusch (1982) found evidence of vertical cultural transmission by surveying the opinions and attitudes of Stanford university students and their parents, finding high parent-offspring correlations for religion (r = 0.71), politics (0.61), superstitious beliefs (0.49) and entertainment (0.44), traits which are presumably not entirely genetically inherited. Hewlett and Cavalli-Sforza (1986) found even stronger parent-offspring cultural inheritance in the Aka pygmies of central Africa. Seventy-two members of a community of Aka were interviewed to find out from whom they learned a variety of practical skills, such as hunting techniques, tool-making skills and food preparation. For the 50 traits that were assessed, 80.7% of acquisitions were attributed to parents, 5.2% to other family members, 12.3% to unrelated others and only 0.9% to independent learning. Similarly, Aunger (2000a) found that among horticulturalists in the Democratic Republic of Congo, children acquire knowledge about food primarily from their parents. Barry, Josephson, Lauer and Marshall (1976), meanwhile, showed varying strengths of transmission (‘inculcation’) of personality traits (toughness, maturity, dutifulness, submission and sociability) from adults to children among 182 societies world-wide.

Examples of horizontal cultural transmission include aspects of language acquisition (Pinker, 1995; Tomasello, Kruger, & Ratner, 1993), where children acquire the features of a specific language, from phonemes to complex rules of grammar, from other adults and children. Nagell, Olguin and Tomasello (1993) and Whiten *et al.* (1996) showed that 2-4 year olds imitate tool use and other manipulative behaviour modelled by non-kin, even when individual learning would have been more efficient. Bandura's social learning experiments (e.g. Bandura, Ross, & Ross, 1961) also demonstrate children's wide-ranging imitative capacity. Finally, the vast literature on the diffusion of innovations reviewed by Rogers (1995) constitutes evidence for the transmission of a wide range of inventions and practices. For example, Ryan and Gross (1943) traced the diffusion of hybrid seed corn use through a community of Iowan farmers, and Coleman, Katz and Menzel (1966) the diffusion of a new antibiotic amongst doctors.

While parent-offspring correlations could in principle be generated through individual adaptation to similar environments rather than inheritance, there is considerable evidence for the role of descent in culture. There are many instances when environmental conditions change but culture does not, due to the lag caused by the inheritance process. For example, McGovern (1981) describes the case of a Viking colony in Greenland who failed to relinquish their Scandinavian farming methods and adapt to their new climate. The colony ultimately died out when conditions deteriorated during the Little Ice Age that began in the 13th century, while the Inuit, living under even harsher conditions but using better adapted technology, survived. Cultural inheritance can also be observed in the different responses to the same environmental changes by societies with different cultural histories. For example, LeVine (1966) found that Nigerian tribes categorised as scoring high on a ‘need for achievement’ trait, such as the Ibo, were more successful than tribes low in this trait, such as the Hausa, when Western capitalist societies became more influential.

In other cases, the transmission biases of cultural inheritance may lead to the spread of traits that fulfil a specific function less well than other competing traits. A familiar example is the spread of the VHS format of video recorder at the expense of the supposedly technically superior Betamax recorder. Arthur (1990) has argued that this was due to a process of positive feedback in which consumers chose not the best product but the most popular product, a possible example of Boyd and Richerson’s (1985) frequency-dependant conformist bias.

The issue of inheritance, however, gives rise to an immediate and common objection to the application of Darwin’s theory of evolution to culture: that culture sometimes exhibits Lamarckian inheritance, or the inheritance of acquired phenotypic characteristics. Clearly cultural inheritance is not *literally* Lamarckian, insofar as acquired cultural knowledge is not transmitted genetically to the next biological offspring (a position held by early writers such as Semon, 1921), so in this sense the application of the term ‘Lamarckian’ does not discredit or disprove cultural evolution. A more common characterisation is that people often adopt a cultural trait, modify it, and then transmit that modified trait to someone else. Whether this is regarded as Lamarckian, however, depends on how the replicator-interactor distinction is drawn (Hull, 2000), and it is generally unclear whether the term ‘Lamarckian’ can be meaningfully applied outside of its original context. This also does not mean to say that all cultural evolution occurs through the individual modification of transmitted cultural variants, and it is quite possible that the inheritance of some cultural traits resembles Mendelian inheritance, in a strict analogy with biological evolution as it is now understood.

2.4.4 Accumulation of Modifications

It is one thing to demonstrate the transmission of culture from parent to offspring, or child to child, but quite another to demonstrate the long-term accumulation of modifications (Boyd & Richerson, 1996; Tomasello *et al.*, 1993) that is characteristic of biological evolution.

> If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down. (Darwin 1859, p. 219)

Curiously, the accumulation of material culture was demonstrated shortly after publication of *The Origin*. Pitt-Rivers (1875) used a wide collection of archaeological artifacts to illustrate the gradual changes that occurred for stone tools and spears. Each new specimen can be recognised as a slight modification on the one before, much as the fossil record shows a succession of related biological forms. A detailed quantitative analysis of the cultural selection and drift processes responsible for changes in lithic technology can be found in Cavalli-Sforza and Feldman (1981).

A similar case for the evolution of technology has been made more recently by Basalla (1988), who amassed extensive historical evidence against the commonly held ‘great leaps by great minds’ view of technological change. That is, rather than single ‘genius’ inventors making unprecedented advances, technological change is more accurately seen as a series of successive modifications. For example, the idea of the steam engine did not spontaneously emerge from James Watt’s inventive mind, but was actually a modified version of the existing Newcomen steam engine, with which Watt had had extensive experience, and which in turn was a modification of a previous model, and so on back through history (Basalla, 1988).

Mathematics, like technology, has evolved through the accumulation of successive innovations by different individuals in different societies over vast periods of time, with each new innovation paving the way for the next. Wilder (1968) details how even the basic base 10 decimal system took over 4000 years to emerge. Only after the Sumerians began to use written symbols to represent numbers in around 2400 BC could the Babylonians invent the place value system, in which the position of a digit with respect to the decimal place determines its value. This then allowed the Hindus and Mayans to invent a written symbol for zero, which in turn allowed calculations to be performed. This accumulation of directly related successive inventions proceeded for centuries, with major additions from the Greeks (e.g. geometry), Arabs (e.g. algebra) and Europeans (e.g. calculus), through to present day mathematics.

2.4.5 Adaptation

> We see these beautiful co-adaptations..in the structure of the beetle which dives through the water; in the plumed seed which is wafted by the gentlest breeze; in short, we see beautiful adaptations everywhere and in every part of the organic world. (Darwin 1859, pp. 114-115)

Darwin's theory aimed to explain the fit between organisms and their environments. Cultural traits, such as clothing or farming practices, also commonly show a functional appropriateness to environmental conditions that has allowed humans to exploit an unprecedented range of habitats across most of the planet. The work of human behavioural ecologists has been to show that many cultural differences act as adaptations to different environmental conditions (e.g. Smith & Winterhalder, 1992). By contrast, some evolutionary psychologists argue that cultural diversity is largely the result of a (biologically) evolved universal human cognition responding to different environmental conditions, characterised as 'evoked culture' (Cosmides & Tooby, 1992, pp. 209-210). Approaches such as these would not be fruitful if there were no correspondence between human cultural practices and ecological variations.

Darwin knew only too well, however, that perfect biological adaptation is not to be expected:

> Natural selection will not produce absolute perfection, nor do we always meet, as far as we can judge, with this high standard under nature. (Darwin 1859, p. 229)

It is, in fact, the imperfections in organisms that gave Darwin's theory some of its greatest support. We have already seen evidence that cultural evolution also does not inevitably lead to perfect adaptation, in those cases where cultural inheritance prevents culture from changing in response to environmental flux. Further instances are seen in the existence of cultural vestiges discussed in Section 2.4.8.

Another consideration, when discussing human adaptation, is that cultural traits will not necessarily promote the inclusive fitness of the humans expressing them (Cavalli-Sforza & Feldman, 1981). In the same way that parasites can manipulate behaviour to their own ends (Moore, 2002), cultural variants that exhibit high rates of (non-vertical) transmission (such as smoking) can spread whether or not they enhance fitness and promote adaptation in the individuals who adopt them.

2.4.6 Geographical Distribution

> ..neither the similarity nor the dissimilarity of the inhabitants of various regions can be accounted for by their climatal and other physical conditions. (Darwin 1859, p. 344)

Darwin realised that the geographical distribution of species could often better be explained by descent than by environmental conditions per se. To illustrate this he compared species at the same latitude in Australia, Africa and South America, finding great differences despite similar environments. Is cultural variation similarly predicted by descent?

Hallpike (1986) found that East African and Indo-Iranian cattle pastoralists shared the same ecology and means of subsistence, but differed in their social organisation and religious beliefs (the East African societies were structured around age and were monotheistic, while the Indo-Iranian societies had no age-based rank structure and were polytheistic). Conversely, Hallpike (1986) also found essentially identical social institutions, religious beliefs and cultural values between two Ethiopian societies, the Konso and the Borana Galla, despite very different ecologies and means of subsistence. These observations led Hallpike (1986) to conclude that '[r]ather than ecology, it seems that historical relationship..is a more reliable predictor of social organisation and religion." (p. 181). Similar observations concerning Melanesian and Polynesian societies had earlier been made by Sahlins (1963).

Further evidence of descent was found in an analysis of the geographical distribution of 47 cultural traits in 277 African societies by Guglielmino *et al.* (1995). First, it was found that ecology alone could not account for the distribution of any of the traits. Second, family and kinship traits (e.g. the degree of polygamy, or how property is inherited by kin) were found to follow the geographic pattern of language, suggesting descent from a common ancestor. Third, sexual division of labour, religious beliefs, sexual behaviours and house structure were found to cluster around specific geographical areas, suggesting the role of cultural diffusion. This also fits with potential inheritance mechanisms. For example, family and kinship traits tend to be inherited vertically from parents to offspring and so change slowly, allowing descent to be more easily observed. A similar study by Hewlett, de Silvestri and Guglielmino (2002) found that, in 36 African populations, 20 cultural traits (called 'semes' rather than 'memes' by the authors, to underline their semantic or symbolic aspect), predominantly kinship, family and political traits, correlated with genetic and/or linguistic similarities, suggesting vertical transmission. Twelve traits, including house building and sex taboos, correlated with geographical proximity, suggesting cultural diffusion. Only four traits correlated with ecological variations.

A second way to test for descent is by constructing cross-cultural phylogenies for cultural traits, as is done in comparative analyses of biological traits. Mace and Pagel (1994) presented a phylogeny for nine Kenyan pastoralist cultures, suggesting that the distribution of camel-keeping can be explained most parsimoniously by a minimum of four independent instances of cultural change (i.e. invention or diffusion), with all other similarities due to descent. Gray and Jordan (2000) similarly found that the distribution of 77 Austronesian languages could most parsimoniously be accounted for with a phylogenetic tree branching from a single common ancestor in Taiwan. Also using phylogenetic methods, Barbrook *et al.* (1998) and Tehrani and Collard (2002) found evidence for cultural descent in manuscripts of *The Canterbury Tales* and the decorative patterns of Turkmen textiles respectively.

Darwin also recognised the importance of barriers, such as oceans, to evolutionary change:

> ..barriers of any kind, or obstacles to free migration, are related in a close and important manner to the differences between the productions of various regions. (Darwin 1859, p. 345)

Just as Darwin used the flora and fauna of island ranges, such as the Galapagos, to illustrate his point, Cavalli-Sforza and Wang (1986) studied differences in the languages of the Caroline Islands in Micronesia. It was found that the degree to which languages shared words declined according to a negative exponential of the distance between those islands, in a manner directly equivalent to biological traits. This suggests that the islands originally shared a common linguistic ancestor and have since diverged, just as species on island ranges have diverged from a common ancestor in relation to distance.

Darwin realised that where migration does not occur, such as on isolated oceanic islands, the resultant paucity of introduced species and loss through drift may result in proportionately fewer species than in mainland areas.

> The species of all kinds which inhabit oceanic islands are few in number compared with those on equal continental areas (Darwin 1859, p. 379)

The same observation for culture has been made for the indigenous population of Tasmania (Diamond, 1978; Henrich, 2004). When first contacted by European settlers in 1798, the Tasmanians had been isolated from any other society for 12,000 years. As a result, the Tasmanians had the simplest material culture of any modern humans, lacking agriculture, domesticated animals, bone tools, bows and arrows, and effective clothes, dwellings or fire technology. The archaeological record even shows a *reduction* in material culture since isolation, with the loss of bone tools and fishing.

2.4.7 Convergent Evolution

Of course, an evolutionary approach does not preclude the independent invention of identical cultural traits, just as it does not preclude the convergent evolution of similar biological traits in distinct lineages. This very point was recognised by Darwin, who noted that

> ..in nearly the same way as two men have sometimes independently hit on the very same invention, so natural selection..has sometimes modified in very nearly the same manner two parts in two organic beings, which owe but little of their structure in common to inheritance from the same ancestor. (Darwin 1859, p. 223)

Darwin himself famously confirmed this when he and Alfred Russel Wallace independently proposed the theory of natural selection. Better examples might involve more isolated cases, such as the independent inventions of writing by the Sumerians around 3000 BC, the Chinese around 1300 BC, and the Mexican Indians around 600 BC (Diamond, 1998). A striking case of convergent evolution in action is the tendency for Mickey Mouse to become increasingly neotenous over successive cartoons (Gould, 1980), in precisely the same way, and over the same period, as teddy bears (Hinde & Barden, 1985).

Convergent evolution occurs because of similar selection pressures, which in the case of culture might be due to universals of human cognition, such as a preference for neoteny, or the result of other cultural traits in the population (in the case of writing, for example, the trading of material goods necessitated some method of stocktaking, which makes up the vast majority of early manuscripts: Diamond, 1998).

2.4.8 Change of Function

Darwin also used morphological evidence to demonstrate descent with modification, specifically when a trait originally used for one function is modified to perform another function or to perform no function at all.

> I believe that disuse..has led in successive generations to the gradual reduction of various organs, until they have become rudimentary, - as in the case of the eyes of animals inhabiting dark caverns, and of the wings of birds inhabiting oceanic islands, which have seldom been forced to take flight, and have ultimately lost the power of flying. (Darwin 1859, p. 431)

With respect to culture, Darwin himself drew a linguistic analogy:

> Rudimentary organs may be compared with the letters in a word, still retained in the spelling, but become useless in the pronunciation, but which serve as a clue in seeking for its derivation (Darwin 1859, p. 432)

As well as vestigial letters, language provides many other instances of vestiges, such as irregular verbs (Pinker, 1999). Vestigial features are also common in technological artifacts, especially when new raw materials become available. Indeed, Basalla (1988) notes that such cases are common enough to merit their own label, namely a 'skeuomorph', which is defined as an "element of design or structure that serves little or no purpose in the artifact fashioned from the new material but [which] was essential to the object made from the original material" (Basalla 1988, p. 107). Stone columns, for example, retained the masonry joints of their wooden precursors, despite no longer serving a function. A familiar vestige is the QWERTY keyboard layout, designed in the 19th century to reduce jamming of the hammers in typewriters by making typing as slow as possible (Rogers, 1995). This layout has nevertheless been preserved in modern computer keyboards, despite no longer serving its original purpose.

A second feature of morphology that suggests descent is the presence of traits that have adopted new functions.

> ..an organ originally constructed for one purpose..may be converted into one for a wholly different purpose..(Darwin 1859, p. 220)

Darwin gave the example of the swimbladder in fish becoming the lung in terrestrial animals (although recent evidence suggests that this may not be the case: Perry, Wilson, Straus, Harris, & Remmers, 2001). Again, Basalla (1988) notes similar cases for technology, such as Edison's gramophone, originally used for dictation in offices, being turned into jukeboxes and record players, and the derivation of nuclear energy from the atomic bomb. In fact, Basalla (1988) argues that very few technological innovations were originally designed for their eventual function.

2.5 POSSIBLE POINTS OF DEPARTURE

It was noted earlier that there is no reason to expect all cultural phenomena to map to biological evolution. Two points of departure, the inheritance of acquired characteristics, and the transmission of information between non-relatives, have already been discussed. This final section concerns three others that have been proposed by various authors.

2.5.1 Convergent Lineages

The only diagram in *The Origin* displays the tree-like branching of continually separating lineages, seemingly very different to the cross-fertilisation that can occur in cultures. Indeed, this has been seized upon by opponents of cultural evolution.

> Biological evolution is a system of constant divergence without subsequent joining of branches. Lineages, once distinct, are separate forever. In human history, transmission across lineages is, perhaps, the major source of cultural change. (Gould, 1991, p. 65)

However, to elevate this contrast to a dichotomy would be a distortion of both biology and culture. That cultural evolution occurs predominantly through convergence is an assumption. Examining this empirically in the context of Turkmen textile artifacts, Tehrani and Collard (2002) found that divergent phylogenesis accounts for much more of the variation in their data than convergent 'ethnogenesis' does. Conversely, certain kinds of convergence of biological lineages occur. Symbionts such as lichen represent the converging of distinct biological lineages, as do the symbioses between protoeukaryotes and the alpha-proteobacteria that went on to become mitochondria, and the cyanobacteria that became chloroplasts (Schwartz & Dayhoff, 1978). Genetic material may be transmitted across species boundaries (introgression), and horizontal transmission of genetic material occurs through the action of viruses and plasmids. Doolittle (1999) reviews examples of exchanges across archaeal and bacterial lineages, through the process of lateral gene transfer. In all these respects there is, therefore, a less distinct difference between cultural and biological evolution than implied by Gould's assertions.

2.5.2 The Nature of Selection

If cultural inheritance is sometimes seen as Lamarckian, as noted above, then this inheritance of acquired variation means that human decision-making processes will determine the adoption and expression of cultural traits, and hence affect the cultural evolutionary process. The idea that cultural evolution is *directed* towards some specific goal has been used to discredit the theory:

> Memes such as the theory of relativity are not the cumulative product of millions of random (undirected) mutations of some original idea, but each brain in the chain of production added huge dollops of value to the product in a non-random way. (Pinker, cited in Dennett, 1995, p. 355)

Although Pinker talks of 'memes' - Dawkins' (1976b) term for a cultural replicator - the criticism that cultural evolution is 'directed', 'intentional' or 'conscious' can equally be made for a mechanism-neutral theory of cultural evolution as presented here.

The case of directed selection is analogous to artificial selection as discussed by Darwin in the first chapter of *The Origin*. Darwin described how human selection for certain naturally existing variants over successive generations has led to the emergence of domestic breeds of plants and animals. However, the reason Darwin drew this analogy between artificial and natural selection was that the process – the selective preservation of favourable variants over time – is identical. Darwin further argued that while the immediate selection of the best individual in any one generation may be 'intentional' or 'conscious', this need not imply an intention to create the long-term cumulative change that may eventually result in diverse breeds.

> ..a man who intends keeping pointers naturally tries to get as good dogs as he can, and afterwards breeds from his own best dogs, but he has no wish or expectation of permanently altering the breed. (Darwin 1859, p. 93)

The same applies to cultural selection. Indeed, one might argue that dog breeding *is* an aspect of our culture and that in Darwin's example artificial selection *is* cultural evolution.

2.5.3 Species and Conceptual Lineages

At first sight, culture does not contain separate species. Hull (1982), however, has developed a potential cultural analogue of the species. Hull (1982) argued that scientific communities (e.g. Darwinians) are a collection of interacting scientists that have in common one or more cultural beliefs (e.g. natural selection or Mendelian genetics) that are expressed in an evolving conceptual system (e.g. Darwinism). What unites them is the notion that they derived their beliefs from preceding Darwinians. We can tell whether a scientist is part of a scientific community in exactly the same way we can tell whether an individual organism is a member of a particular species, by determining whether they have inherited shared information from the same source. To belong within the same conceptual lineage, people must have gained their information from each other, rather than merely holding similar views. It follows that 'speciation' events can occur when previously sharing conceptual lineages become isolated.

2.6 CONCLUSIONS

Even if it has been shown that culture evolves in a Darwinian manner, why is this of any interest or use? First, at a practical level, researchers can borrow sophisticated techniques originally developed for studying evolutionary change in biology to analyse cultural change. Population dynamic models designed to track changes in gene frequencies are already being used to analyse culture (e.g. Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981), as are phylogenetic methods (e.g. Gray & Jordan, 2000; Mace & Pagel, 1994).

Second, on a theoretical level, the synthetic framework provided by evolutionary theory (Mayr, 1982) has successfully integrated several disparate disciplines into a coherent research programme, evolutionary biology, and has the potential to do the same for the study of culture. Just as Darwin drew upon evidence from zoology, botany, geology, palaeontology and physiology, this chapter has incorporated findings from anthropology, psychology, sociology, linguistics and history, with the hope of integrating these traditionally separate disciplines. Furthermore, the synthetic evolutionary framework has resulted in biology, since *The Origin*, becoming an enormously productive scientific discipline. Conversely, the field of cultural (or social) anthropology emerged at about the same time as Darwin's writings, but has become preoccupied with self-examination (Bloch, 2000; Kuper, 2000) that questions its status as a progressive research discipline comparable to evolutionary biology or genetics.

Finally, an evolutionary perspective gives focus to future empirical work. Some of the studies cited here were specifically designed to test cultural evolution, but most originated from unrelated theoretical perspectives. By recognising that our current understanding of culture is comparable to that attained by biology in 1859, perhaps some shortcuts can be taken by learning lessons from the succeeding 150 years of biological research. Cultural equivalents of biological concepts such as character displacement can be tested for (Laland & Brown, 2002). Studies of social learning are needed, such as more extensive transmission chain studies, in a manner analogous to Mendel's transmission studies with pea plants. The cultural 'Watson and Crick', meanwhile, are likely to be neuroscientists, looking at how information is stored in the brain. Cultural information may be stored and transmitted in a different way to genetic information, but this just makes the fact that culture evolves more interesting. In short, the unifying framework of Darwinian evolution has the potential to synthesise the social sciences as it has the natural sciences, as explored in the next chapter.

CHAPTER 3 - TOWARDS A UNIFIED SCIENCE OF CULTURAL EVOLUTION[2]

3.1 ABSTRACT

If it is accepted that human culture exhibits key Darwinian evolutionary properties, then it follows that the structure of a science of cultural evolution should share fundamental features with the structure of the science of biological evolution. This chapter tests this claim by outlining the methods and approaches employed by the principal sub-disciplines of evolutionary biology and assessing whether there is an existing or potential corresponding approach to the study of cultural evolution. Existing approaches within anthropology and archaeology demonstrate a good match with the macroevolutionary methods of systematics, paleobiology and biogeography, while mathematical models derived from population genetics have been successfully developed to study cultural microevolution. Much potential exists for experimental simulations and field studies of cultural microevolution, where there are opportunities to borrow further methods and hypotheses from biology. Finally, the cultural equivalent of molecular genetics is somewhat restricted by limitations in neuroscience. It is argued that studying culture within a unifying evolutionary framework has the potential to integrate a number of separate disciplines within the social sciences.

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[2] Submitted as Mesoudi, A., Whiten, A. & Laland, K.N. Towards a unified science of cultural evolution. *Behavioral and Brain Sciences*.

3.2 INTRODUCTION

Parallels or analogies between biological and cultural evolution have been noted by a number of eminent figures from diverse fields of study (e.g. Darwin, 1871; Dawkins, 1976b; Dennett, 1995; Dobzhansky, Ayala, Stebbins, & Valentine, 1977; Hull, 1982; Huxley, 1955; James, 1880; Medawar, 1982; Popper, 1979; Skinner, 1981), and in the last few years a burgeoning literature exploring this relationship has emerged (e.g. Aunger, 2002; Aunger, 2000b; Blackmore, 1999; Boyd & Richerson, 2005; Danchin, Giraldeau, Valone, & Wagner, 2004; Mace & Holden, 2005; Mesoudi *et al.*, 2004; Mufwene, 2001; Pagel & Mace, 2004; Plotkin, 2002; Richerson & Boyd, 2005; Runciman, 2005; Shennan, 2002; Wheeler *et al.*, 2002; Ziman, 2000).

The implication of this growing body of theory is that culture exhibits key evolutionary properties (see Chapter 2). If this is accepted, it follows that the same tools, methods and approaches that are used to study biological evolution may productively be applied to the study of human culture, and furthermore that the structure of a science of cultural evolution should broadly resemble the structure of evolutionary biology. In this chapter this comparison is made explicit, by examining the different approaches and methods used by evolutionary biologists and assessing whether there is an existing corresponding approach or method in the study of cultural evolution. Where such an existing correspondence is not found, we will explore whether there is the potential to develop one. Potential differences between biological and cultural evolution will also be explored.

The purpose of this comparison is primarily to stimulate a more progressive and rigorous science of culture. While evolutionary biology has become enormously productive since Darwin's theory of evolution was formulated, the discipline most directly engaged in the study of culture - cultural or social anthropology - has been much less demonstratively productive over the same time period, particularly in terms of establishing a secure body of data and theory that earns and deserves the attention of researchers working in sister disciplines. This is increasingly acknowledged by many of its own practitioners (e.g. Bennett, 1999; Bloch, 2000; Kuper, 1999). For example, in a recent review of the history of anthropology, Bennett (1999) states that 'the cultural side of the discipline tends to smother its data with personal and arcane theorizing" (p. 951), while another anthropologist, Bloch (2000), states that cultural anthropology 'with time, has become theoretically more and more vague, pretentious and epistemologically untenable" (p. 202).

Why has biology been so much more successful than anthropology over the past 150 years? It is doubtful that biologists are on average more able than researchers who have traditionally studied culture, nor is biology significantly easier to study than culture. While many non-human species are practically and ethically easier to experiment on, for example, they cannot tell us about their actions and do not keep historical records. Rather, two factors are likely to be of particular importance. First is the relative willingness of biologists to make simplifying assumptions and use what may be comparatively crude but workable methods, in order to make complex systems tractable and contribute to the steady accumulation of knowledge that will ultimately form the basis of a sophisticated understanding of the phenomena in question. While many social scientists frequently object that human culture is too complex to be amenable to such simplifying assumptions and methods, the relative success of biologists in studying enormously complex biological systems suggests such objections may be misguided.

Second, and particularly relevant to this chapter, the theory of evolution encompasses and integrates a multitude of diverse sub-disciplines within biology, from behavioural ecology to paleobiology to genetics, with each sub-discipline stimulating and contributing to several others (see Mayr, 1982 for further details of this 'evolutionary synthesis'). In a similar way, applying evolutionary theory to the cultural domain has the potential to integrate a number of currently separate disciplines, such as cultural anthropology, archaeology, psychology, economics, sociology and history. Such an integration could serve to highlight how these disciplines are, in fact, studying complementary aspects of the same problems, and emphasize how multiple and multidisciplinary approaches to these problems are not only possible but necessary for their full exposition. At present, many of the individual studies considered below are the result of independent developments at the fringes of separate fields of study. Placing these disparate studies side-by-side within a broader evolutionary framework, as is done here, will hopefully contribute towards creating a coherent unified movement and bring evolutionary analyses of cultural phenomena into the mainstream.

An evolutionary framework also brings with it a set of proven methods that have rich potential within the study of culture. A number of cases are noted below in which methods developed within evolutionary biology have been adapted for use in the study of culture (e.g. phylogenetic analyses or population genetic models). As shown below, several of these evolutionary methods have already contributed to significant advances over more traditional non-evolutionary methods.

The left hand side of Figure 3.1 illustrates the overall structure of evolutionary biology, as described by Futuyma (1998 pp. 12-14) in what is, perhaps, the most widely used undergraduate textbook in the field. The study of biological *macroevolution* deals with change at or above the species level, while biological *microevolution* concerns changes within populations of a single species. The former comprises systematics, paleobiology and biogeography, while the latter involves population genetics (theoretical, experimental and field-based), evolutionary ecology and molecular genetics. In Sections 3.3 and 3.4 each of the sub-disciplines of evolutionary biology are examined in turn, first outlining their general methods then briefly describing examples of recent studies to illustrate how those methods are applied and the kind of results they yield. This is followed in each case by a discussion of existing analogous methods within the social sciences regarding human culture, again describing recent key studies. These cultural disciplines, and the way in which they map onto the structure of evolutionary biology, are illustrated on the right hand side of Figure 3.1. While there may be no obvious precedent for two distinct fields to exhibit the same internal structure, the similarity of the underlying processes (see Chapter 2) leads us to expect a correspondence. It is hoped that this mapping will (1) help make sense of actual developments in the study of cultural evolution; (2)

suggest new research programmes and hypotheses; and (3) help identify the most promising research strategies.

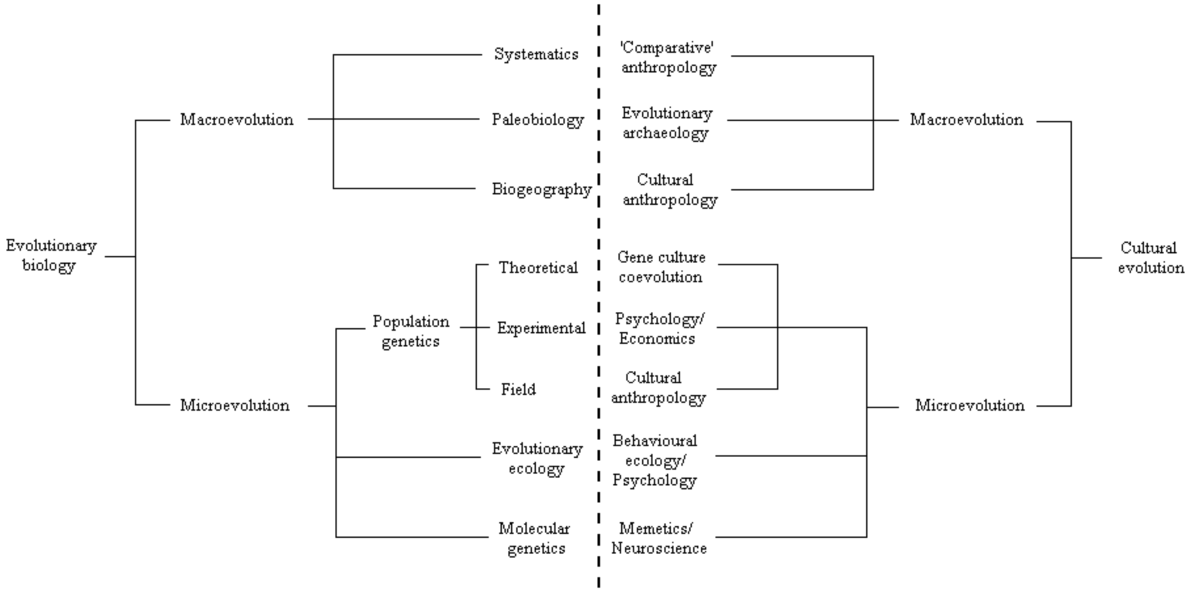

Figure 3.1 - Major subdivisions within evolutionary biology (left hand side; after Futuyma 1998) and corresponding disciplines currently or potentially employed in the study of cultural evolution (right hand side)

The definition of culture and the precise theory of cultural evolution that this comparison is based on were specified in Chapter 2. It should further be emphasised that the field of cultural evolution outlined in this chapter is distinct from the field of *evolutionary psychology* (e.g. Barkow *et al.*, 1992; Pinker, 1997), which deals with *biologically* evolved features of the human mind, shaped by genetic rather than cultural inheritance. Evolutionary psychology therefore more accurately belongs on the left hand side of Figure 3.1 (although it is not shown), and should be distinguished from the separate cultural inheritance system outlined on the right-hand side. Although some evolutionary psychologists tend to downplay the role of transmitted culture (e.g. Tooby & Cosmides, 1992, pp. 115-117), there is ample evidence that culture plays a powerful causal role in determining human behaviour and cognition (Richerson & Boyd, 2005; Tomasello, 1999). This is not to say, however, that biologically evolved features of cognition do not affect cultural processes in important ways, as emphasised by gene-culture co-evolutionists (e.g. Durham, 1992). This interaction is discussed further in Section 3.4.5.2.

3.3 MACROEVOLUTION

3.3.1 Systematics

3.3.1.1 Biology.

Systematics is the study of the diversity of organisms and of the relationships between them. Modern systematists adopt the principles of *cladistics*, which holds that these relationships should be based exclusively on *phylogeny*, or descent (Futuyma, 1998; Harvey & Pagel, 1991; Hennig, 1966). Hence modern systematists seek to reconstruct the evolutionary history of species based on similarities in their morphological, behavioural or genetic characters. (A biological *character* is defined as an inherited trait or feature, while a *character state* describes the form or value of that character. For example, ‘blue’ and ‘brown’ are character states of the character ‘eye colour’.) This section only concerns the analytical techniques used to identify these relationships, rather than the methods used to obtain the geographical or archaeological data used in these analyses, which are discussed in the following sections.

Two species might share a character or character state either because they each inherited it from a common ancestor (*homology*) or because the character evolved independently in the two species' separate lineages (*analogy*). In order to eliminate the latter and determine phylogenetic relationships, systematists identify *shared derived characters*, i.e. traits that evolved only once in a pair of species' common ancestor, but are not observed in close relatives. Because shared derived characters are unique to species directly related by descent, they can be used to identify branching points in the phylogeny. The principle of parsimony can then be used to construct a phylogenetic tree which requires the fewest number of these branching points, often using computer programs such as PAUP (Swofford, 1998) or MacClade (Maddison & Maddison, 1992).

For example, Burns, Hackett and Klein (2002) recently applied phylogenetic analyses to the morphological features of 88 species of Darwin's finches of the Galapagos Islands, finding that all descended from a common ancestor originating in the Caribbean, rather than South America as had commonly been thought. The evolutionary history of specific traits can also be studied using phylogenetic methods, such as Whiting, Bradler and Maxwell's (2003) finding that, while the common ancestor of all insects is thought to have possessed wings for flight, the common ancestor of the stick insects was wingless, and wings re-emerged in the stick insect lineage on a number of independent occasions.

Phylogenetic methods are also used to identify general patterns of evolution. For instance, Goodwin, Balshine-Earn and Reynolds (1998) found that ‘mouthbrooding’ behaviour in cichlid fish, in which eggs are incubated in the mouth of the parent, has evolved on 10-14 independent occasions from the ancestral state of guarding eggs in nests, illustrating convergent evolution. The association of mouthbrooding with reduced fecundity and larger eggs additionally illustrates the selective effects of one trait on others.

3.3.1.2 Culture.

Just as biologists seek to reconstruct a species’ evolutionary history using shared characters, anthropologists seek to reconstruct the history of groups of people based on cultural traits, such as language, tools, customs or beliefs. In doing so, anthropologists have faced the same problem as evolutionary biologists, that of distinguishing between homologous and analogous traits. Indeed, this was recognised within anthropology as long ago as 1889 by Francis Galton, which has led to it being referred to as ‘Galton’s problem’.

The fact that Galton’s problem is virtually identical to the problem faced by biologists has recently led a number of anthropologists to adopt the same solutions. Mace and Pagel (1994) argued that the phylogenetic analyses used by systematists are superior to previous attempts to solve Galton’s problem, such as Murdock’s cross-cultural sample (Murdock & White, 1969) or the statistical removal of inherited traits (e.g. Dow, Burton, White, & Reitz, 1984), both of which involve the loss of important aspects of the data. Mace and Pagel (1994) treated cultural traits as equivalent to biological characters, with independent instances of cultural change occurring when a cultural trait is invented, acquired from another culture, changed or lost. Shared, derived characters can then be identified, and the parsimony-based computer programs developed by systematists can be used to reconstruct the most likely evolutionary history of those cultural traits of interest.

For example, Holden (2002) applied cladistic methods to linguistic data from 75 Bantu languages spoken in sub-Saharan Africa. Items of basic vocabulary whose meanings were common to all groups (e.g. ‘man’, ‘woman’) were taken as characters, and the different lexical forms used to represent these meanings were treated as character states. A shared character state was therefore one in which the same word form was used for the same meaning in both languages. Geographical and archaeological data were also obtained (see next sections). It was found that the linguistic data showed a good fit with the phylogenetic tree model, and that this tree correlated with geographical proximity and archaeological data suggesting that language was associated with the spread of farming across prehistoric Africa. A further study on the same populations (Holden & Mace, 2003) suggested that the acquisition of cattle led to a change from matrilineal to patrilineal inheritance of wealth.

Using similar methods, Gray and Jordan (2000) found that the distribution of 77 Austronesian languages was most consistent with a single common ancestral form in Taiwan which rapidly spread through the region, while Gray and Atkinson (2003) found evidence supporting the theory that the Indo-European language group was associated with the spread of agriculture from Anatolia around 8000-9500 years ago.

The recognition that cultural traits may be directly acquired from other cultures, i.e. transmitted horizontally, raises possible objections (e.g. Moore, 1994) to the use of these biological methods, which were originally developed to deal only with vertical (genetic) transmission and hence might be unsuitable for studying some cultural evolution. This echoes the more general criticism already discussed in Section 2.5.1 that culture is convergent and cross-fertilising, whereas biology is divergent and branching (Gould, 1991). As argued in that section, however, this dichotomy represents a distortion of both biology and culture. Another potential objection to the use of cladistic methods in anthropology is the difficulty of identifying distinct 'characters' in cultural artifacts (see also criticisms of memetics in Section 3.4.5.2.). The identification of characters in culture is undoubtedly difficult (O' Brien & Lyman, 2003a, p.143), but it is important to acknowledge that it is probably no more difficult than for biological characters, and this difficulty has not prevented biologists from producing valuable work using the character concept (Wagner, 2000).

3.3.1.3 Conclusions.

Treating cultural traits as equivalent to biological characters allows anthropologists to apply the same rigorous phylogenetic methods to cultural data as used by evolutionary biologists. This is because anthropologists and biologists share the same crucial goals: to reconstruct the history of certain traits and to identify general patterns of change. A number of studies applying phylogenetic methods to cultural data demonstrate that such methods can be successfully used to achieve these goals, for example in determining whether a group of traits are related by descent, whether their spread was associated with other traits, or whether they generated selection for other traits.

3.3.2 Paleobiology

3.3.2.1 Biology.

The aim of paleobiology is to use the fossil record to identify prehistoric species and reconstruct their evolutionary history (Futuyma, 1998; Simpson, 1944), consequently helping to explain the present diversity and distribution of living species. The principle methods involve the collection of fossils and analysis of their features, with age and environment reconstructed based on these features and the characteristics of the surrounding rocks. Analysis of these data often involves the use of the phylogenetic methods described above in order to distinguish between homologous and analogous traits. The fossil record is a much more direct (albeit incomplete) source of evidence about the evolutionary past than the distribution of existing species, and additionally allows paleobiologists to provide an absolute time scale for evolutionary events using radio-decay dating techniques.

For example, Zhou, Barrett and Hilton (2003) describe exceptionally well-preserved fossils from north-eastern China from the Early Cretaceous period, the forms of which support the theories that birds are direct descendants of the dinosaurs, that feathers evolved before flight, and that there was rapid adaptive radiation of bird ancestors. Seiffert, Simons and Attia’s (2003) phylogenetic analysis of strepsirrhine primate fossils, meanwhile, suggests that the group is much older than was previously thought and has an Afro-Arabian origin. These studies, and countless others, show that fossil evidence can be used to date evolutionary events, support hypotheses concerning the origin of traits, and reveal general evolutionary patterns such as adaptive radiation.

3.3.2.2 Culture.

In general, archaeologists have similar goals to paleobiologists – to identify prehistoric artifacts, to reconstruct lineages of these artifacts and of the people associated with them, and to reveal the evolutionary relationships between these lineages. The basic methodology – extracting specimens from the ground – is also similar. It is only recently, however, that some archaeologists have begun to adopt explicitly evolutionary models and tools (for overviews see O' Brien & Lyman, 2002; Shennan, 2002). The key assumption underlying both paleobiology and archaeology is that similar forms which vary through time are causally connected by inheritance (which O' Brien & Lyman, 2000 term the assumption of ' heritable continuity). Such sequences of causally connected forms constitute evolutionary lineages. Simpson (1961) proposed that evolutionary lineages should be used as a means of defining a species, rather than requiring reproductive isolation (Mayr, 1963), and this ‘evolutionary species’ concept is increasingly being used in evolutionary biology (Wiens, 2004). The same lineage-based species concept has been suggested by Hull (1982) for culture, and extended by O’Brien and Lyman (2000) specifically for prehistoric artifacts.

O’Brien and Lyman (2000) have argued that evolutionary lineages can be reconstructed using the method of seriation, in which a collection of artifacts is ordered according to their similarity: the more features two artifacts share, the closer they are in the order; the fewer they share, the further apart they are placed. O'Brien and Lyman (2000) argue that where such orderings exhibit gradual, overlapping change, it can be assumed that the seriation represents an evolutionary lineage causally connected by cultural transmission.

Early archaeologists used the method of seriation to identify lineages of coins (Evans, 1850), stone tools (Pitt-Rivers, 1875) and Egyptian pottery (Petrie, 1899). The method fell out of favour, however, in the mid-20th century, which O'Brien and Lyman (2000) attribute to the increased popularity of an essentialist stance in archaeology, in which types are perceived to have distinct 'essences' and change only occurs when one type suddenly transforms into another. This contrasts with evolutionary 'population thinking' (Mayr, 1982) which recognises naturally occurring variation within populations, rather than focusing on typological essences. O'Brien and Lyman (2000) have consequently made efforts to reintroduce the seriation into archaeology as a method of studying evolutionary change in artifacts. This is demonstrated by their analysis of projectile points from south-western U.S.A., which they show to exhibit continuous, gradually changing variation rather than a small number of distinct types. O'Brien and Lyman (2000) argue that forcing artifacts into distinct categories often distorts their true phylogenetic relationships.

The method of seriation is nonetheless vulnerable to the same problem as similar methods in paleobiology: distinguishing between homologies and analogies. Hence O'Brien, Darwent and Lyman (2001) and O'Brien and Lyman (2003a) have argued that it is also necessary to adopt the cladistic methods described above to reconstruct evolutionary lineages accurately. For example, O'Brien *et al.* (2001) and O'Brien and Lyman (2003a) carried out a phylogenetic analysis of 621 Paleoindian projectile points from south-eastern United States (see Figure 3.2), while Tehrani and Collard (2002) used similar methods to reconstruct the history of Turkmen textile patterns.

Figure 3.2 - A phylogenetic tree of 17 projectile points from south-eastern United States, from O'Brien and Lyman (2003a), illustrating divergence from a single common ancestor.

Other evolutionary archaeologists have adapted neutral drift models from evolutionary biology (e.g. Crow & Kimura, 1970) to account for 'stylistic variation' in artifacts. For example, Neiman (1995) demonstrated that changes in decorative styles of Illinois Woodland ceramics can be predicted by a model incorporating the selectively neutral but opposing forces of drift and innovation. Bentley and Shennan (2003) found that the frequencies of West German pottery decorations over 400 years can be predicted by a similar model of unbiased cultural transmission, with some anti-conformist bias in later periods.

As well as prehistoric artifacts, past cultures - unlike past species - have often left detailed written records or direct historical evidence of their knowledge, skills and technology. For example, Hinde and Barden (1985) found that the facial dimensions of teddy bears became increasingly baby-like over an 80 year period, which they attributed to a biologically evolved human preference for baby-like faces. Basalla (1988), meanwhile, collected numerous examples of technological change, which exemplify the gradual modification of preceding technology (see also Petroski, 1994; Ziman, 2000). For example, while Eli Whitney's cotton gin is commonly described as unprecedented, it was in fact based on existing mechanical cotton gins used to extract other varieties of cotton seed, which were in turn derived from previous Indian gins and before that an older still sugar cane press (Basalla, 1988, pp. 32-33). Such gradual, cumulative change suggests the presence of evolutionary lineages of artifacts linked by cultural transmission.

Methods developed within evolutionary biology can also be applied to historical data. Howe *et al.* (2001) describe how different manuscript versions of the same text can be used to reconstruct the evolution of that text. This was demonstrated by Barbrook *et al.* (1998), who used cladistic methods to reconstruct the historical relationships between 58 different manuscripts of Chaucer's 'The Canterbury Tales', improving on previous non-phylogenetic reconstructions. Similarly, Bentley, Hahn and Shennan (2004) found that the frequencies of first names and patent applications in 20th century U.S.A. both conform to a simple model of random copying originally developed in evolutionary biology (Crow & Kimura, 1970). This neutral model represents a useful null hypothesis describing the case where no selection is operating.

3.3.2.3 Conclusions.

Archaeologists face essentially the same task as paleobiologists - to identify earlier forms of the phenomena of interest (often now extinct or superseded) and reconstruct their history. It is therefore not surprising that the tools and approaches used by paleobiologists have been successfully imported into archaeology. Adopting evolutionary 'population thinking' (O' Brien & Lyman, 2000)using the methods of cladistics (Mace & Holden, 2005), and importing models of neutral drift (Neiman, 1995) can produce a more accurate understanding of history than traditional archaeological methods. Historical records of cultural artifacts will often be more complete and accurate than the fossil record, offering a potentially important role for historians in the study of cultural evolution.

3.3.3 Biogeography

3.3.3.1 Biology.

Biogeography is the study of how biological, ecological, geographical and historical factors determine the spatial distribution of organisms (Brown & Lomolino, 1998; Futuyma, 1998). Members of a population may adapt to their new environments when they disperse, or populations may be divided by physical barriers and evolve distinctively. Islands are often of particular interest to biogeographers (e.g. MacArthur & Wilson, 1967) because of their isolation from other terrestrial ecosystems. Long-term geographical factors such as climate change or tectonic plate movement can affect organisms' spatial distribution, as well as shorter-term ecological factors such as competitors or pathogens. Fossil evidence and phylogenetic analyses are used to infer the past distribution of organisms, which can help to explain their present distribution, and which has led biogeography to become intimately linked with both paleobiology and systematics.

The methods of biogeography can be classed as either descriptive or analytical. Descriptive methods consist of documenting the present distribution of organisms in space, along with their ecology and physical environment. Once these data have been gathered, analytical models, including the cladistic techniques described above, can be constructed and tested to try to explain this distribution.

For example, Stephens and Wiens (2004) sought to explain the geographical distribution of emydid turtles in eastern North America, which exhibit two broad patterns of community structure. Phylogenetic analyses of morphological and molecular data combined with details of habitat and diet revealed that the differences between the two groups are predominantly due to ‘phylogenetic conservatism’ (i.e. descent from two distinct evolutionary lineages), although the dispersal of several species from one group to the other has reduced these differences.

Roca *et al.* (2004) used fossil data to explain the distribution of an island species. Phylogenetic analyses of genetic and fossil evidence suggest that around 76 million years ago the solenodons - small, burrowing insectivores from the West Indies - diverged from other insectivores rather than from the tenrecs or the rodents. This date coincides with the separation of the islands from mainland North America due to tectonic movement and/or rising sea levels, supporting the hypothesis of divergence due to geographical separation.

3.3.3.2 Culture.

The geographical distribution of cultural traits is shaped, at least in part, by similar factors to those affecting the distribution of organisms. Just as the past distribution of organisms can help to explain the present distribution due to biological inheritance, cultural traits can also persist through time due to trans-generational cultural transmission. While organisms can disperse to new environments, cultural traits can spread by the movement of culture-bearing people and the diffusion of ideas and technology among non-kin. Cultural traits may also arise as adaptations to local ecological conditions.

The field of social science most equivalent to biogeography is again anthropology. One of the main goals of cultural anthropology has been to document and map the worldwide distribution of cultural traits, resembling the descriptive methods of biogeography. This has resulted in databases such as Murdock's Ethnographic Atlas (Murdock, 1967), the Human Relations Area Files (Murdock *et al.*, 1987) and, for languages, the Ethnologue (Grimes, 2002).

More recently, evolutionarily-informed analytical models have been developed to attempt to account for the distributions of cultural traits captured by these databases. The field of human behavioural ecology (see section 3.4.4.2) operates, with some success, on the premise of a correspondence between cultural and ecological variation (Smith & Winterhalder, 1992). Other researchers have endeavoured to distinguish ecological from 'inherited tradition' explanations. Guglielmino *et al.* (1995), for example, used the Ethnographic Atlas to analyse the distribution of 47 cultural traits in 277 African societies. Most of the traits, particularly family and kinship traits, correlated with linguistic group, suggesting vertical transmission. A minority of traits were distributed according to geographical proximity, consistent with horizontal diffusion between groups, while the distribution of none of the traits could be explained by ecology alone.

Similarly, Hewlett, de Silvestri and Guglielmino (2002) combined data from the Ethnographic Atlas and the Ethnologue with newly emerging genetic data to study the distribution of cultural traits in 36 African populations. Twenty of these traits were distributed according to language and/or genes, suggesting vertical cultural transmission, twelve traits correlated with geographical proximity, suggesting diffusion, and four followed ecology, suggesting independent adaptation to local conditions.

A further parallel with biogeography lies in the use of cladistic methods to help explain the present distribution of cultural traits, which we have already seen, for example, for African and Austronesian languages (Gray & Jordan, 2000; Holden, 2002). Yet another parallel lies in the value of physical barriers in studying the spatial distribution of culture. For example, Cavalli-Sforza and Wang (1986) applied a 'stepping-stone' model, developed within biology to study genetic distributions, to linguistic data from 17 Micronesian islands, finding that the degree to which languages shared words declined with the negative exponential of the distance between those islands, just as has been found for biological traits.

Another example of the use of islands to study cultural evolution involves the case of the prehistoric inhabitants of Tasmania, whose cultural repertoire significantly decreased in size and complexity since their isolation from mainland Australia (Diamond, 1978; McGrew, 1987). Henrich (2004) developed a model showing that the reduction in population size caused by this physical separation was sufficient to cause the breakdown and loss of relatively complex cumulative skills and tools, due to the paucity of models from whom to learn such skills. Henrich's (2004) analysis demonstrates the interactive effects of demography and geography on the distribution of cultural traits.

3.3.3.3 Conclusions.

There is a clear parallel in the aims, methods and findings of biogeography and anthropology. Both disciplines aim to explain the spatial distribution of traits, and do this descriptively by documenting spatial variation in forms, and analytically by developing theoretical models to account for patterns in this variation. While the descriptive stage has been carried out by anthropologists for decades independently of a Darwinian model of cultural evolution, analytical models have benefited from biological tools such as the methods of cladistics and fitness maximisation models. Similar factors have moreover been found to influence the distribution of biological and cultural traits, such as transmission dynamics (e.g. vertical/descent or horizontal/diffusion), geographical phenomena (e.g. physical barriers) and ecological factors.

There is also much potential here for the science of cultural evolution to become more predictive, along the lines of evolutionary biology, by specifying *a priori* which traits should follow these different evolutionary dynamics and under which conditions. For example, Boyd and Richerson (1985) predict that cultural traits which constitute adaptations to relatively rapidly changing environmental conditions should be transmitted horizontally, whereas cultural traits that constitute adaptations to environmental conditions that are stable across biological generations (although not stable enough to have become genetically specified) should show evidence of conservative vertical transmission. Further predictions are given in Section 3.4.3.

3.3.4 Macroevolution: General Conclusions

The evidence concerning macroevolutionary patterns reveals a broad fit between the methods and approaches of evolutionary biology and those of the social sciences. This is primarily because a number of anthropologists and archaeologists are already importing biological methods and models into their fields, with considerable success. Phylogenetic methods have been used by anthropologists to explain the spatial distribution of various cultural traits, and by evolutionary archaeologists to reconstruct evolutionary lineages of material artifacts. As this suggests, there is already considerable cross-fertilisation of ideas and methods in these disciplines, which is a key benefit of adopting a unified evolutionary framework. We have also seen cases where the evolutionary methods have proved significantly more effective than traditional non-evolutionary methods, such as the adoption of evolutionary 'population thinking' in archaeology, or the cladistic solution to Galton's problem.

3.4 MICROEVOLUTION

One of the central principles of the evolutionary synthesis of the 1930s was that large-scale macroevolutionary patterns of change are the result of small-scale microevolutionary changes in gene frequencies within populations (Mayr, 1982). A complete theory of cultural evolution would therefore require studies of small-scale changes in populations of cultural traits. The following sections outline the approaches to microevolution developed by evolutionary biologists – population genetics (theoretical, experimental and field), evolutionary ecology and molecular genetics – along with corresponding methods in the study of cultural evolution.

3.4.1 Theoretical Population Genetics

3.4.1.1 Biology.

Significant advances were made in the study of biological evolution before its molecular basis was understood, in no small part through the use of simplified mathematical models, pioneered by Fisher (1930), Wright (1931) and Haldane (1932). In the simplest models, sexually reproducing individuals in a large ('infinite-sized') population each contribute to an aggregate gene-pool. Under the assumptions of random mating, and with no migration, selection or mutation, allele frequencies will remain constant over successive generations (the Hardy-Weinberg principle). Deviations from this simple case can be incorporated into population genetic models, such as mutation, non-random (e.g. assortative) mating, or the impact of processes such as natural selection or random genetic drift. Overall allele or genotype frequencies in successive generations can be tracked mathematically to simulate the process of evolution, often to find out whether a particular genetic trait can invade and spread through a population and, if so, to explore the possible evolutionary consequences of this invasion.

For example, McKone and Halpern (2003) developed a population genetic model of androgenesis, a rare phenomenon seen in freshwater clams, Saharan cypress trees and stick insects, where the offspring acquire nuclear DNA from the male parent only. The model predicted that mutations causing androgenesis will often spread rapidly to fixation in an initially nonandrogenetic population, and in some cases cause extinction of that population due to the loss of females, perhaps explaining its rarity.

3.4.1.2 Culture.

Models of *gene-culture co-evolution* (sometimes also referred to as *dual-inheritance theory*) adopt essentially the same methods as above, incorporating cultural inheritance into population genetic models (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Feldman & Cavalli-Sforza, 1976; Laland, Kumm, & Feldman, 1995). These models exploit parallels in the demographic consequences of biological and cultural change with, for instance, differential adoption and innovation in culture modelled as equivalent to natural selection and mutation within biology, and with other processes such as drift, migration and assortative mating operating equivalently in both cases.

In gene-culture coevolution models, each individual is often described in terms of a combination of genetic and cultural traits, or their ‘phenogenotype’. This requires that transmission rules for both genes and culture must be considered, with selection on genes affecting the adoption of cultural traits and vice versa. As well as adopting the same general methods and principles as population genetics, in many cases gene-culture coevolution researchers have adapted specific established population genetic models to render them suitable to features of culture that are not directly analogous to their biological counterpart.

Researchers in these fields recognise that cultural transmission can be very different to biological transmission. While the latter is primarily vertical (from parent to offspring), Cavalli-Sforza and Feldman (1981) have modelled the consequences of horizontal (within-generation) and oblique (from unrelated members of the parental generation) cultural transmission. Boyd and Richerson (1985) and Henrich and Boyd (1998) have demonstrated mathematically that a ‘conformist’ cultural bias, in which individuals are predisposed to adopt the most popular cultural trait in a group, can evolve in a wide variety of environmental conditions and leads to stable differences between cultural groups, potentially leading to cultural group selection (Boyd & Richerson, 1985). Other models consider a variety of other forms of transmission biases (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Feldman & Cavalli-Sforza, 1976). Importantly, many of these biases are unique to cultural transmission and will generate evolutionary dynamics with no obvious parallel in biology. Such differences do not, however, invalidate an evolutionary analysis of culture.

Models have also been developed for specific cases of gene-culture coevolution. For example, Feldman and Cavalli-Sforza (1989) modelled the coevolution of genes for lactose absorption and the cultural trait of dairy farming, finding that the allele for lactose absorption will spread provided there is a high probability that the offspring of dairy farmers themselves become dairy farmers, but not otherwise, even with a significant viability advantage. Another case study examined the evolution of handedness (Laland, Kumm, Vanhorn, & Feldman, 1995), proposing a model that gave a better fit to patterns of handedness in families and among twins than leading purely genetic models.

As well as population genetic methods, biological models of neutral genetic drift (Crow & Kimura, 1970) have been adapted to study the evolution of cultural traits such as names and patents (Bentley *et al.*, 2004), demonstrating that the distribution of such traits can be accounted for by chance events. Boyd and Richerson (1985), meanwhile, have developed a model of runaway cultural selection similar to runaway sexual selection, which they argue can account for oversized yams in Ponapae and extensive tattooing in Polynesia (paralleling elaborate sexually selected biological traits such as the peacock's tail).

Mathematical models such as these are often treated with suspicion and even hostility by some social scientists, who consider them to be gross oversimplifications of reality (see Laland, Kumm, & Feldman, 1995 and associated comments). The alternatives to gene-culture coevolutionary analyses, however, are usually either analyses at a single (purely genetic or purely cultural) level or vague verbal accounts of 'complex interactions', neither of which are productive. Gene-culture analyses have repeatedly revealed circumstances under which the interactions between genetic and cultural processes lead populations to different equilibria than those predicted by single-level models, or anticipated in verbal accounts (Laland, Kumm, & Feldman, 1995), as illustrated by the examples of dairy farming and handedness.

Interestingly, fifty years ago the same reservations about simplifying assumptions were voiced about the use of population genetic models in biology by the prominent evolutionary biologist Ernst Mayr (1963). He argued that using such models was akin to treating genetics as pulling coloured beans from a bag (coining the phrase 'beanbag genetics'), ignoring complex physiological and developmental processes that lead to interactions between genes. In his classic article "A defense of beanbag genetics", J.B.S. Haldane (1964) countered that the simplification of reality embodied in these models is the very reason for their usefulness. Such simplification can significantly aid our understanding of processes that are too complex to be considered through verbal arguments alone, because mathematical models force their authors to explicitly and exactly specify all of their assumptions, to focus on major factors, and to generate logically sound conclusions. Indeed, such conclusions are often counterintuitive to human minds relying solely on informal verbal reasoning. Haldane (1964) provided several examples where empirical facts follow the predictions of population genetic models in spite of their simplifying assumptions, and noted that models can often highlight the kind of data that need to be collected to evaluate a particular theory.

Ultimately, Haldane (1964) won the argument and population genetic modelling is now an established and invaluable tool in evolutionary biology (Crow, 2001). The same arguments apply to the use of similar mathematical models in the social sciences (see also Laland, 1993; Laland, Kumm, & Feldman, 1995; Mace & Pagel, 1994; Pagel & Mace, 2004).

3.4.1.3 Conclusions.

A number of researchers have imported the methods of theoretical population genetics to study the coevolution of genes and culture, and the dynamics of cultural change over time. These methods have provided a rigorous analysis of many cultural evolutionary processes and case studies. The differences between biological and cultural inheritance are not ignored and do not invalidate such models, while many of the criticisms of the use of such analytical models in the social sciences have been addressed in a parallel debate within evolutionary biology.

3.4.2 Experimental Population Genetics

3.4.2.1 Biology.

As well as using the theoretical models described above, population geneticists have studied microevolutionary processes experimentally by breeding multiple generations of study organisms in the laboratory, in order to simulate evolution under controlled conditions. Laboratory-based experiments have been used to estimate the rate and effect of mutation, detect adaptation to experimentally induced environmental conditions (e.g. different temperatures), and measure responses to the artificial selection of single or multiple traits (Futuyma, 1998; Hartl & Clark, 1997).

In a typical artificial selection experiment, a population of a species, such as *E. coli* or *Drosophila*, is measured for some desired trait (e.g. temperature resistance). In each generation only a subset of the population is allowed to reproduce, with the reproducing individuals chosen according to the desired trait (e.g. those most resistant to high temperatures). After a number of generations the population is again tested for the trait to estimate the response to this selection regime.

For example, Torres-Vila *et al.* (2002) employed a laboratory-based artificial selection paradigm to investigate the genetic basis of polyandry (females mating with more than one male) in a normally non-polyandrous species of moth. Initially 150 pairs of moths were allowed to mate freely, and all of the fertilised females were assessed for their tendency to solicit further matings. In five subsequent generations only females displaying polyandrous behaviour were allowed to mate, resulting in a significant increase in the frequency of polyandry and indicating the successful artificial selection of this trait.

Natural selection can also be simulated more directly by manipulating environmental conditions and allowing the population members to compete naturally amongst themselves, with those individuals best suited to the imposed conditions out-breeding less suited individuals. After a number of generations the population is tested for adaptation to the imposed conditions. Kennington *et al.* (2003), for example, experimentally simulated the natural selection of body size in *Drosophila* in response to humidity. Separate populations were maintained at either high or low humidity and were allowed to breed freely. After 20 weeks (5-10 generations) it was found that the low humidity lines were significantly smaller than the high humidity lines, which Kennington *et al.* (2003) argued occurred because large flies have a low surface area relative to weight, lose less water and so are better adapted to low humidity. This experimental result also helps to explain the geographical distribution of *Drosophila* in the wild, with large body sizes found at high latitudes with low humidity.

3.4.2.2 Culture.

One parallel with this work lies in laboratory based psychological experiments simulating cultural transmission. Where population genetic experiments simulate biological evolution by studying the transmission of genetic information from generation to generation through the reproduction of individuals, psychological experiments can potentially simulate cultural evolution by studying the transmission of cultural information (e.g. texts or behavioural rules) from one individual to another through social learning.

One method for simulating cultural evolution was developed by Gerard, Kluckhohn and Rapoport (1956) and Jacobs and Campbell (1961). This involves establishing a norm or bias in a group of participants, usually by using confederates. One by one these participants are replaced with new, untrained participants. The degree to which the norm or bias remains in the group after all of the original group members have been replaced represents a measure of its transmission to the new members.

For example, Baum *et al.* (2004) studied the transmission of traditions using a task in which participants received financial rewards for solving anagrams. Groups of individuals could choose to solve an anagram printed on either red or blue card: the red anagrams gave a small immediate payment, while the blue anagrams gave a larger payoff but were followed by a 'time-out' during which no anagrams could be solved. By manipulating the length of this time-out, the experimenters were able to determine which of the two anagrams gave the highest overall payoff (i.e. where the blue time-out was short, blue was optimal, and where the blue time-out was long, red was optimal). Every 12 minutes one member of the group was replaced with a new participant. It was found that traditions of the optimal choice emerged under each experimental condition, with existing group members instructing new members in this optimal tradition by transmitting either accurate or inaccurate information about payoffs, or through coercion.

Key similarities exist between this study and the experimental simulations of natural selection described above. In Kennington *et al.*'s (2003) study with *Drosophila*, where the experimentally determined conditions of low humidity favoured small body size, smaller individuals out-reproduced larger individuals. Hence genetic information determining 'small body size' was more likely to be transmitted to the next generation through biological reproduction, and the average body size of the population became gradually smaller. In Baum *et al.*'s (2004) study, where the experimentally determined conditions favoured red anagrams (when the blue time-out was relatively long), choosing red anagrams gave a larger payoff to the participants. Hence the behavioural rule 'choose red' was more likely to be transmitted to the new participants through cultural transmission, and the overall frequency of choosing red gradually increased.

Baum *et al.*'s (2004) method could easily be adapted to study the cultural evolution of attitudes or beliefs. Groups of participants could be asked to discuss a contentious issue, then every generation the participant with the most extreme opinion in a certain direction removed and replaced with a random participant. After a number of generations the group should hold more extreme views (in the opposite direction to those of the removed participants) than average members of the larger population.

Experimental economists have also recently begun to study the transmission of behavioural traditions that emerge when chains of successive participants play economic games. For example, Schotter and Sopher (2003) had successive pairs of participants play a game in which two players chose one of two options without communicating. If they chose different options, neither got any payoff, encouraging coordination. If both chose the first option then the first player benefited more than the second, while if both chose the second option the second player benefited more, creating conflict. Transmission was effected by allowing each player to view the behavioural history of all previous players and/or to receive explicit advice from the preceding player in the chain. It was found that stable conventions emerged in which both players consistently chose one option, and that these conventions were mainly due to explicit advice rather than behavioural history.

A similar methodology exists within experimental psychology. The *transmission chain method*, as developed by Bartlett (1932), involves a text or picture being passed along a linear chain of participants (see Chapter 4). The first participant in such a chain reads or views the stimulus material and later recalls it. The resultant recall is then given to the next participant in the chain to recall, the result of which is given to the third, and so on along the chain. Studying how the material changes as it is transmitted, and comparing the degradation rates of different types of material, can reveal specific biases in cultural transmission.

For example, Chapter 6 (Mesoudi & Whiten, 2004) used this method to study the cultural transmission of event knowledge. Everyday events, such as going to a restaurant, are thought to be represented in memory hierarchically, in which a global high-level proposition (e.g. ‘go to restaurant’) can be subdivided into lower-level propositions (e.g. ‘sit down’, ‘order’, ‘eat’, ‘pay’), each of which can be sub-divided further (e.g. ‘look at menu’, ‘select food’, ‘call waiter’). It found that when descriptions of such events expressed entirely at a low hierarchical level were passed along multiple chains of participants, they were spontaneously transformed into higher hierarchical levels.

Linear transmission chain studies such as those of Schotter and Sopher (2003) and Mesoudi and Whiten (2004) bear less similarity to the experimental paradigms of population genetics. Nevertheless, Schotter and Sopher’s (2003) study provides important data on the mode of cultural transmission (explicit advice versus behavioural history), data which might be needed as a preliminary to more advanced experimental manipulations. Studies such as Bartlett (1932) and Mesoudi and Whiten (2004), while not imposing a selection regime on the transmission of cultural traits, are in a sense simulating selection ‘in the wild’ (see Section 3.4.3.2), as cultural information is being shaped by the minds of the participants it passes through. In Mesoudi and Whiten (2004), the implicit hierarchical structure of memory causes the selection of event knowledge at high hierarchical levels; hence, there is selection due to evolved or implicit features of human cognition. A design more explicitly along the lines of a natural selection population genetic experiment might involve exposing different chains of people to different experimental conditions, or having each chain composed of different types of people with alternative pre-existing knowledge.

Finally, as well as simply detecting the *presence* of directional selection, population geneticists may obtain quantitative estimates of the *strength* of selection. Cultural transmission experiments would benefit from the development of similar measures, and once again there are opportunities to borrow usefully from biology. Stabilising selection might also be studied in this manner, by testing whether certain beliefs or ideas are converged upon following an experimentally induced deviation (see Section 3.4.3).

3.4.2.3 Conclusions.

Although laboratory based experiments are an established approach to the study of biological evolution, relatively little experimental work exists in psychology or economics that has studied the dynamics of cultural transmission. Such studies are essential for a full understanding of cultural evolution. Psychological studies of cultural transmission would benefit from explicitly drawing on the methods of experimental population genetics, both in the design of experiments and in the analysis of data.

3.4.3 Population Genetics Field Studies

3.4.3.1 Biology.

The third approach within population genetics is the study of evolution in naturally occurring populations. Observational studies or field experiments can give estimates of the heritability of traits by measuring parent-offspring correlations, and measures of mortality and reproductive success can be used to estimate the mode and strength of selection on those traits (Endler, 1986; Futuyma, 1998).

The *mode* of selection (Endler, 1986; Simpson, 1944) refers to whether selection is *directional* (i.e. individuals at one end of a distribution are favoured, causing a change in the mean trait value), *stabilising* (i.e. intermediate individuals are more successful than those at the extremes, decreasing variation in the trait) or *disruptive* (i.e. extreme individuals do better, increasing variation in the trait).

The *strength* of selection is commonly represented by the *selection gradient*, a multiple regression-based measure of the relationship between relative fitness and variation (Arnold & Wade, 1984; Lande & Arnold, 1983). Selection gradients have become a common currency within evolutionary biology for estimating the strength and mode of selection, and for making comparisons between populations (e.g. Endler, 1986; Hoekstra *et al.*, 2001; Kingsolver *et al.*, 2001). The actual methods used to obtain these measures are varied. Endler (1986) lists ten common methods for detecting natural selection in the wild, and the corresponding results that would suggest its operation, as summarised in Table 3.1.

There are literally hundreds of examples of natural selection being demonstrated in natural populations of organisms by the above methods (Endler, 1986). Recent examples include Donley *et al.*'s (2004) analysis of similar morphological and biomechanical specialisations in lamnid sharks and tuna, such as a 'thunniform' body shape, in both cases caused by selection for fast movement through water. This convergent evolution (Endler's 3rd method) has occurred independently during the 400 million years since the two groups diverged from a common ancestor. Marko (2005), meanwhile, found evidence for character displacement (Endler's 2nd method) in two closely related species of rocky-shore gastropods. Significant differences in shell shape were observed only where the two species overlapped, caused by divergent selection as a result of competition.

	Method	Result indicative of selection
1	Exploring the relationship between a trait and an environmental factor (source of selection)	Correlation between the trait and an independent environmental (selective) factor
2	Comparing closely related species living in the same region	Homologous traits affected in same manner, e.g. divergence in similar traits due to competition (character displacement)
3	Comparing unrelated species living in similar habitats	Similarities in analogous traits due to convergent evolution
4	Comparing gene frequencies with those predicted by a null (no selection) model	Deviation of gene or genotype frequencies, number of alleles, or disequilibrium, from the null model
5	Long-term study of trait distribution	Long-term stability or regular directional change in the trait
6	Perturbation of natural populations	The trait diverges from the new post-perturbation mean
7	Long-term study of demography (e.g. survivorship, fecundity)	Particular demographic patterns are associated with particular trait values over time
8	Comparing the trait distribution of different age-classes or life-history stages	Differences in trait frequency distributions between age classes
9	Using knowledge of fitness, genetics, physiology etc. to predict short-term change in a trait	Predictions confirmed
10	Using fitness-maximisation models to predict an observed trait frequency or distribution at equilibrium	Predictions confirmed

Table 3.1 - Methods for the detection of natural selection in the wild and results that would suggest the presence of selection as given by Endler (1986: chapter 3 esp. Table 3.1).

3.4.3.2 Culture.

Cultural traits have similarly been studied in natural human populations, although mostly not within an explicit evolutionary framework and hence without the formalised hypotheses, methods and measures of selection employed within evolutionary biology as seen above. Three relevant research traditions - anthropological field studies, rumour research, and the diffusion of innovations - are now briefly discussed (more details can be found in Chapter 4), before outlining how more formal, theoretically-driven methods developed within biology might be applied to cultural data.

First, anthropological field studies have examined the acquisition of cultural knowledge in traditional societies. Members of a community are typically interviewed to find out from whom they acquired their knowledge or skills. For example, Hewlett and Cavalli-Sforza (1986) interviewed members of the Aka of central Africa, finding that the majority (80.7%) of practical skills were said to be acquired from parents, 5.2% from other family members and 12.3% to unrelated individuals. Similarly, Aunger (2000a) found that food taboos are acquired predominantly from biological parents in a horticultural society from the Democratic Republic of Congo, with a subsequent less influential phase of learning from non-kin.

Second, the field of social psychology devoted to rumour research (Rosnow, 1980, 1991) has generated a number of field studies examining the transmission of rumours through naturally occurring populations. A rumour is defined as a belief passed from person to person without secure standards of evidence being present (Allport & Postman, 1947, p. ix). Studies have used questionnaires to track either naturally occurring or experimentally introduced rumours through a small population. Jaeger, Anthony and Rosnow (1980), for example, used confederates to plant a rumour in a college that some students had been caught smoking marijuana during final exams, obtaining details of transmission using questionnaires. Bordia and Rosnow (1998) have more recently studied the transmission of a rumour through an internet community, with the electronic record of communications allowing the longitudinal study of all stages of transmission, rather than relying on retrospective accounts.

Finally, research in sociology on the diffusion of innovations (Rogers, 1995) examines how new ideas and technologies are transmitted through naturally occurring populations. Typically, questionnaires or interviews are employed to assess the past and present use of the innovation by the respondent, and used to compile a picture of diffusion through the population. Classic studies have examined the diffusion of new types of seed amongst farmers (Ryan & Gross, 1943) and antibiotic amongst doctors (Coleman *et al.*, 1966). A recurring finding from over 3000 diffusion studies is an S-shaped cumulative adoption curve (Rogers, 1995), which indicates a slow initial uptake, followed by a rapid increase in adoption, and finally another slow period as the population reaches saturation. Similar sigmoidal dynamics characterise the diffusion of alleles.

Many of these diffusion studies, however, can be criticised for not clearly identifying *a priori* the putative selection pressure responsible for the diffusion, and then testing this prediction in natural populations, as is commonly done in evolutionary biology (Endler's method 1). Instead, diffusion of innovations research has produced a list of *a posteriori* and somewhat vague qualities that supposedly explain diffusion rates, such as ‘trialability’, or ‘complexity’ (Rogers, 1995). One recent study that did specify *a priori* a hypothesised selection pressure is Bangerter and Heath’s (2004) study of the ‘Mozart effect’, the idea that exposure to classical music enhances intelligence, especially during childhood. While having very weak scientific support, this idea has gained wide currency in the U.S. mass media, which Bangerter and Heath (2004) hypothesised was because it offers a cheap and easy way of supposedly enhancing one’s child’s development. This hypothesis predicts that the Mozart effect should be more prevalent in the mass media of states where there is poor academic performance and low spending on education, which Bangerter and Heath (2004) showed to be the case.

3.4.3.3 Conclusions.

There are some weak similarities between the methods used by evolutionary biologists to study evolution in naturally occurring populations of organisms and those which have been used to study cultural change ‘in the wild’. Rumours and innovations are studied as they colonise novel environments, while anthropological studies provide estimates of heritability. The shorter time scale of some cultural evolution and the ability of people to report its means of transmission suggest that cultural evolution might be easier to detect than biological evolution (although such verbal reports would need to be supplemented with observational data).

The study of cultural evolution, however, is distinctly lacking in formal tests for cultural selection, as opposed to other forms of cultural change such as drift. Laland and Brown (2002) have argued that each one of Endler’s (1986) methods for detecting natural selection in the wild (Table 3.1) can be adapted to study the selection of naturally occurring cultural traits. As mentioned above, sociological studies have successfully tracked changes in the frequencies of various traits following their natural or artificial introduction into a novel environment. The next step would be to demonstrate that these changes in frequency are the result of selection, for example by comparing a newly introduced idea with the same idea in the parent population from which it diffused, predicting directional change. An alternative approach would be to test whether stabilising selection was operating on the character prior to the perturbation by investigating whether it returns to the original equilibrium, as predicted. More studies are needed like Bangerter and Heath (2004), which identify *a priori* a putative selection pressure - anxiety over child development - responsible for the spread of a cultural trait, and successfully predict the distribution of the trait from that selection pressure.

Another method is to investigate cultural character displacement, where two competing cultural lineages in the same region diverge in order to reduce direct competition (Laland & Brown, 2002). We might, for example, predict that the religious beliefs of people who live side-by-side with people of different, opposing beliefs (e.g. Muslims and Jews in Palestine, or Catholics and Protestants in Northern Ireland) are more divergent and extreme than the beliefs of people not in immediate contact with competing beliefs (e.g. Muslims in neighbouring Islamic countries such as Syria and Jews in Jewish-only regions of Israel, or Catholics in the Republic of Ireland and Protestants in mainland Britain). Convergent cultural evolution, meanwhile, might be detected where cultural lineages from distant yet similar environments have evolved similar features. History is likely to be littered with examples of similar, independently evolved solutions to common problems, such as the independent evolution of writing by the Sumerians around 3000 B.C., the Chinese around 1300 B.C. and the Mexican Indians around 600 B.C., all in response to a need for stocktaking (Diamond, 1998).

Studies of cultural evolution could also adapt the measures of selection strength developed by biologists, such as the selection gradient. Quantitative measures of the rate of microevolution, like the darwin or the haldane (Hendry & Kinnison, 1999), might also be adapted to the cultural case. There is much opportunity here for the fertile transfer of good ideas from biology to the social sciences, with many of the methods currently being used by evolutionary biologists to investigate natural selection in the wild yet to be tried by researchers studying culture.

3.4.4 Evolutionary Ecology

3.4.4.1 Biology.

Ecology is the study of interactions between organisms and their environments (Begon, Harper, & Townsend, 1996). Evolutionary ecology focuses on the evolutionary processes by which organisms have become *adapted* to their environments (Cockburn, 1991; Futuyma, 1998). Such environmental features can be *abiotic*, such as temperature or rainfall, or *biotic*, such as food sources, predators, parasites, competitors or helpers, of both the same and different species. Ecologists have adopted a range of methods to study these processes, including field studies, natural and laboratory experiments and mathematical models. There is therefore a great deal of overlap with biogeography and population genetics.

For example, Korpimäki *et al.* (2002) set out to determine whether predation was responsible for the 3-5 year cycles in population densities of voles in northern Europe. By experimentally reducing numbers of the voles' predators, Korpimäki *et al.* (2002) were able to show a corresponding increase in the population density of voles compared to non-manipulated vole populations. This response was supported by a demographically-based population model which predicted that reduced predation produces a shift from 3-5 year cycles of vole population density to 1-year cycles.

3.4.4.2 Culture.

Cultural traits can also be said to interact with, and adapt to, their environment. The environment in this case can be divided into three categories, two of which roughly correspond to the abiotic and biotic features that affect organisms. Hence cultural traits may adapt to physical features of the environment such as temperature or rainfall. Cultural traits may also compete with, and adapt to, other cultural knowledge, equivalent to the biotic environment. Finally, cultural traits may adapt to biologically evolved or implicit features of human cognition. This has no exact equivalent in the biological world, although perhaps there is a loose parallel in genetic or developmental constraints on adaptation, or in the coevolution of symbionts and hosts (Dennett, 2001, 2002).

As their names suggest, cultural ecologists (e.g. Steward, 1955) and human behavioural ecologists (e.g. Smith & Winterhalder, 1992; Winterhalder & Smith, 2000) have studied the adaptation of cultural traits to the physical and social environment. The more rigorous and explicitly Darwinian human behavioural ecology is discussed here, which is directly equivalent to (and indeed emerged from) behavioural ecology within biology, usually using the same theoretical tools and models, such as optimal foraging theory (Stephens & Krebs, 1986). Although human behavioural ecologists often choose to downplay transmitted cultural processes, such work is valuable within a cultural evolutionary framework in specifying the microevolutionary process of adaptation which may (or may not) then be transmitted to subsequent generations.

The practical methods of human behavioural ecology, like those of anthropology in general, involve observing and recording behaviour in natural environments, typically in small communities within traditional societies. Unlike conventional anthropology, however, these observations are guided by the predictions of formal mathematical models. This fieldwork, as well as the theoretical models it is designed to test, resemble the methods of evolutionary ecology. An example is the occurrence in Tibet of polyandry which has been shown to be functionally adaptive under the particularly harsh environmental conditions of the region (Crook & Crook, 1988).

As well as adapting to the physical environment, cultural traits may also adapt to other pre-existing cultural information. The study of this form of adaptation would incorporate competition between cultural traits, for which ecological concepts such as exploitation or interference might be useful. Mufwene (2001) has recently proposed a detailed ecological theory of language evolution along these lines.

Finally, because cultural traits predominantly rely on human minds for their storage and transmission, there is the possibility of adaptation to biologically evolved or developmentally acquired cognitive features of those minds. Hence transmission experiments and field studies can draw on findings from cognitive and developmental psychology concerning implicit memory structures, such as Mesoudi and Whiten's (2004) demonstration that the hierarchical structure of memory shapes the cultural transmission of event knowledge. Evolutionary psychology (e.g. Barkow *et al.*, 1992) also provides a rich theoretical and empirical body of research on biologically evolved features of human cognition that might be predicted to bias cultural transmission in particular directions. Sperber and Hirschfeld (2004) similarly argue that the diversity of some cultural traits, such as religious beliefs or classifications of animals and plants, are the result of adaptation to biologically evolved domain-specific cognitive capacities (e.g. folk-biology: Atran, 1998). There is also evidence that biomechanical properties of the human vocal apparatus significantly constrain the form of words (MacNeilage & Davis, 2000). The infant vocal tract, for example, favours simple consonant-vowel alternations such as 'dada' and 'mama' (MacNeilage & Davis, 2000), which may explain why such word forms are used in many languages to denote parents.

The aforementioned study by Bangerter and Heath (2004) concerning the 'Mozart effect' also demonstrated that the content of this scientific myth adapted over time to fulfil the role of reducing anxiety about childhood education. Although the original scientific study used college students, media articles in the following eight years increasingly reported the effect as applying to children and babies.

Of course, cultural knowledge does not exist solely in human brains, and does not exclusively rely on face to face communication for transmission. It may also be fruitful to study the adaptation of cultural traits to alternative transmission media such as printed documents or the internet, and to examine whether such media are merely direct extensions of cognitive capacities or whether they generate their own novel transmission constraints (see Donald, 1991).

3.4.4.3 Conclusions.

Cultural traits may adapt to the physical environment, to other cultural knowledge, or to biologically evolved or implicit features of cognition. While behavioural and cultural ecologists have produced a large body of work relating ecological factors to cultural beliefs, knowledge and skills, there is much less work on adaptation to the other two 'cultural environments'. Anthropological field work and psychological experiments are needed which measure features of these environments and make testable predictions regarding corresponding features of culture.

3.4.5 Molecular Genetics

3.4.5.1 Biology.

One of the major achievements of 20th century biology was the discovery that sequences of DNA comprise the major part of the molecular basis of biological inheritance. Considerable progress has been made in biology as a result of this knowledge. The fields of molecular biology and genetics involve the study of the structure of DNA, RNA and proteins and the processes involved in their inheritance and expression (Futuyma, 1998; Watson, Hopkins, Roberts, & Weiner, 1987). Molecular genetics has a number of specific uses in evolutionary biology (Futuyma, 1998). As mentioned above, molecular markers can be used to reconstruct and date phylogenetic relationships, as well as provide information on genetic variation, population structure and gene flow. Molecular techniques can also be used to investigate the functions of specific genes in the development of biochemical, morphological or behavioural phenotypic features.

3.4.5.2 Culture.

One approach to culture that is explicitly analogous to genetics is *memetics*. In order to illustrate the universality and substrate-neutrality of his replicator-centred theory of evolution, Dawkins (1976b) coined the term *meme* to describe a cultural replicator, or a unit of cultural transmission. Memetics has been developed further by Hull (1982), Dennett (1995), Blackmore (1999) and Aunger (2002; 2000b), amongst others. A common assumption of memetics is that cultural knowledge is stored in brains as discrete packages of semantic information, comparable to how biological information is stored as genes. Once expressed in behaviour or artifacts, these packages of learned information can be replicated in the heads of other individuals through social learning.

The recently burgeoning literature promoting memetics has attracted a number of criticisms (Laland & Brown, 2002). Some of these, such as the need to accommodate the merging of lineages, apply equally to any unified theory of cultural evolution and have been discussed elsewhere in this chapter. Specific to memetics, however, is the criticism that culture cannot be divided into discrete units with clearly specified boundaries (Bloch, 2000; Midgley, 2000).

However, the same putative 'criticism' could equally be levelled at modern concepts of the gene (Laland & Brown, 2002). As documented by Portin (1993; 2002), the concept of the gene has undergone significant changes over the last 150 years. The classical view, held from Mendel (1866) until the 1930s, saw the gene as an indivisible unit of transmission, recombination, mutation and function. That is, a gene is a unit of information that is transmitted whole, within which no recombination occurs, which mutates independently from other genes, and which produces a single molecular product (as captured by James Watson's famous canon "DNA makes RNA makes protein"). This simple and dated gene concept seems to be the view of the gene held by many social anthropologists, including those critical of memetics.

Advances in genetics since the 1930s, however, have shown this unitary gene concept to be inadequate and overly restrictive. Reconceptualisation began in the

1970s following the discoveries of such phenomena as *overlapping genes*, where the same stretch of DNA codes for more than one protein; *movable genes*, DNA sequences that move around the genome; and *nested genes*, which reside inside other genes. Such revised conceptions have continued in the wake of modern discoveries, such as alternative splicing, nuclear and messenger RNA editing, cellular protein modification and genomic imprinting.

In alternative splicing, for example, one of several alternative versions of an exon is transcribed into a coding segment. Depending on which one is chosen, different proteins can be produced from the same gene. It can even involve the splicing in of exons from other genes, and in some cases it produces not just one or two variants but hundreds or even thousands. Alternative splicing is not a rare or occasional event, and seems to occur in approximately half of all human genes (Modrek & Lee, 2002). Gone is the notion of 'one gene - one protein'. In fact, genes seem much more like ideas - information that can be expressed in a multitude of different ways.

The modern concept of the gene is hence characterised as abstract, general and open, with fuzzy boundaries that change depending on the context in which the term is used (Portin, 1993, 2002). Indeed, there are now multiple, mutually incompatible gene concepts prevalent within biology (Stotz & Griffiths, 2004). So while the critics of memetics are probably correct in pointing out the vaguely and flexibly specified nature of the meme concept, exactly the same problem applies to the gene concept, which undoubtedly has been of enormous value in the study of biological evolution.

The crucial point here is that both empirical and theoretical traditions within population biology have thrived in spite of this biological complexity, by using simple, discrete gene concepts.

However, there is still a gap between the detailed understanding of the cellular and molecular bases of genetic inheritance and the somewhat informal ideas of memetics. A more detailed picture of the mechanisms of cultural transmission requires an understanding of how the brain processes relevant information. Here, the most obvious analogy might be thought to be between molecular genetics and the molecular and cellular bases of social learning and memory. However, such learning can be usefully studied at levels other than the molecular, ranging from purely cognitive analyses which say little directly about underlying neural bases, to studies that explicitly focus on supra-cellular aspects of how imitative and related processes are executed in the brain, studied through methods such as *f*MRi. These considerations suggest that because the storage and transmission of culturally transmitted information is so physically different to the genetic, it is here that scientists studying cultural transmission will need to venture further beyond the analogies between cultural and biological evolution that have been considered so far. Already, one can perceive the beginnings of a 'social cognitive neuroscience' that will integrate all the required levels of analysis, but this prospect remains in its infancy. Here, there is space only to indicate the principal twigs on this branch of the scheme sketched in Figure 3.1.

First, at the *neural* level, the social learning community (see Hurley & Chater, 2005) has hailed as highly significant the discovery of 'mirror neurons' in the prefrontal cortex of monkeys, which activate both when the monkey observes a specific goal-directed hand action, such as grasping an object, and also when the monkey performs that same action (Gallese *et al.*, 1996; Rizzolatti *et al.*, 1996). This match between observation and execution of motor actions has led some researchers to suggest that the mirror neuron system forms the basis for *imitation* (Melzhoff & Decety, 2003; Rizzolatti *et al.*, 2002; Williams *et al.*, 2001), which is one possible cultural transmission mechanism, and *theory of mind* (Gallese & Goldman, 1998), which has also been argued to be important in human cultural transmission (Tomasello, 1999; Tomasello *et al.*, 1993).

However, it has long been argued that rather than single memories or functions being determined by single neurons, memory is more likely to be determined by patterns of activation within neural circuits and the resulting connection strengths between neurons (Hebb, 1949). Phenomena such as long-term potentiation (Bliss & Lomo, 1973) and long-term depression (Dunwiddie & Lynch, 1978) offer potential electrophysiological mechanisms underpinning certain long-term memories (see Keysers & Perrett, 2004 for a Hebbian-based model of social cognition). These views of memory, in which single neurons are implicated in a range of functions and functions are determined by more than one neuron, resemble the complexity found in the genetic system discussed above, where one gene has a potentially wide range of functions and expressions.

Aunger (2002) has recently attempted to integrate memetics with neuroscience, arguing that a robust conceptualisation of the 'meme' must specify its material basis in the brain. Aunger (2002) proposes that memes should be seen as electrochemical states of multiple neurons, and offers a definition of a 'neuromeme' as "a configuration in one node of a neuronal network that is able to induce the replication of its state in other nodes" (p. 197). As acknowledged by Aunger (2002), however, any attempt to provide a more detailed description and theory of a neuromeme is severely limited by the current lack of understanding within neuroscience concerning the precise neural and molecular basis of how learned information is stored in the brain. One problem specific to the present discussion is that rat and monkey models may be limited in their relevance to studying culturally acquired information given these species' limited capacity for culture, while invasive single neuron recordings are not performed on humans and other great apes.

Second, the charting of imitation and related processes at the *whole brain* level has focused principally on humans, including the study of neurological cases such as apraxia and its associated imitation deficits (Goldenberg & Hermsdorfer, 2002) and *f*MRi studies of imitation in normal (Iacoboni *et al.*, 2001; Rumiati *et al.*, 2004) and other groups, such as autistic individuals who experience difficulties in imitation (Avikainen, Kulomaki, & Hari, 1999).

If neuronal studies have been largely restricted to monkeys, and whole brain studies to adult humans, it is research on social learning in great apes and, more recently, human children that has generated the richest current taxonomies of cultural learning, delineating such processes as program-level imitation, emulation and affordance learning (Byrne & Russon, 1998; Tomasello *et al.*, 1993; Want & Harris, 2002; Whiten & Ham, 1992; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004). Cognitive models that seek to explain how these operate have begun to proliferate, but remain few and quite crude in comparison to our understanding of genetic transmission mechanisms; they include Meltzoff and Moore's (1997) Active Intermodal Matching (AIM), Heyes' (2005) Associative Sequence Learning (ASL) and Byrne's (1999) String Parsing models. Interestingly, all of these models appeal to a foundation of mirror-neuron function, leading Whiten (2005) to question whether they really solve, or instead merely assume solved, the essential 'correspondence problem' (Nehaniv & Dautenhahn, 2002) of mapping between equivalent actions in a model and a cultural learner. Others have explicitly tackled this problem in offering neural network models proposed to be capable of learning the appropriate correspondences (Keysers & Perrett, 2004; Laland & Bateson, 2001). Keysers and Perrett (2004) review data consistent with their hypothesis that in monkeys this is achieved by circuits linking premotor area F5, inferior parietal cortex PF/PFG and the superior temporal sulcus, and by the homologues of these areas in humans.

3.4.5.3 Conclusions.

While genetic information is known to be represented in sequences of DNA molecules, cultural information is represented primarily in the brain. Viewing culture as comprised of discrete units of information, or memes, can potentially make a complex system theoretically and empirically tractable, in the same way as the gene concept advanced biologists' understanding of biological evolution. Although memes can be characterised as vague entities with flexible and fuzzy boundaries, so can the modern concept of the gene. It should be remembered that there was at least 50 years of productive investigation into biological microevolution before the molecular basis of genetic inheritance was determined, and even now it is only partly understood. Moreover, even if it is revealed that cultural transmission is *not* particulate, cultural evolution may still occur (Henrich & Boyd, 2002).

A deeper understanding of the neural and molecular basis of culturally acquired information must rely on technological advances such as neuroimaging techniques. However, we should also reserve the possibility that the same cultural information is specified by different neural substrates in different brains, severely limiting such methods for studying cultural transmission. In this case there may be no cultural equivalent to molecular biology, although models and methods examining cultural transmission at the behavioural and cognitive levels can still provide important insights.

Delineation of the neural basis of cultural information will also bear on an oft-cited disanalogy between biological and cultural evolution, that there is no clear equivalent to the genotype-phenotype (or replicator-interactor) distinction in culture. Loosely, we can speak of culturally acquired semantic information stored in brains as replicators and the expression of that information in behaviour or artifacts as their interactors. However, without further advances in memetics and neuroscience such a division is somewhat speculative. It may prove that forcing cultural inheritance too tightly into the biological model is in this case unproductive (Aunger (2002), for example, has developed an alternative model of cultural transmission based on signal theory).

The delineation of the genotype-phenotype distinction will also bear on whether cultural inheritance can be described as ‘Darwinian’ or ‘Lamarckian’, the former maintaining Weismann’s barrier between replicator and interactor, and the latter involving the inheritance of acquired phenotypic variation (see also Chapter 2). Ultimately, researchers should get too distracted by whether strict analogies to the replicator-interactor distinction can be drawn or whether cultural inheritance is Darwinian or Lamarckian, especially when the necessary neuropsychological evidence is lacking. Many of the methods described elsewhere in this chapter can be pursued despite a poor understanding of cultural transmission at the neural level.

3.4.6 Microevolution: General Conclusions

The comparison between biological and cultural microevolution has produced mixed results. First, a well-developed body of theory exists which has drawn on the mathematical population genetic models within biology to provide a rigorous and successful analysis of cultural evolution. This is predominantly the work of gene-culture coevolution, although neutral models of genetic drift have recently also been successfully applied to cultural traits.

Second, there is currently a poor correspondence between our understanding of molecular genetics and the molecular or neural basis of cultural inheritance. This is primarily due to limitations in the tools of neuroscience, such as imaging techniques, which cannot yet reveal exactly how information is acquired by and stored in the brain, nor the relationship between models of social learning and models of memory (although potential exists to develop further cognitive models of social learning).

Third, the comparison is also less successful with regard to experimental and field studies of cultural microevolution. This is not because of technological limitations, rather it is because explicit tests for selection, such as the artificial selection paradigm of population genetics or Endler's (1986) various tests for selection in natural populations, and quantitative measures of the strength of that selection, such as selection gradients, have not been employed. A number of opportunities therefore exist for psychologists, field anthropologists, sociologists and experimental economists to adapt some of these tools and methods developed in biology to the study of cultural evolution.

3.5 DIFFERENCES BETWEEN BIOLOGICAL AND CULTURAL EVOLUTION

Despite the plethora of studies reviewed above, which have been argued can be viewed as part of a larger field of cultural evolution, many of these studies, as well as the evolutionary approach in general, have yet to gain acceptance by mainstream cultural anthropology and related social sciences. One reason for this resistance is that many social scientists see a number of fundamental differences between biological and cultural change that they argue invalidate an evolutionary analysis of culture. We have already seen in this and the previous chapter that a number of these purported differences, upon closer examination of either the biological or the cultural evidence, become either illusory or unimportant to the validity of the comparison (e.g. the horizontal transfer of cultural information causing cultural lineages to blend and merge (Section 2.5.1); the directed nature of cultural selection (Section 2.5.2); the apparent lack of species in culture (Section 2.5.3); the apparent lack of discrete particles in culture equivalent to genes (Section 3.4.5.2); and the lack of a clear equivalent to the genotype-phenotype distinction (Section 3.4.5.3)). Ultimately, critics have yet to empirically demonstrate that these purported differences do in fact invalidate an evolutionary account of human culture, and moreover explain why many of the evolutionary methods discussed above (e.g. the phylogenetic analyses) work equally well for both biological and cultural evolution despite such alleged differences.

One potentially valid criticism of accounts of cultural evolution not yet addressed is the treating of all cultural traits as equivalent. Chapters 2 and 3 have described beliefs, behaviour, technological artifacts, languages and social systems as examples of a somewhat simplistic notion of the ‘cultural trait’. Undoubtedly, cultural evolutionary processes will sometimes act differently on different forms of cultural variation, frequently generating distinct evolutionary dynamics for each. It is already well established that vertically and horizontally transmitted traits, conformist transmission, and direct and indirect biases will each exhibit different but characteristic dynamics (Boyd & Richerson, 1985). The pattern and intensity of selection acting on fads and fashions will undoubtedly be quite different from that acting on established norms and institutions. In a sense, this is not too dissimilar to the biological case, where alternative traits may be subject to different forms of selection, and where multi-level selection models are commonplace.

Plotkin (2002) has furthermore argued that ‘social constructions’, cultural traits such as justice or money that only exist because of shared agreement, require a fundamentally different explanation to concrete traits such as technological artifacts, and have no real equivalent in the biological domain. As argued by Plotkin (2002), however, this does not invalidate an evolutionary approach to culture, rather it requires a different evolutionary treatment to the one developed within biology. An evolutionary consideration of social constructions, as well as a detailed taxonomy of cultural traits, are, however, beyond the scope of this thesis. The important point is that deviations from the biological case such as this do not necessarily invalidate an evolutionary approach to culture, they merely require novel treatments of cultural phenomena within a single evolutionary framework.

3.6 NONHUMAN CULTURE

This chapter ends by considering the burgeoning literature that has emerged in the last few years regarding non-human social learning and culture (see Avital & Jablonka, 2000; Byrne *et al.*, 2004; Fragaszy & Perry, 2003; Laland & Hoppitt, 2003; Whiten *et al.*, 2003), which suggest parallels with the human work discussed above. Irrespective of the similarities and differences between human and animal culture, here it is asked whether the above methods can fruitfully be employed to study the behavioural traditions of other species.

First, there is evidence from a number of species of behavioural traditions not obviously attributable to genetic or ecological differences, and hence thought to constitute socially learned cultural patterns. For example, Whiten *et al.* (1999; 2001) documented thirty-nine putative cultural traits in chimpanzees from various regions of Africa, such as tool usage or grooming behaviour. Similar regional differences thought to be cultural in origin have been observed in orangutans (van Schaik *et al.*, 2003) and capuchins (Fragaszy & Perry, 2003; Perry *et al.*, 2003), as well as in the vocalisations of birds (Catchpole & Slater, 1995) and mammals (especially cetaceans: Janik & Slater, 1997), and behavioural traditions in fishes (Helfman & Schultz, 1984; Warner, 1990). There are obvious parallels here with the databases compiled by cultural anthropologists documenting worldwide geographical variation in human culture.

Second, Mercader, Panger and Boesch (2002) have used traditional archaeological techniques to excavate a site in Africa used by chimpanzees for at least the past 20 years to crack nuts using stone hammers and wooden anvils. Considerable evidence of past nut-cracking behaviour was uncovered, specifically nutshell and fractured stone, the latter of which the authors claimed was indistinguishable from a subset of the earliest and simplest stone tool assemblages left by hominid ancestors. Although the finds were probably very recent compared with the cultural artifacts studied by archaeologists, this study suggests that the same methods can potentially be used to uncover evidence of past non-human cultural behaviour.

Third, a number of studies have tracked the diffusion of innovations within non-human communities, paralleling the research tradition of the same name for human technology (Rogers, 1995). The most famous case is the diffusion of potato washing in a community of Japanese macaques (Kawai, 1965). Lefebvre (1995) found that 16 of 21 reported cases of the diffusion of foraging innovations in primates exhibit a rapid accelerating pattern of adoption characteristic of cultural transmission (an example of which is the S-shaped distribution reported by Rogers, 1995), although Laland and Kendal (2003) and Reader (2004) have expressed reservations about inferring learning mechanisms from diffusion curves. Perhaps such studies could benefit from the refinements advocated above for the equivalent human work.

Fourth, population genetic modelling has been used to analyse patterns of non-human culture, specifically bird song. Lynch and Baker (1993) found that the geographical distribution of chaffinch songs can be accounted for by a neutral model in which mutation, migration and drift are at equilibrium. Lachlan and Slater (1999) adopted a gene-culture coevolution technique devised by Feldman and Cavalli-Sforza (1976) to find that vocal learning can be maintained in a ‘cultural trap’ formed by the interaction between genes (which specify the constraints on songs) and culture (the songs themselves). Gene-culture coevolutionary methods have also been used to explore how song learning might affect speciation (Beltman, Haccou, & ten Cate, 2004) and the evolution of brood parasitism (Beltman, Haccou, & ten Cate, 2003).

Fifth, the experimental transmission chain method devised by Bartlett (1932) has been used to study the social learning of mobbing in blackbirds (Curio, Ernst, & Vieth, 1978b) and food preferences in rats (Laland & Plotkin, 1990, 1993). Jacobs and Campbell’s (1961) replacement method has been used to study the transmission of food preferences in rats (Galef & Allen, 1995) and route preference in guppies (Laland & Williams, 1997, 1998).

The above studies demonstrate that many of the same methods used to investigate biological evolution or human cultural evolution can be applied to non-human culture. Studying human and non-human culture within the same theoretical framework is likely to provide important insights into the evolutionary origins of, and psychological mechanisms underpinning, human culture.

3.7 CONCLUSIONS

The evidence discussed in this chapter suggests that much potential exists for a comprehensive science of cultural evolution with broadly the same structure as the science of biological evolution, as outlined in Figure 3.1. This potential is already being realised for the study of cultural macroevolution and the mathematical modelling of cultural microevolution, with methods developed within evolutionary biology, such as phylogenetic analyses and population genetic models, being applied to cultural data. One area, the study of the neural basis of cultural transmission, is dependent on further advances in neuroimaging and other new technologies. Finally, a number of opportunities exist for psychologists, sociologists and experimental economists to adopt the methods and tools developed in population genetics to experimentally simulate cultural microevolution, and detect cultural evolution 'in the wild'.

We have also seen some examples where the explicit adoption of an evolutionary framework or evolutionary methods has provided significant advances over traditional non-evolutionary methods. For example, phylogenetic analyses have provided a solution for Galton's problem when comparing societies related by descent, and evolutionary 'population thinking' allows more accurate descriptions of archaeological artifacts than does an essentialist perspective.

One reason why evolutionary biology has been relatively successful is that a unifying evolutionary framework encourages and stimulates cross-disciplinary work. Some cross-disciplinary borrowing has already been seen in the study of cultural macroevolution, with phylogenetic methods increasingly used in both archaeology and cultural anthropology. More such borrowing is anticipated as greater numbers of researchers adopt the evolutionary framework outlined here. For example, experimental studies of cultural transmission would do well to explicitly test the predictions of theoretical models, and in turn empirical findings should be used to inform the assumptions of such models. Experimental work might also simulate the findings of archaeologists and anthropologists to determine the possible transmission mechanisms underlying certain historical and geographical macroevolutionary patterns.

In the above sections it has been argued that the study of culture would benefit from the adoption of a number of methods and approaches developed within evolutionary biology. This should not be taken, however, as advocating the slavish and dogmatic imitation of evolutionary biology. Cultural inheritance is undoubtedly different in many respects from biological inheritance, and novel mathematical analyses and empirical investigations into cultural dynamics that deviate from the biological case are necessary. As noted above, cultural phenomena such as social representations have yet to be dealt with in evolutionary terms. At the same time, however, these deviations do not invalidate an evolutionary framework. For example, subtle refinements of traditional biological methods have been found to enhance the validity of the mathematical modelling tradition described in Section 3.4.1.2.

Furthermore, despite the impression perhaps given in this chapter, we should also bear in mind that evolutionary biology is, like any other science, far from perfect and is continually changing and updating its methods. Indeed, evolutionary biologists may well benefit from considering alternative evolutionary systems to their own, or from utilising methods developed by social scientists.

In short, the fact that culture exhibits a number of key Darwinian properties allows us to use evolutionary biology as a model for integrating a multitude of separate disciplines within the social sciences, and where appropriate borrow some of the methods developed by evolutionary biologists to solve similar problems. Putting disparate studies from presently unconnected disciplines together into a broad evolutionary context adds value to each of the individual studies, because it illustrates that the degree of progress in this area is far more impressive that hitherto conceived. These studies could not yet be said to be aligned with a unified ‘movement’. Nonetheless, the above exercise implies that if such an evolutionary movement could be better co-ordinated, a more persuasive and important direction could be put on much work in the social sciences.

Part B - Cultural Transmission

In Part A it was argued that human culture evolves according to Darwinian principles, and that this evolutionary framework stimulates and integrates a number of diverse empirical lines of investigation. Parts B and C represent two of these empirical approaches - two of the branches of Figure 3.1. Part B concerns the experimental study of human cultural transmission, in which Bartlett's (1932) transmission chain method is used to test for a number of hypothesised transmission biases. Such experiments roughly correspond to experimental population biologists' attempts to simulate biological inheritance in laboratory populations of study species. Like these biologists' experiments, the experiments presented in Part B are highly simplified compared with reality. Viewed within the context of a larger evolutionary framework, however, experimental studies of small-scale cultural transmission are essential for a full understanding of large-scale evolutionary change.

CHAPTER 4 - LITERATURE REVIEW

4.1 INTRODUCTION

A key concept in Part A was *cultural transmission*, defined as the passing of some trait or characteristic from one individual to another through social learning. The evolutionary theory of culture presented in Chapter 2, like Darwin's (1859) theory of biological evolution, is dependent on the transmission (or inheritance) of information from individual to individual (Section 2.4.3). Consequently, Chapter 3 identified the experimental study of cultural transmission as a vital part of a complete science of cultural evolution (Section 3.4.2).

This relationship between cultural transmission and evolution was also recognised by Cavalli-Sforza and Feldman (1981), who noted that:

> ..theories of cultural transmission and evolution can, to some extent, be developed independently of each other, although for a complete theory of cultural evolution rules of cultural transmission are essential. (Cavalli-Sforza & Feldman, 1981, p.54)

The reason that "rules of cultural transmission are essential" is that, as recognised by Cavalli-Sforza and Feldman (1981) and also Boyd and Richerson (1985), cultural transmission can be very different from biological inheritance, with its own unique transmission rules that may produce very different evolutionary dynamics. This would therefore necessitate a body of data from which such transmission rules and biases can be inferred. Although these authors do attempt to draw on empirical studies where possible, they are hindered by first an overall lack of such data, and second the lack of a single discipline dedicated to the study of cultural transmission. As a result, researchers interested in cultural transmission and evolution are forced to draw on isolated pockets of research that are disconnected both from one another and from a wider theory of human culture.

The aim of this literature review is to bring together and critically evaluate studies of cultural transmission from a number of diverse disciplines (psychology, sociology, anthropology, economics, biology and archaeology) which use a number of different methodologies. Section 4.2 concerns the simplest experimental paradigm, the 'transmission chain method', followed by a discussion of the more group-based 'replacement method' (Section 4.3). We then examine the use of the transmission chain method within economics (Section 4.4) and with non-human species (Section 4.5). This is followed by a discussion of the related fields of rumour transmission (Section 4.6) and the diffusion of innovations (Section 4.7), both of which use a more naturalistic, less experimental approach to study cultural transmission. Finally, in Section 4.8 archaeological data is reviewed which can be used to infer historical transmission chains. The review concludes in Section 4.9 by identifying potentially fruitful lines of investigation that have arisen from these studies, some of which are then pursued in subsequent chapters.

4.2 THE TRANSMISSION CHAIN METHOD

The *transmission chain method* represents the simplest experimental procedure for studying cultural transmission. The method is similar to the children's games 'Chinese Whispers' or 'Broken Telephone', and is illustrated in Figure 4.1. The first participant in the chain reads or hears some material, and then attempts to recall it. This recall is then given to the second participant, who does the same. Their recall is passed on to the third participant, and so on along the chain. The changes that occur in the material can then be studied, as well as comparisons of the rates at which different material degrades. Although highly simplified compared with real human culture, the transmission chain method affords a high degree of experimental control and, as will be seen below, has the potential to provide important contributions to the study of human cultural transmission. Indeed, it has been described by Plotkin (1995) as "close to an experiment tailor-made for those interested in culture" (p. 219).

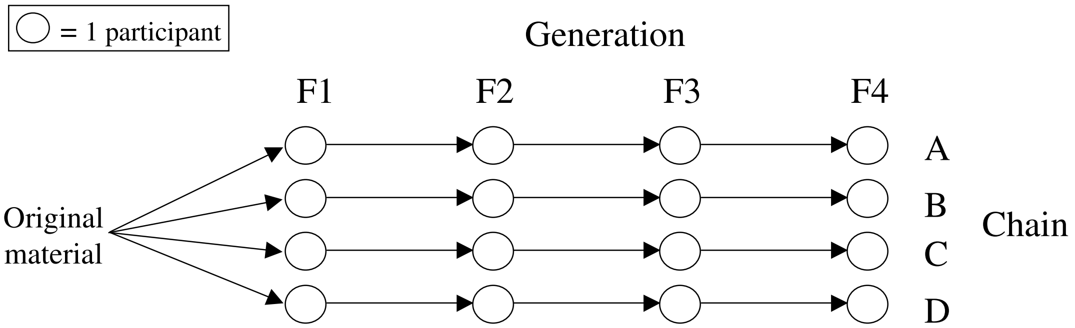

Figure 4.1 - A schematic representation of the transmission chain design. Each circle represents one participant. In this design, the original stimulus material is passed along four replicate chains (A-D), each comprising four generations (F1-F4)

4.2.1 Sir Frederic Bartlett

The transmission chain method has its origin in the work of Bartlett (1932), who, in his classic book *Remembering*, devised the transmission chain method (which he called the 'method of serial reproduction') and described a series of transmission chain studies. One of Bartlett's (1932) main objectives was to move away from the abstract, asocial methods of studying memory at that time, such as having participants memorise sequences of numbers or nonsense letter strings, and towards a more ecologically valid method. He therefore used more meaningful stimulus material, such as stories, and devised the transmission chain method to study the social aspects of memory. Bartlett (1932) was also aware, however, of the wider implications of his transmission chain method for studying human culture:

> Elements of culture, or cultural complexes, pass from person to person within a group, or from group to group, and, eventually reaching a thoroughly conventionalised form, may take an established place in the general mass of culture possessed by a specific group. (Bartlett, 1932, p. 118)

Bartlett's (1932) precise method consisted of a participant reading the material through twice at normal reading speed, then performing a distractor task for 15-30 minutes before recalling the material. That material was then taken by Bartlett (1932) and given to the next participant in the chain, who went through the same procedure, as did each participant in the chain. The material that Bartlett (1932) reports results for are two folk tales, 'The War of the Ghosts' (from native American culture) and 'The Son who Tried to Outwit his Father' (from the Congo); passages describing a cricket match, an air raid and how to play tennis; a joke; two arguments; and a series of pictures. The participants were predominantly Cambridge undergraduates, with some replications with undergraduates from India.

A general finding for all of the material and participants was that the material rapidly became considerably shorter in length and lost much of its detail, with only the overall gist being preserved. A second general finding was that participants tended to distort the material to make it more coherent and consistent with their own pre-existing knowledge. The War of the Ghosts, for example, contained many supernatural elements that were nonsensical to the English participants, and were subsequently removed or replaced with more familiar events. These two processes, loss of detail and rationalisation, led Bartlett (1932) to propose that remembering is primarily a *reconstructive* process, and hardly ever a process of exact replication. Only the gist or overall impression of the material is preserved, and rebuilt around pre-existing knowledge structures, or *schemas*. It was also found that the folk stories were transmitted with greater accuracy than any of the other material, which Bartlett (1932) explained by arguing that people already possess story schemas, that contain the structure of a typical folk tale, thus aiding recall.

Although Bartlett's (1932) work was groundbreaking, it can also be criticised on a number of grounds. First, his analyses are entirely subjective and qualitative, with no attempt at quantitative or statistical analyses. Second, details of the precise methodology that he used are sketchy at best. No detail of the distractor task is given, nor why it varied in length from 15-30 minutes. No mention is made of the instructions given to the participants, or whether they were standardised, despite the use of several different experimenters. Indeed, Gauld and Stephenson (1967) found that instructing participants to reproduce only information that they were absolutely certain was in the original led to significantly fewer errors in transmission of War of the Ghosts. Third, Bartlett's (1932) conclusions were all drawn on single chains. He himself notes that "..the main turning points [in the reproductions] are the work of individual interests or idiosyncrasy, and in the total social product the outstanding individual can be shown to have played a crucial part." (p. 126). Surely it is improper to draw general conclusions about human cultural transmission if the data are so susceptible to individual idiosyncrasies. Such idiosyncrasies also make independent replication of experimental findings impossible.

4.2.2 Early Transmission Chain Studies

During the 30 years following Bartlett's (1932) *Remembering*, a series of transmission chain studies were published, primarily in the *British Journal of Psychology* (probably due in part to Bartlett's position as editor of that journal). These studies all shared Bartlett's (1932) general methodology but varied in the material used or participants tested. A brief summary of these studies is now given.

Northway (1936) studied the transmission of three stories through chains of 10, 14 and 15 year old children. Like Bartlett, Northway (1936) found that "the essential situation and broad outline of the story is preserved" (p. 21), and unfamiliar events were omitted or took a more familiar form. Unlike Bartlett (1932), there was an attempt to quantify the recall, although only gross differences between whole chains were examined, rather than within-chain generational changes, and statistical tests were not applied. Nevertheless, there were trends towards the younger children and children from state schools showing more invention and less accuracy than older children and children from private schools.

Maxwell (1936) investigated the transmission of a murder story containing several errors through chains of different participants, including students, priests, soldiers and children, with the intent that the different participants would respond differently to the mistakes. For example, the priests should be more likely to correct an error concerning the time of Mass. All of the groups preserved the murder incident, although from what can be ascertained without any quantitative or statistical analyses of the results, there seemed to be very few systematic differences between the groups. Talland (1956) similarly investigated whether participant differences affected the transmission of texts, this time comparing students from six different Western nations. There were some group differences, the strongest occurring for a description of a cricket match, which all groups except the English reproduced extremely poorly, except the Americans who distorted it into baseball. Participants from Catholic countries transmitted a description of priesthood more accurately, although an historical account of the 15th century French invasion of Italy showed little differential distortion by French and Italian participants, against the author's prediction. Although Talland (1956) did attempt to quantify recall by dividing the texts into 'units of content', these were not accurately defined and were not subsequently used to statistically compare the groups.

Tresselt and Spragg (1941) examined whether previous experience of information increased its likelihood of later replication. Chains of participants were first presented with one of two anthropological texts concerning traditional pottery: half of the chains read Passage A, concerning technical aspects of how traditional societies made pottery, and half read Passage B, describing the religious significance of pottery. These were not recalled. All chains then received a novel Passage C that contained within it elements of both Passages A and B. This passage was recalled, and reproduced along the chain. It was found that, as predicted, elements from Passage A were preserved for more generations in the chains that had previously read Passage A, compared with controls who had read neither A or B. Reading Passage B, however, yielded no preference in transmission for B elements. Although the authors intended that the two passages would be identical in impact, it seems that the technological information (Passage A) had a greater priming effect than religious information (Passage B), although this is somewhat speculative given the limited nature of this investigation. Nevertheless, the hypothesis that previously experienced information is transmitted with greater fidelity than novel information warrants further investigation.

Ward (1949) attempted perhaps the most innovative use of the transmission chain method of this period, by experimentally simulating the actual transmission of an artefact through history. Ward (1949) obtained a series of coin designs found across Europe, whose dates suggested that the design originated in Macedonia in approximately 350 BC and proceeded to be copied through France and England, reaching Yorkshire *circa* 50 BC. The original Macedonian design was then used as the starting point in a series of laboratory transmission chains, the results of which were compared with the historical artifact chain. Although Ward (1949) claimed that changes in his experimental reproductions did indeed mirror actual changes in the historical artefacts, there was unfortunately no quantitative analysis, and the few reproductions that were published in the paper are somewhat unconvincing.

Nevertheless, the idea of experimentally simulating the actual transmission of an artefact is intriguing, and warrants more detailed investigation.

Bartlett (1932) also studied the transmission of pictorial stimuli, concluding that the same process of loss of detail and conformity to pre-existing knowledge that he found for verbal material applied equally to pictorial stimuli. He also found that the title or label of a picture can significantly affect its transmission. For example, an abstract squiggle that was labelled 'portrait d'homme' gradually acquired face-like qualities. These findings were replicated by Hall (1951) with different stimuli. For example, when a picture of a dog containing stars was labelled 'dog', it gradually lost the stars and retained the dog-like outline during transmission, but when labelled 'constellation' the stars were retained and emphasised and it lost its dog-like shape.

Around the same time as these studies, a slightly modified version of the transmission chain method was being used by researchers in the United States who were interested in how rumours spread through societies. This work originated in attempts by the U.S. government during the Second World War to control the spread of rumours that could potentially damage public morale and reduce support for the war. Allport and Postman (1947) presented the first participant, and only the first participant, with a picture or photograph, and instructed them to describe what they could see to the second participant. The second participant then retold that description to the third participant, who told the fourth, and so on down the chain. Like Bartlett (1932), they found that the descriptions rapidly lost detail ('leveling'), certain salient features were emphasised ('sharpening'), and the descriptions were distorted according to the participants' pre-existing expectations or prejudices ('assimilation'). For example, in one trial a picture of a white man threatening a black man with a razor became distorted according to the white participants' prejudicial notions of black people as criminal and dangerous, so that after a few generations the black man was holding the razor and threatening the white man. Again, however, only single chains were run, making it difficult to draw any general conclusions, and Allport and Postman (1947) report performing their studies as part of their university lectures, with each reproduction relayed out loud in front of an audience, hardly ideal experimental conditions.

Brissey (1961) used a similar design to Allport and Postman (1947), except that instead of pictures, the first participant in the chain watched a film of a car crash, and then wrote a description of the film. This description was passed on to the second participant to recall, and so on down 36 chains of five participants each, representing a significant advance on the previous single-chain studies. Recall accuracy was scored at each point in the chains by participants rating as true or false a series of statements concerning the original film. It was found that both the number of correct and incorrect true/false responses decreased with generation, due to a marked increase in omitted responses. There was a general effect, then, of omission rather than distortion. It was also found that items rated by non-participating independent judges as most important were least likely to be omitted during transmission than items rated less important.

Several conclusions can be drawn from these early studies from the thirty-year period following Bartlett's (1932) original experiments. First, there is universal confirmation of Bartlett's (1932) original findings that there is a general reduction in the length of the material, that much of the detail is lost, and only the overall impression or gist of the text is preserved. Second, most of the studies also unfortunately inherited the flaws from Bartlett's (1932) work, specifically a lack of quantitative or statistical analyses, poorly specified experimental procedure, and a reliance on single chains that are vulnerable to individual idiosyncrasies or breakdowns. However, the fact that the general results just mentioned were found across all studies despite these shortcomings suggests that they are robust. These authors should also not be criticised too harshly for not adopting standards of scientific practice that seem obvious today but had yet to become standard practice when the studies were carried out. There were occasional attempts at quantitative analysis (Talland, 1956) and the use of multiple chains (Brissey, 1961). Even in the absence of these, however, there remain many innovative ideas, such as Ward's (1949) recreation of an actual historical transmission chain, or Tresselt and Spragg's (1941) study of the effect of priming on transmission.

4.2.3 Recent Transmission Chain Studies

As time passed, transmission chain studies benefited from modern scientific standards, such as the reporting of standardised experimental procedures, the use of statistics, and sample sizes large enough to yield significant results. However, there was also a marked decline in the popularity of the transmission chain method, perhaps due to the rise of cognitive psychology during this period, which has tended to ignore social processes. Conversely, social psychologists are often suspicious or hostile of highly simplified simulations of reality, of which these experiments are prime examples (see Chapter 12). Only in the last few years has the transmission chain method been used by a handful of researchers interested in the experimental study of social transmission and culture.

Kurke, Weick and Ravlin (1989) introduced an innovative twist to the transmission chain method. Following transmission down a chain of participants, the final product was sent back up the same chain to see whether the information that had been lost could be restored. The intention was to see whether the degradation that occurs to instructions when they are passed down organisational command chains can be reversed. In the first phase of the study, five participants, A-E, performed the transmission chain method as per Bartlett (1932) using War of the Ghosts as the starting material. Participant E's recall was then given back to participant D, who was instructed to use it to reconstruct the original version that he or she had read previously. This reconstruction was then passed on to participant C who did the same, and so on back to participant A. The result was that each generation restored a large part of the information they had lost the first time around. This is illustrated by the mean numbers of 'information units' (a measure of recall similar to Kintsch's (1974) propositions: see below) recalled by each generation: moving down the chain produced means for A→B→C→D→E of 67.6→49.7→39.9→30.9→24.9, while moving back up E→D→C→B→A gave means of 24.9→29.7→37.7→46.9→63.2. Despite this apparent restoration of information, the final restored generation (63.2) contained significantly fewer units than the first (67.6), indicating that some information had been lost. The two did not significantly differ, however, in the number of themes (a more gross measure of recall, roughly defined as an important element of the plot). So although some of the finer details were not restored, it was possible to reconstruct the more general themes of the story by passing the recall back through the chain. It should be noted, however, that when the material was passed back up the chain, the participants had already read and recalled a previous version of the material, and the second reconstituted material would be acting as a cue for earlier recall.

Two other recent studies both used the transmission chain method to investigate gender stereotyping. Kashima (2000a) had twelve chains of five generations each transmit a single story containing both stereotype-consistent (SC) and stereotype-inconsistent (SI) behaviour. An example of the latter was a husband staying home to prepare dinner while his wife goes out drinking. Interestingly, although the first two generations were more likely to recall SI than SC information, in the final two generations this trend was reversed, with better recall of SC information. Kashima (2000) used this finding to argue that gender stereotyping only occurs 'collectively'. The effect was in fact due to the different degradation rates of the two types of material: although SI information was initially recalled more accurately, it then underwent faster degradation than the SC information, so that by the last two generations it had fallen below the SC recall level. It is not clear, however, why the two should have different rates of degradation, and whether they are independent of each other, that is, whether SI information has a steep degradation curve in the absence of SC information, or whether both types of material must be present in the same chain. In any case, the process of cultural transmission shows effects that cannot be predicted by patterns of individual recall, demonstrating the benefit of the transmission chain method compared with standard single-generation memory studies. It was also found that the instructions given, either emphasising accuracy of recall or instructing the participant to reproduce the story as if they were telling someone else, had no effect on transmission.

Bangerter (2000) similarly used the transmission chain method to test whether participants' gender stereotypes would distort a scientific text describing conception. Twenty chains each containing four participants were run. Two statistically significant effects were found. First, the sperm and ovum described in the text were anthropomorphised, moving from the object to the subject position of sentences. Second, the sperm tended to be given an active role and the ovum a passive role, which Bangerter (2000) argued was the result of gender stereotyping. However, the link between descriptions of sex cells and gender stereotyping might be a little tenuous, and perhaps a more plausible explanation might be that the participants were applying their folk biological knowledge that 'things with tails swim', and 'things with no appendages' do not. This might also explain why Bangerter (2000) found no effect of individual differences in gender stereotyping.

4.2.4 Transmission Chain Studies: Conclusions

These later studies demonstrate that the transmission chain method can be a valid means of testing hypotheses concerning human cultural transmission. Bartlett's (1932) original method can be updated to meet modern standards of scientific practice, specifically by the use of multiple parallel chains, quantitative and statistical analyses, and properly standardised and controlled methodology. The modern studies also confirm the earlier general findings of a reduction in length and loss of detail that occurs during transmission. One general limitation of this method, however, lies in the linearity of the one-to-one chains. Actual cultural transmission may frequently involve more than one model and more than one receiver, and to study these more group-based aspects of transmission a slightly different methodology is needed. Before moving on to discuss such a method, there are two general points to be made concerning the quantitative analysis and the distractor task.

Although one of the first results to be found using the transmission chain method was that only the gist or overall meaning of material is preserved, with the loss of surface detail, there is still no real consensus on how to represent this underlying meaning for the purposes of a quantitative analysis. Text is usually divided into ‘idea units’ or ‘propositions’, although these are often defined differently from study to study. It is suggested here that the quantitative analysis of material should take advantage of Kintsch’s (1974) propositional analysis that seems ideally suited to the task. Kintsch (1974) proposed that the underlying meaning of text can be represented by propositions, which consist of a single predicate and a series of ordered arguments. The predicate is a relational term, such as a verb or adjective, that describes the links between the arguments, which are the agents, objects or other propositions in the text. For example, the sentence ‘Mary bakes a cake” would be written as

(BAKE, MARY, CAKE)

where BAKE is the predicator and MARY and CAKE are the arguments. Because the precise wording of the proposition as written in Standard English is unimportant for the propositional representation, the proposition above could equally represent ‘Mary is baking a cake” or “A cake is being baked by Mary”, as well as ‘Mary bakes a cake”.

Evidence for the psychological reality of propositions was provided by Bransford and Franks (1971), who found that participants could not discriminate between sentences that they had and had not previously heard when those sentences were composed of the same underlying propositions. Kintsch and Keenan (1973), meanwhile, found that the number of propositions in a sentence determined its reading time, independently of the number of words in the sentence. Ratcliff and McKoon (1978) found a greater priming effect for two words taken from the same proposition than for two words from the same sentence but different propositions. This effect remained even when the two within-proposition words were further apart in the surface structure of the sentence than the between-proposition word pair. Finally, Goetz, Anderson and Schallert (1981) found that when participants recalled sentences containing three propositions, for over 90% of the words recalled, if one part of the proposition (the predicate or an argument) was recalled, the rest of the proposition was also recalled. That is, propositions tended to be recalled in an all-or-nothing or particulate fashion. Propositional analysis is, therefore, an empirically supported and theoretically ideal method of quantifying the information present at each generation of a transmission chain.

Another general point concerns the distractor task. The studies described above all vary in whether they use a distractor between reading and recalling the material, and if so, the type of distraction used and its duration, with no discernable effects on their results. For example, both Bartlett (1932) and Northway (1936) used the story The War of the Ghosts, the former using a 15-30 minute distractor, the latter using none, with reportedly identical results. Indeed, at no point in any of the studies is the purpose of the distractor mentioned. It could be that its purpose is to eliminate primacy or recency effects that have been shown to affect short term memory, but Northway (1936) found neither of these effects in her results, and Bartlett's (1932) theory of memory predicts that simple effects apparent for lists of nonsense words, such as primacy or recency, will not apply to meaningful stimuli. Perhaps, then, the distractor task should be abandoned unless there is a clear rationale for including it.

4.3 THE REPLACEMENT METHOD

In the *replacement method*, originally proposed by Gerard *et al.* (1956), a norm or bias is established in a group of participants and one by one these participants are replaced with new, untrained participants (see Figure 4.2). Each replacement represents one 'cultural generation'. The degree to which the norm remains in the population during successive replacements/generations hence represents a measure of its transmission to the new members.

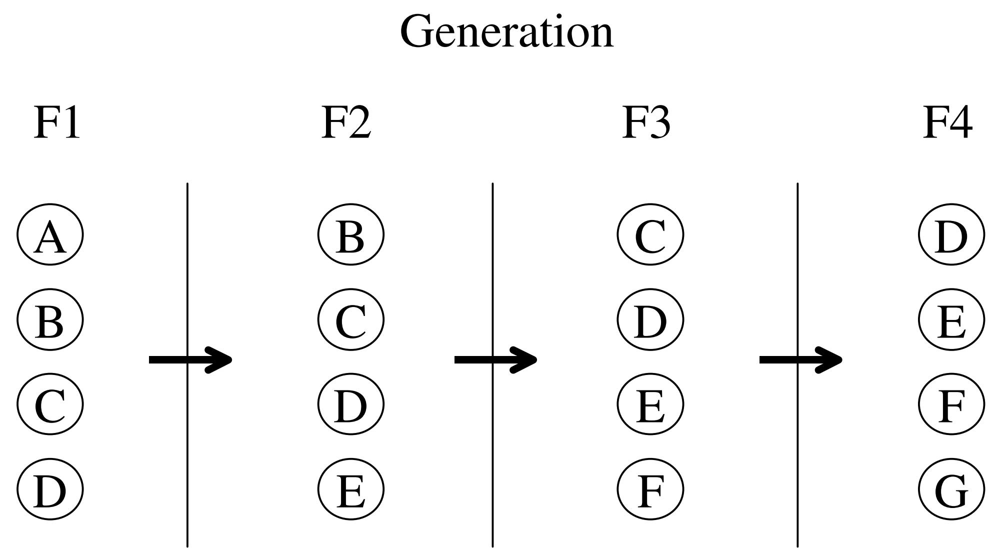

Figure 4.2 - A schematic representation of the replacement method. The first generation, comprising participants A-D, completes the experimental task. In the second generation participant A is replaced with a new participant E, and the group (B-E) completes the task again. This replacement is repeated for each generation.

Jacobs and Campbell (1961) used the replacement method to study the persistence of an artificially exaggerated perceptual judgement of the 'auto-kinetic effect'. The auto-kinetic effect is a perceptual illusion in which a stationary point of light is perceived as constantly moving a few centimetres when viewed in an otherwise pitch-black room. In earlier work by Sherif (1936), a group of participants were all shown this illusion, and asked one by one to estimate how much they thought the light was moving. The group was in fact composed of only one genuine participant, the rest being confederates of the experimenter who had been instructed to give unrealistically exaggerated estimates of the light's movement. Sherif's (1936) now-classic finding was that the majority of the participants he tested gave similar estimates to the confederates despite that estimate being obviously false, illustrating the powerful effect of conformity in group settings. Jacobs and Campbell (1961) repeated Sherif's (1936) experiment with the addition that, after each round of estimating, one group member was replaced with a new naïve participant. Significant evidence of the inculcated norm was found for about four or five generations after the replacement of all of the confederates, after which the perceptual judgement returned to that exhibited by naïve control groups. A follow-up investigation by Zucker (1977), using the same methodology, found that transmission of the arbitrary norm increased in fidelity when the participants were given instructions emphasising membership of an institution or organisation.

Weick and Gilfillan (1971) used the replacement method with a different task. Participants in a group had to individually call out numbers, without being able to hear the other members' numbers, so that the sum total of all group members' numbers equalled a specified target value. Groups were taught either hard or easy strategies for coordinating their responses, and members were replaced in the normal way after each trial. As predicted, Weick and Gilfillan (1971) found that the easy strategies persisted for about eight generations after the last trained member had been replaced, while the difficult strategies were hardly transmitted at all, demonstrating that high fidelity transmission of problem-solving strategies is possible when the strategy is both effective and easy to implement.

Insko *et al.* (1980), meanwhile, used the replacement method to study the trading of goods. Three groups of four participants each were taught to produce different products, specifically paper models, and earnings would be maximised if these different products were combined, encouraging trade. One group was placed in a position of economic and communicative superiority: its products were more valuable than the other two groups, and all trade had to be conducted through it. After each round of trading, one member of each group was replaced with a new participant, with a total of nine replacements (generations). The results showed that while the dominant group earned more than the other two groups, all groups increased their earnings over the generations. This increased productivity can be attributed to increasingly efficient trading and division of labour, rules concerning which were being transmitted to each new generation. Insko *et al.* (1980) also noted that seniority rules for leadership (i.e. that the member who had been in the group the longest took charge of trading and production) were also transmitted to each new generation.

In a follow-up study, Insko *et al.* (1983) found that the trading model implemented above was more productive than a situation in which the central advantaged group was additionally allowed to confiscate the products of the other two groups. Productivity was greater both for the two subordinate groups and for the central group. A key feature of both of these studies is that unlike the studies described above, the transmitted culture was not arbitrary or introduced by the experimenter, it was a functional response to environmental conditions produced and maintained by the participants themselves. This introduction of selection pressures also resulted in an *increase in complexity* that is characteristic of some aspects of long-term evolutionary change in biological species, in contrast to the degradation or loss of complexity that has been repeatedly found by the transmission chain studies described above[3].

A slightly different version of the replacement method was adopted by Rose and Felton (1955), who had three groups of three participants discuss their interpretation of two Rorschach ink-blots in nine successive 16 minute sessions (‘generations’). Between each generation participants were swapped from group to group in order to see how cultural transmission, in this case of ink-blot interpretations, occurred under conditions of migration. The somewhat surprising result was that closed societies in which no participant migration occurred were significantly more productive in generating interpretations than open societies in which members frequently switched groups.

More recently, Baum *et al.* (2004) have used the replacement method to study the transmission of traditions in an anagram-solving task. Groups of participants could choose to solve an anagram printed on either red or blue card. The red anagrams gave a small immediate payoff, while the blue anagrams gave a larger payoff but were followed by a ‘time-out’ during which no anagrams could be solved. By manipulating the length of this time-out, the experimenters were able to determine which of the two

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[3] Note that an increase in complexity in biological evolution is meant only in a broad sense, such as the successive transitional stages of Szathmary and Maynard Smith (1995), and in no way implies that an increase in complexity is inevitable or irreversible.

anagrams gave the highest overall payoff (i.e. where the blue time-out was short, blue was optimal, and where the blue time-out was long, red was optimal). Every 12 minutes one member of the group was replaced with a new participant. It was found that traditions emerged, defined by whichever choice gave the highest payoff under each experimental condition (the optimal choice), with existing group members instructing new members in this optimal tradition by transmitting either accurate or inaccurate information about payoffs, or through coercion.

The replacement method offers a useful complement to the transmission chain method. Whereas the transmission chain method has been mainly used to study the transmission of complex verbal material along one-to-one chains, the replacement method has been used to study the emergence and persistence of group-wide behavioural traditions. The replacement method is therefore more suited to investigating the effects of social/interpersonal factors on cultural transmission, such as conformity (Jacobs & Campbell, 1961) and power (Insko *et al.*, 1980).

4.4 INTERGENERATIONAL ECONOMIC GAMES

A recent development in the field of experimental economics is the use of intergenerational games to study the transmission of behavioural traditions along chains of participants, much like the transmission chain method employed by psychologists.

For example, Schotter and Sopher (2003) had successive pairs of participants play the ‘Battle of the Sexes’ game, in which two players must choose one of two possible options without communication. The payoffs were determined by two rules. First, if the players chose different options, then neither player got any payoff, while if both players chose the same option, then they both got a payoff. Second, the two options differed in their payoffs to the two players: if both players chose the first option, then Player 1 got a larger payoff than Player 2, while if both players chose the second option, then Player 2 got the larger payoff. Hence the first rule encouraged the players to cooperate in coordinating their responses, while the second rule created a conflict in that one player will always get a larger payoff than the other. Transmission between successive generations was effected by giving each pair two sources of information from the previous pair(s) in the transmission chain. This was either a behavioural *history* of every previous generation (i.e. which option was chosen by previous players and what outcomes they received) or explicit verbal *advice* given by the previous generation as to which option they should choose and why. After approximately 50 generations one of these two sources of information was removed, to assess their independent effects.

Schotter and Sopher (2003) found that the repeated games exhibited clear conventions, which the authors likened to the pattern of punctuated equilibrium seen in the fossil record. Hence there were long periods during which both players chose one of the options, followed by a brief period of instability and rapid change, followed by a long period during which both players again chose a single option. This tendency to coordinate over many generations was attributed to the role of advice: removing the option to view the behavioural history of previous generations had no significant effect, while removing the explicit advice from the previous generation significantly disrupted the stable conventions. Schotter and Sopher (2003) also obtained players' guesses of which option their partner would choose, and hence which option the player should choose to maximise their payoff. In those cases where this rational choice conflicted with the choice recommended in the advice, half of the players selected the latter. These results suggest that conformity to explicitly provided social norms plays a powerful role in developing cultural traditions. In general, this study highlights the usefulness of the transmission chain method in the field of experimental economics, which has traditionally neglected social influences in favour of a non-social 'rational actor' model of human behaviour.

4.5 ANIMAL STUDIES

Although originally developed to study human culture, the transmission chain method is equally suited to the study of socially learned traditions in animal populations. Curio, Ernst and Vieth (1978a; 1978b), for example, used the transmission chain method to show that European blackbirds culturally transmit information concerning enemy recognition. Observer birds saw a conspecific exhibit a mobbing response toward a novel species of bird, a stuffed Australian honeyeater. The observer consequently exhibited a mobbing response towards the honeyeater comparable to that exhibited toward a genuine predator, and greater than control blackbirds that had not observed the model. That observer then acted as a model for the next blackbird in the chain, who in turn demonstrated for the next bird, and so on down the chain. The mobbing response was transmitted with no reduction in strength through a total of six birds. The transmission of a mobbing response to a plastic bottle was also demonstrated, but with less fidelity, suggesting biological constraints on transmission.

Laland and Plotkin (1990), meanwhile, set up transmission chains in Norway rats for a socially learned foraging behaviour, digging for food items. The first rat was explicitly trained in digging, and then observed by the second rat in the chain. The second rat subsequently acted as a demonstrator to the third rat, which demonstrated for the fourth, and so on up to the eighth and final rat. Eight parallel chains were run in total. As only the first rat was explicitly trained in digging, any improved digging ability after this first demonstrator must be attributed to social transmission. This was indeed found, with rats in the transmission chain digging up significantly more food items than rats in a no-transmission control condition. A follow-up study by Laland and Plotkin (1993) also involving transmission chains of Norway rats showed successful transmission of a food preference via excretory deposits and/or gustatory cues.

The replacement method has also been applied to non-human species. Galef and Allen (1995) taught an arbitrary food preference to groups of Norway rats, and then replaced the group members one-by-one with naïve rats. Three generations after the last trained rat had been replaced there was still significant evidence of the arbitrary preference, indicating that the preference had been transmitted to each new member. Similarly, Laland and Williams (1997) trained groups of guppies to take one of two routes to a food source, and gradually replaced the group members with naïve, untrained fish. Three days after all of the original members had been removed, there was still a significant preference for the route the founder members had been trained to take, suggesting that the route preference had been culturally transmitted. Laland and Williams (1997) concluded that this transmission was driven by the guppies' tendency to shoal, where individuals follow conspecifics in order to reduce the risk of predation.

The results of these studies demonstrate that some non-human species can transmit behaviours along chains of several individuals. This is not too surprising given that social learning allows the acquisition of information about the environment that changes too fast for genetic adaptation (such as the edibility or location of novel foods or the characteristics of novel predators), yet without the cost of individual learning (Aoki, Wakano, & Feldman, 2005; Boyd & Richerson, 1985).

Such findings suggest that some culturally transmitted behaviours may spread and eventually fixate in a population, and generate distinct cultural traditions within species. Such behavioural traditions have been proposed for chimpanzees (Whiten *et al.*, 1999, 2001), orangutans (van Schaik *et al.*, 2003) and capuchins (Perry *et al.*, 2003), as well as in the vocalisations of birds (Catchpole & Slater, 1995) and cetaceans (Janik & Slater, 1997). The results of the transmission studies additionally demonstrate that, in the species so far experimented with, such traditions might be maintained by very simple social learning mechanisms, such as via the odours of excretory deposits (as in Laland & Plotkin's rats) or as a by-product of shoaling behaviour (as in Laland & Williams' guppies).

Although these social learning mechanisms and behaviours may be much simpler than the complex verbal information that is commonly transmitted along human chains, this does not mean that the results of the animal studies have no bearing on the human studies. One such result is the finding of biological constraints on transmission. Curio *et al.* (1978a; 1978b) noted that transmission of the mobbing response was stronger for a stuffed bird, which resembles the observers' natural predators, than for a plastic bottle. Laland and Plotkin (1993), meanwhile, found that an innate preference for one food over another in rats prevented the transmission of the unfavoured food. Similar biological constraints on transmission can also be tested in humans (e.g. Chapter 5). Indeed, the burgeoning fields of evolutionary psychology and human behavioural ecology provide a wealth of hypotheses pertaining to biologically evolved constraints on cognition that can be adapted for use in transmission chain studies.

4.6 RUMOUR TRANSMISSION

Allport and Postman's (1947) use of the transmission chain method to study the spread of rumour led other researchers to modify the methodology to more accurately capture the dynamics of real life rumour transmission. Rather than a laboratory-based approach, the transmission of either genuine or planted rumours through a naturally occurring population was studied, in examples of what can be called the *naturalistic approach*. Allport and Postman (1947) defined rumour as "a specific (or topical) proposition for belief, passed along from person to person, usually by word of mouth, without secure standards of evidence being present" (p. ix). This definition thus asserts that rumour concerns the cognitive rather than the behavioural aspects of cultural transmission ('proposition for belief'), then emphasises that rumour is culturally transmitted ('passed from person to person'), suggests a medium for that transmission ('word of mouth'), and finally asserts that rumour is characterised by a lack of evidence. Although rumour researchers often used the terms 'rumour' and 'gossip' interchangeably, *gossip* is defined here as 'culturally transmitted information concerning complex third party social relationships' (see Chapter 5 for the theoretical justification of this definition). Gossip may (or may not) be classified as rumour, depending on the quality of the supporting evidence, while rumour may (or may not) be gossip, depending on the content of the rumour.

Schachter and Burdick (1955), for example, introduced a rumour into a girls' school and measured its uncontrolled spread through the population in a single day. The rumour, that some exam papers had been stolen, was planted by teachers in an offhand manner during what were ostensibly routine morning meetings with eight pupils. Transmission of the rumour was then measured at the end of the day by interviewing each girl. It was found that all but one of the 96 girls had heard the rumour, with no distortion. Furthermore, there was more frequent transmission and more invention of novel rumours under conditions of 'cognitive unclarity', when, before the rumour was planted, one girl from each class was removed by the headteacher without explanation. Schachter and Burdick (1955) went on to argue that the lack of distortion of the rumour contradicts Bartlett's (1932) findings of information loss and distortion. This is somewhat unfounded, however, as Bartlett (1932) and the subsequent transmission chain studies described above all used lengthy and complex prose passages, rather than a simple fact. No doubt if an experimental transmission chain study were performed with the sentence ‘Some exam papers have been stolen”, very little distortion would occur, or conversely, if complex material had been used by Schachter and Burdick (1955), there would have been considerable distortion.

In a similar study, Jaeger, Anthony and Rosnow (1980) used confederates to plant a rumour in college classes that some students had been caught smoking marijuana during a final exam, measuring a week later whether they had heard, passed on or believed the rumour. It was found that rumour transmission was less frequent when the confederate who introduced the rumour was immediately discredited by a second confederate, and that the rumour was more likely to be transmitted by participants rated high in anxiety, and who rated drug use as of little importance. A similar effect of anxiety was found by Anthony (1973), measuring the spread of a rumour about the axing of a school club amongst pupils.

Rosnow, Yost and Esposito (1986), instead of planting a rumour, studied naturally occurring rumours that arose during intense labour negotiations at a university. Questionnaires were used to obtain any rumours that participants had heard, their confidence in the truth of those rumours, and whether they had transmitted the rumour. It was found that rumours rated as most believable were more likely to be passed on. A similar study tracking the transmission of rumours concerning the murder of a student (Rosnow, Esposito, & Gibney, 1988) replicated these findings, and also replicated the earlier findings that cognitive unclarity and high anxiety levels fostered transmission.

More recently, Bordia and Rosnow (1998) studied the transmission of a rumour through an internet community. The rumour emerged naturally in an internet discussion group and alleged that an internet service provider was secretly accessing the hard drives of its subscribers. Content analyses on the contributions to the discussion group revealed similar findings to the studies outlined above, with the rumour characterised by conditions of credulity, uncertainty and anxiety. The major advantage of studying rumour on the internet, however, was that the entire history of every contribution to the discussion was perfectly preserved, and every contributor could be identified. This allowed the identification of individual differences in the contributors to the discussion board. For example, some contributors tended to make predominantly 'apprehensive' statements, while others made predominantly 'disbelieving' statements. The preservation of contributions also allowed examination of the history or development of the rumour over time. Bordia and Rosnow (1998) identified several 'developmental stages' in the transmission of the rumour, such as an initial period of conflict followed by more cohesive group-solving activity, although these stages were somewhat descriptive and vague.

To summarise, there have been general findings in the rumour literature that rumour transmission is more likely to occur under conditions of anxiety, uncertainty and credulity (Rosnow, 1980, 1991). Experiments on rumour offer the advantage of studying cultural transmission as it occurs naturally through a population, with none of the artificiality of the laboratory. An important point is that participants can choose *not* to transmit the information, unlike the experimental transmission chain situation, in which transmission is a necessary condition of participating. The naturalistic approach is also ideal for investigating factors such as anxiety, which would be hard to induce in an experimental situation. The analysis of internet-based rumour, as pioneered by Bordia and Rosnow (1998), additionally allows the study of individual differences in transmission and an examination of the time-course of the rumour by preserving a record of all contributions to the rumour.

However, as noted above, with increased ecological validity comes a decrease in experimental control. Except for the internet study, there is a reliance on participants' retrospective recall of whether they transmitted the rumour. There are also limitations on the complexity of the material used, which tends to be limited to single propositions or statements. It would be fruitless to plant a 300 word story as, if it is transmitted at all, it would rapidly degrade to a single statement with no means of recording and measuring that degradation. The field of rumour transmission also suffers from a vague and descriptive sociological perspective, and would benefit from an integration with the other work cited in this chapter.

4.7 DIFFUSION OF INNOVATIONS

The naturalistic approach adopted in the rumour literature has also been used within the 'diffusion of innovations' literature, which is thoroughly reviewed by Rogers (1995). Diffusion of innovation studies examine how new ideas and technologies are transmitted through populations. For example, Ryan and Gross (1943) traced the diffusion of hybrid seed corn use through a community of Iowan farmers, finding that there was a considerable gap between a farmer learning of the seed and using it, and that neighbouring farmers were most influential in adoption of the seed. Coleman, Katz and Menzel (1966) examined the diffusion of a new antibiotic amongst doctors in 1953, finding that early adopters tended to be more educated, of higher social status and have a wider social network than late adopters.

Rogers (1995) also describes cases in which an innovation fails to diffuse, such as the resistance met by health workers in Peru when they tried to get villagers to boil their water. This basic health practice failed to spread because the health workers' germ theory of illness conflicted with the villagers' beliefs linking illness to hot food. It was also argued that diffusion is most likely when the model and the adopter are similar, not the case for Western health workers and Peruvian villagers. As well as failure to diffuse, other studies have found that diffusion often has unexpected and unpredictable consequences. For example, Sharp (1952) studied the introduction by missionaries of steel axes to Australian aborigines to replace their traditional stone axes. Although the steel axes were more efficient as cutting and chopping instruments, stone axes could no longer be used as status symbols, leading to disruption of the status hierarchy and the trading system, eventually causing men to prostitute their wives and daughters for the steel axes. This example demonstrates not only the unpredictable outcome of introducing an innovation, but also the complex inter-linking of technology, beliefs and social systems that affects cultural transmission.

A recurring finding in these studies and over 3000 others from the diffusion of innovation literature is an S-shaped cumulative adoption curve (Rogers, 1995). That is, there is an initial slow uptake of the innovation, followed by a rapid increase in adoption, followed by another period of slower uptake. Rogers (1995) argued that this represents a few influential and high-status ‘opinion leaders’ initially adopting the innovation, then rapid diffusion through the population, followed by a slowing in the diffusion as the population becomes saturated. Lefebvre (1995) found that an S-shaped cumulative adoption curve is also characteristic of the diffusion of food washing and diet preferences through macaque and chimpanzee populations.

Rogers (1995) also identified several features of innovations which made them more or less likely to be adopted and transmitted. In general, innovations were more likely to be adopted and transmitted if they were (1) perceived to be better than existing ideas or practices (*relative advantage*), (2) consistent with existing values and past experiences (*compatibility*), (3) simple to understand and use (*complexity*), (4) easy to try out and experiment with (*trialability*) and (5) visible to others (*observability*).

The diffusion of innovations literature is almost identical to the rumour literature in its naturalistic study of cultural transmission, in this case in the form of behavioural practices or new technologies, as they are transmitted freely through a naturally occurring population. As such, the same advantages and disadvantages apply: whilst there is greater ecological validity than the experimental approaches described earlier, there is a corresponding decrease in experimental control. Nevertheless, innovations research reinforces the rumour studies’ findings on individual differences (people of high-status and wider social networks are more likely to transmit culture), and adds important new findings such as the S-shaped adoption curve and the disassociation between knowledge and behaviour, as shown by the delay between the farmers learning of and using the hybrid seed.

4.8 HISTORICAL TRANSMISSION CHAINS

Long before experimental psychologists started running their own simulated transmission chains, archaeologists were collecting evidence of actual cultural transmission from historical artifacts. This was achieved through the method of *seriation*, in which a collection of artifacts is ordered according to their similarity: the more features two artifacts share, the closer they are in the order; the fewer they share, the further apart they are placed. As noted by O'Brien and Lyman (2000), the use of seriation rests on two assumptions: firstly that similarity of features corresponds to closeness in historical time, so that a sequence of gradually changing artifacts is also a chronological sequence of artifacts. This is the assumption of *historical continuity*. The second assumption is that the reason why similarity of features corresponds with closeness in time is that the artifacts in the sequence are part of a lineage of inherited information, causally connected by cultural transmission. O'Brien and Lyman (2000) therefore named this *heritable continuity*. As only heritable continuity involves cultural transmission, it is this that we are interested in here.

Although the existence of historical continuity often denotes heritable continuity, it is possible that the former could occur without the latter. An example of historical continuity without heritable continuity is the anti-Darwinian progressive culture stages of anthropologists such as Service (1962), in which all human societies develop through a sequence of fixed and inevitable stages, such as band, tribe, chiefdom and state. Another example of historical continuity without heritable continuity is the case of convergence, in which the same trait emerges more than once independently, with no connection through transmission.

O'Brien and Lyman (2000) argue that heritable continuity can be demonstrated by showing that the different types of artifacts in the seriation overlap in time. For example, type A might occur during periods 1-3, type B during periods 2-4, and type C during periods 4-6. Types A, B and C therefore show heritable continuity: their similarities are due to inheritance through cultural transmission. In general, however, if the change is continuous and gradual, then heritable continuity can be assumed.

The earliest recorded use of seriation was probably Evans' (1850) sequence of gold coins found in Britain, dating back to before the Roman invasion of 54 B.C. This work is familiar as being the historical baseline for Ward's (1949) experimental simulation described above. Evans' (1850) sequence of artifacts begins with coins featuring the head of Phillip II of Macedon on one side and a horse-drawn chariot on the other. As the seriation progresses, these images become less lifelike and more schematised, with the head of Phillip II eventually being lost altogether and replaced with an abstract pattern. The horse-drawn chariot, meanwhile, lost the chariot and became either just a horse or a horse with a rider. This simplification closely resembles the changes that Bartlett (1932) observed in his experimental chains of stories and pictures (although in other lineages of Evans' (1850) coins the simplification was reversed and the design again became naturalistic).

Seriation was then used by Pitt-Rivers (1875) to reconstruct lineages of stone tools, muskets and copper and bronze axes, all demonstrating gradual change in which each specimen can be seen as a slight modification on the one before. Petrie (1899) also used seriation to order approximately 4000 items of pottery excavated along the Nile in Egypt. Petrie's (1899) seriation revealed firstly significant overlapping of features, confirming the assumption of heritable continuity. Second, various lineages of designs can be observed in the seriation, with some lineages becoming extinct, and others merging to form new lineages. Third, the seriation allowed Petrie (1899) to speculate that the handles on the pots, while originally serving a practical purpose, gradually became less functional and more decorative, eventually becoming vestigial. Kidder (1915) performed a similar seriation using pottery from New Mexico, finding that the decorative patterns on the pottery became gradually less intricate through time.

In a striking parallel with the transmission chain method in psychology, the method of seriation then fell out of favour with most archaeologists, and when it *was* used it was to determine a chronological time-line, rather than to denote heritable continuity. O'Brien and Lyman (2000) attribute this in large part as due to the widespread adoption of an essentialist stance, in which types are perceived as having 'essences' and change occurs when one type suddenly transforms into another. This contrasts with a materialist viewpoint which focuses on the variation that naturally occurs within types, resulting in the 'population thinking' (Mayr, 1982) and gradual, continuous change that is essential to Darwinian evolution (see Chapter 2).

Lipo *et al.* (1997) and O'Brien and Lyman (2000) have attempted to reintroduce the method of seriation as a means of identifying lineages in prehistoric artifacts, making explicit the assumption of heritable continuity, and hence cultural transmission. Lipo *et al.* (1997) used seriation to reconstruct lineages of ceramic sherds of the lower Mississippi Valley and help to explain the spatial distribution of these sherds. O'Brien and Lyman (2000), meanwhile, used seriation to analyse projectile points from south-western USA, which they show to exhibit continuous, gradually changing variation rather than a small number of distinct types as had been previously assumed.

In summary, the method of seriation has been used by archaeologists to reconstruct cultural transmission chains from prehistoric artifacts. Some of these seriations show similar changes as do the early transmission chain studies described above. Evans' (1850) lineages of coins, for example, demonstrate the reduction of an image to a schematised form much as Bartlett's (1932) studies with pictures showed. More recently, O'Brien and Lyman (2000) have made more explicit the assumption underlying the method of seriation, that it denotes heritable continuity and hence cultural transmission, and have used it as a starting point for full evolutionary explanations for prehistoric lineages of material artifacts.

4.9 CONCLUSIONS

The literature reviewed above demonstrates how cultural transmission has been studied using diverse methodologies (experimental, observational, historical), within a number of diverse disciplines (psychology, sociology, anthropology, economics, biology, archaeology) and involving different types of transmitted information (written or spoken verbal material, technological artifacts, behaviour).

However, it is apparent that in many cases cultural transmission is being studied with little understanding of either the other disciplines and methods or a wider theory of human culture. The study of cultural transmission would benefit from a cross-fertilisation of methods and ideas across disciplines for a number of reasons. First, theories or models that are supported by more than one empirical method have inherently greater validity. Furthermore, the different methods discussed above each have complementary strengths and weaknesses. For example, while the historical lineages of Section 4.8 are the result of actual cultural transmission in real populations, they are often incomplete and the mechanism that produced them is unknown. The experimental methods of Sections 4.2 and 4.3 might be used to simulate these historical lineages to get at those underlying transmission mechanisms, affording as they do all the advantages of experimental methods (control over variables, complete data etc.). Indeed, Ward's (1949) attempt to simulate an historical lineage from the archaeological record using the transmission chain method (Section 4.2.2) represents a sadly isolated and methodologically flawed example of such a cross-disciplinary integration which deserves to be pursued further.

Experimental work might also benefit from an integration with mathematical models such as those of Cavalli-Sforza and Feldman (1981) or Boyd and Richerson (1985). Predictions derived from these models could be tested with experimental methods, the results of which can then be used to inform further models and theories.

The non-human studies discussed in Section 4.5 highlight the importance of testing for the precise mechanisms of transmission. The wider literature on non-human social learning (Whiten & Ham, 1992; Whiten *et al.*, 2004) has identified a number of precisely defined mechanisms such as imitation, emulation and stimulus enhancement, each of which has different implications for larger-scale cultural change (Heyes, 1993). So far, however, psychologists have tended to ignore these distinctions (Want & Harris, 2002). The experimental methods described above might be used to test the effects of these different mechanisms by having chains of participants transmit the same behaviour or material but only allowing certain forms of social learning (e.g. comparing an 'imitation only' condition, a 'spoken language only' condition and a 'written language only' condition).

However, before pursuing these more advanced proposals for future work involving interdisciplinary integration and social learning mechanisms, it might be useful first to obtain more basic data on cultural transmission using simpler methods. This is particularly important given the paucity of such data at present and the fact that few psychologists are currently interested in cultural transmission. It was noted in Section 4.2 that the original Bartlett-style transmission chain method represents a potentially very effective yet under-used means of experimentally investigating human cultural transmission. Although the early transmission chain studies featured a number of methodological flaws such as a lack of quantitative statistics or standardised procedures, the recent studies show that these issues can be resolved. Perhaps the main advantage of the transmission chain method is that it is quick and easy to implement yet can still generate theoretically interesting results.

The general aim of Chapters 5-9 was therefore to demonstrate that the transmission chain method can be successfully used in the empirical study of human cultural transmission, the results of which can be used to inform the wider theory of cultural evolution outlined in Part A. The specific aim of each chapter was to test for the presence of a different transmission bias: a social bias (Chapter 5), a hierarchical bias (Chapter 6), a status bias (Chapter 7), an anthropomorphic bias (Chapter 8) and a neoteny bias (Chapter 9).

CHAPTER 5 - A BIAS FOR SOCIAL INFORMATION[4]

5.1 ABSTRACT

Evolutionary theories concerning the origins of human intelligence suggest that cultural transmission might be biased toward social over non-social information. This was tested by passing social and non-social information along multiple chains of participants. Experiment 5a found that gossip, defined as information about intense third-party social relationships, was transmitted with significantly greater accuracy and in significantly greater quantity than equivalent non-social information concerning individual behaviour or the physical environment. Experiment 5b replicated this finding controlling for narrative coherence, and additionally found that information concerning everyday non-gossip social interactions was transmitted just as well as the intense gossip interactions. It was therefore concluded that human cultural transmission is biased toward information concerning social interactions over equivalent non-social information.

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5.2 INTRODUCTION

In seeking to investigate the social nature of memory, Bartlett (1932) formulated the ‘transmission chain method’, in which material, typically a text, is passed through a chain of participants, in a manner similar to the children’s game ‘Chinese Whispers’ or ‘Broken Telephone’. The first participant reads the material, and is later asked to recall it. The resultant recall is then given to the second participant to reproduce, whose recall is in turn given to the third, and so on along the chain. Using this method, Bartlett (1932) demonstrated that traditional folk tales were transmitted more fully than a range of other stimuli, such as a newspaper report, a description of a scene and a scientific text. In the following two decades a series of transmission chain studies were published in the *British Journal of Psychology* investigating various hypotheses and participant groups (Hall, 1951; Klugman, 1944; Maxwell, 1936; Northway, 1936; Ward, 1949).

Following this initial period of research activity, the transmission chain method fell from favour within psychology, perhaps due to the rise of behaviourism, and then of cognitive psychology, both of which have tended to ignore social processes. However, a handful of recent studies have sought to reintroduce the transmission chain method, updating it according to modern standards of experimental psychology by reporting standardised instructions, using multiple parallel chains and introducing the statistical analysis of quantifiable data (e.g. Bangerter, 2000; Kashima, 2000a). These recent studies demonstrate that the transmission chain method can be uniquely effective in revealing cumulative and systematic biases in recall that affect cultural transmission.

The present study used this method to investigate the cultural transmission of information regarding third party social relationships, including what is commonly called ‘gossip’. As acknowledged by Emler (2001), there has been very little social psychological theory developed in this area, and even less systematic hypothesis testing. In contrast, the topic is here approached from an evolutionary and comparative perspective, in which there is a large body of work devoted to the social function of human intelligence. Such an approach can add theoretical rigour to a traditionally underdeveloped and under-researched topic.

The *Machiavellian Intelligence* (Byrne & Whiten, 1988; Whiten, 1999b; Whiten & Byrne, 1997) or *Social Brain* (Dunbar, 1998, 2003) hypothesis asserts that primate intelligence evolved primarily to deal with complex social problems, rather than non-social ecological or technological problems such as locating food, extractive foraging or using tools. Support for the hypothesis comes from correlational analyses of a number of primate species showing a link between a proxy of intelligence, the ratio of neocortex to the rest of the brain, and various measures of social complexity, such as group size (Barton & Dunbar, 1997), frequency of tactical deception (Byrne & Corp, 2004) and frequency of social play (Lewis, 2001). Measures of non-social complexity, such as range size or foraging style, show no such correlation with neocortex ratio (R. I. M. Dunbar, 1995).

Although such analyses encompass the entire primate order, the Machiavellian intelligence hypothesis should not be taken as excluding the evolution of human intelligence, and the studies cited above include data from several ancestral hominid species (as well as modern humans). Indeed, Whiten (1999a) outlines how social factors may have shaped cognition during human evolution to produce what he terms a 'deep social mind', exhibiting faculties such as mind-reading and co-ordinated co-operation. Dunbar's (1993; 1996) *social gossip theory* argues that language evolved in humans in response to social selection pressures, in order to track complex social relationships and ensure their coherence in the unusually large social groups characteristic of modern humans.

The Machiavellian intelligence hypothesis can also be taken to imply that, as a result of selection pressures in the past favouring social cognitive complexity, the cognition of modern-day humans should exhibit certain specialisations to deal with social problems (Whiten, 2000b). If modern-day human cognition is indeed moulded to deal with social problems, then people should preferentially attend to, recall and transmit social information over equivalent non-social information. Observational evidence consistent with this claim was provided by Dunbar, Duncan, and Marriott (1997), who found that freely forming conversational groups spent approximately two-thirds of their time discussing social topics (personal relationships, personal experiences or social activities) - more than work, leisure, politics and the arts combined.

To date, there has been no equivalent *experimental* test of the Machiavellian intelligence hypothesis with regard to cultural transmission. However, an earlier memory study by Owens, Bower, and Black (1979), while not intended to be such a test, can be considered relevant. Participants in Owens *et al.*'s (1979) study read and recalled descriptions of a female student involved in five everyday events: making a cup of coffee, going to the doctor's, buying some milk, attending a lecture and going to a party. The experimental group, but not the control group, was in addition told of a motive for the character (that she is pregnant by her professor) that could be used to make sense of and connect the five episodes, in effect turning the neutral events into gossip. The result was that the experimental group recalled significantly more episodes than the control group.

The aim of the present study was to expand upon and extend Owens *et al.*'s (1979) findings in two ways, in order to provide an explicit test of the Machiavellian intelligence hypothesis with regard to human cultural transmission. First, rather than having single participants reading and recalling experimental material (i.e. social and non-social material), Bartlett's (1932) transmission chain method was used to pass the material along chains of participants, in order to investigate the longer-term persistence of any 'social bias' in cultural transmission. If an effect can be demonstrated to have a degree of stability or persistence along chains of multiple participants, we can more confidently extrapolate from this necessarily simplified experimental setting to a larger group- or population-level and draw wider conclusions regarding human culture as a whole.

Information		Definition	Predicted by	
Social	Gossip	Concerning intense third-party social relationships and interactions	Machiavellian intelligence/social brain hypothesis	Strong Machiavellian intelligence hypothesis/Exploitative theories of language evolution
	Social non-gossip	Concerning everyday third-party social relationships and interactions		
Non-social	Individual	Concerning interactions and relationships between a single person and the physical environment	Ecological hypotheses of primate intelligence	
	Physical	Concerning interactions and relationships solely within the physical environment		

Table 5.1 - Definitions of each category of information tested in Chapter 5, with the theory which predicts the information to be favoured during transmission

Second, we explicitly draw on the Machiavellian intelligence hypothesis in order to provide precise definitions of 'social' and 'non-social' information, as shown in Table 5.1. The Machiavellian intelligence hypothesis holds that it is not merely being 'social' in the sense of 'living in groups' that has been a key factor in the evolution of primate intelligence, but rather the degree of social *complexity*, characterised by frequently changing coalitions and alliances (Whiten, 1999b). Hence we define 'social' information as information concerning interactions and relationships between a number of third parties. This social category is sub-divided according to the quality of those interactions or relationships: '*Gossip*' involves particularly intense and salient social interactions and relationships, such as the illicit affair and the pregnancy of Owens *et al.*'s (1979) material, while *'Social Non-Gossip'* involves more everyday interactions and relationships. This social category is contrasted with 'non-social' information, which we divide into information concerning a single individual's interactions with the physical environment (*'Individual'*) and information solely concerning that physical environment (*'Physical'*).

The Machiavellian intelligence hypothesis would predict that social information (both Gossip and Social Non-Gossip) would be transmitted in greater quantity and with greater accuracy than the non-social information (both Individual and Physical). Ecological hypotheses of the evolution of primate intelligence (e.g. Clutton-Brock & Harvey, 1980) might predict in contrast that the Individual information (how to do things) and the Physical information (about the non-social environment) would be transmitted at least as well as the Social information. A stronger version of the Machiavellian intelligence hypothesis might additionally predict that social interactions which are more intensely 'Machiavellian' and gossip-like, featuring exploitative behaviour such as deception or infidelity, would elicit a stronger appeal than commonplace everyday social interactions. This stronger form would thus additionally predict that the Gossip information would be transmitted in greater quantity and with greater accuracy than the Social Non-Gossip information.

This additional difference between the Gossip and the Social Non-Gossip information might also be predicted by theories which argue that the function of gossiping is to transmit information about other people' s anti-social behaviour, in order to learn about their reputation and protect against exploitation. Enquist and Leimar (1993) argued that gossiping is a behavioural adaptation to protect against potential free-riders by spreading information about their past behaviour, preventing the free-riders from moving from population to population in order to find and exploit naïve individuals. Wilson, Wilczynski, Wells, and Weiser (2000), meanwhile, argued that gossiping acts as a means of preventing behaviour which acts to promote individual gain at the expense of the group. This argument was backed up by a series of experiments in which participants rated speakers of self-serving gossip more negatively than speakers of group-serving gossip. If these theories are correct, information about exploitative or anti-social behaviour such as deception and infidelity (the Gossip material) should be favoured over simple everyday social interactions (the Social Non-Gossip material).

Note that these predictions are only intended to apply to information that is equivalent in dimensions other than the social/non-social comparison. The word ‘equivalent’ here is intended to exclude non-social information that is particularly salient or significant to people for other specific reasons: it is not claimed that *all* social information is *always* transmitted better than *all* non-social information, but rather that when the only difference between two pieces of information is the social component, then the social will be preferred over the non-social.

5.3 EXPERIMENT 5A

In line with the theoretical predictions outlined above and in Table 5.1, in Experiment 5a three paragraphs matched for number of words, sentences and propositions were constructed, each constituting a different class of information. The Gossip information featured an illicit affair and pregnancy (following Owens *et al.*, 1979), the Individual information comprised simple facts about a single character such as their age and occupation, and Physical information described the geography, history and commerce of a city. (Note that the social category is represented here solely by the Gossip material; a distinction between Gossip and Social Non-Gossip information is made in Experiment 5b.) These paragraphs were then transmitted along multiple chains of participants using the methodology developed by Bartlett (1932).

5.3.1 Materials and Methods

5.3.1.1 Design

A within-chain transmission chain design was adopted (Figure 5.1), in which the first participant in each of ten replicate chains was given material containing information representing all three categories (Gossip, Individual and Physical). Each of the ten chains comprised four participants, or ‘generations’. This within-chain design was intended to reduce random between-chain variation, which pilot studies with a between-chain design (Mesoudi, 2002) found obscured any differences between the material types.

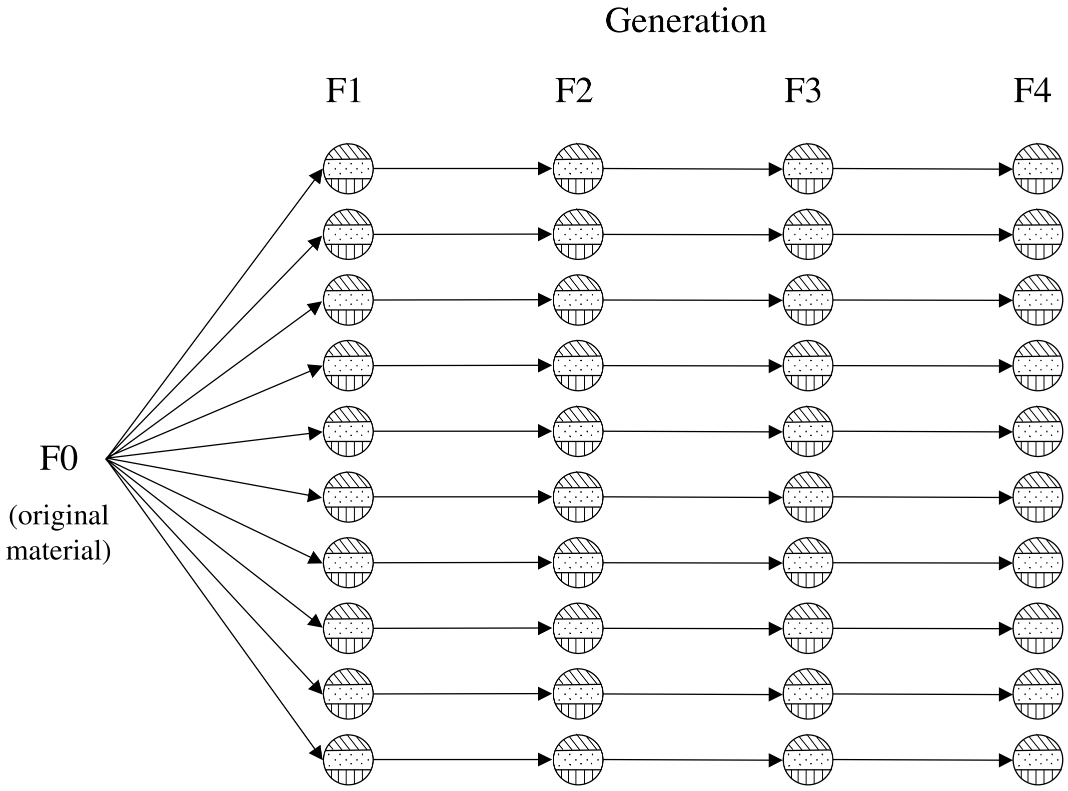

Figure 5.1 - The design of Experiment 5a. Each circle represents one participant, and the three different patterns represent the three different types of material.

The independent variable was the transmission generation, of which there were four (F1-F4). The dependent variables were the total number of propositions recalled (recall quantity), and the number of propositions that were present in the original material (recall accuracy), as detailed in the Coding section below. It was predicted that Gossip would be transmitted in greater quantity and with greater accuracy than both the Individual and the Physical material.

Note that each chain of four participants was here treated as an independent unit of analysis, rather than each participant. This is because the focus of interest is the material and how that material changes as it passes through the chain, rather than any single participant’s memory performance. Furthermore, the recall of second, third and fourth generation participants is constrained by each previous generation’s recall, with anything omitted in one generation unavailable to subsequent generations to recall. Hence the recalls of each participant within a single chain are not statistically independent of one another, and in the ANOVAs reported below each chain is treated as an independent unit of analysis, rather than each participant (e.g. ‘between-groups’ implies ‘between-chains’ rather than ‘between-subjects’).

It was judged that four participants constituted an optimum chain length, i.e. this number was long enough to capture the long-term cumulative effects of cultural transmission, yet short enough to be practical in terms of recruiting participants and performing replications. Previous transmission chain studies (e.g. Bangerter, 2000) have successfully demonstrated transmission effects using four participants per chain.

5.3.1.2 Material

The original material given to the first participant in each chain was composed of three paragraphs, each paragraph representing one of the three types of information: Gossip, Individual and Physical (although these labels were not given to the participants). These paragraphs are reproduced in Appendix A.1. Each of the paragraphs was matched for number of words, sentences and propositions.

The original material contained the three paragraphs in a fixed order: Individual, then Gossip, then Physical. The order was not counterbalanced, as it was felt that the material as a whole would make less sense to the participant if, for example, the Physical material came first. Pilot studies (Mesoudi, 2002) suggested that order of presentation has no effect on recall, and in any case any primacy or recency effect would favour either the Individual or the Physical material, *against* the main experimental hypothesis.

5.3.1.3 Participants

Forty participants of mean age 20.98 years (standard deviation = 3.30) performed the experiment. Seven of the chains were composed of female participants (n = 28) and three of the chains were composed of male participants (n = 12) to check for possible sex differences, although based on the results of Owens *et al.* (1979) and Dunbar *et al.* (1997), none were predicted. All participants were students, participated voluntarily, were unpaid and had normal reading and writing ability.

5.3.1.4 Procedure

The procedure adopted here involved the experimenter physically passing the material from individual to individual, rather than the participants directly transmitting the material (e.g. Bartlett, 1932). This allowed greater control over transmission, and removed the need to gather groups of participants together. Participants were thus run in groups of between one and five.

A booklet was produced which contained on the first page the instruction, ‘Please read the following text through once. When you have finished turn the page.” followed by the material. The second page contained the instruction, ‘Now, without turning back, please write out as best you can the text you just read. Be as accurate as possible, but don't worry if you can't remember it all. When you have finished turn the page." followed by a blank space for recall. A final sheet solicited the age and sex of the participant and thanked them for participating, whereupon the experimenter debriefed them as to the nature of the study. The recall was then typed up and inserted into the next participant's booklet as appropriate.

No distractor task was performed, and no time limit was set. At no point in the procedure did either the printed instructions or the experimenter state that the experiment was a memory test, that the material had come from another participant, or that their recall would be passed on to another participant.

5.3.1.5 Coding

A propositional analysis (Kintsch, 1974) was performed on each participants' recall (see Chapter 4). This propositional analysis was used to calculate the total number of propositions recalled, a measure of *recall quantity*, and the number of propositions also contained in the original material, a measure of *recall accuracy*. Note that recall in each generation was always compared with the *original* (F0) material, not the previous generation's recall, as it is the gross cumulative changes that are important rather than any single individual's memory achievement.

To assess inter-rater reliability, an independent coder blind to the hypothesis and to the material type coded two of the chains from Experiment 5a and three of the chains from Experiment 5b (the same propositional analysis was used in both experiments). The coding of the blind second coder and myself was highly consistent, with a Pearson's correlation coefficient of 0.97.

5.3.2 Results

5.3.2.1 Recall quantity

A mixed 2x3x4 ANOVA with sex as a between-groups factor and material and generation as within-groups factors showed an overall effect of material ($F_{(2,16)} = 63.71$, $p < 0.01$) and of generation ($F_{(3,24)} = 26.49$, $p < 0.01$) but no effect of sex ($F_{(1,8)} = 2.37$, ns). Planned comparisons were made between each pair of material types, using 2x4 within-groups ANOVAs at a Bonferroni corrected significance level of $\alpha^* = \alpha / n$ where n = no. of comparisons (hence $\alpha^* = 0.05 / 3 = 0.017$). Significant differences were found between Gossip and Individual ($F_{(1,9)} = 131.44$, $p < 0.01$) and between Gossip and Physical material ($F_{(1,9)} = 112.46$, $p < 0.01$), although there was no significant difference between Individual and Physical ($F_{(1,9)} = 3.80$, ns). The prediction that a larger quantity of the Gossip material is transmitted than the other material is therefore supported, and can be observed in Fig. 5.2, with a larger quantity of the Gossip material transmitted in every generation than of the Individual and Physical material.

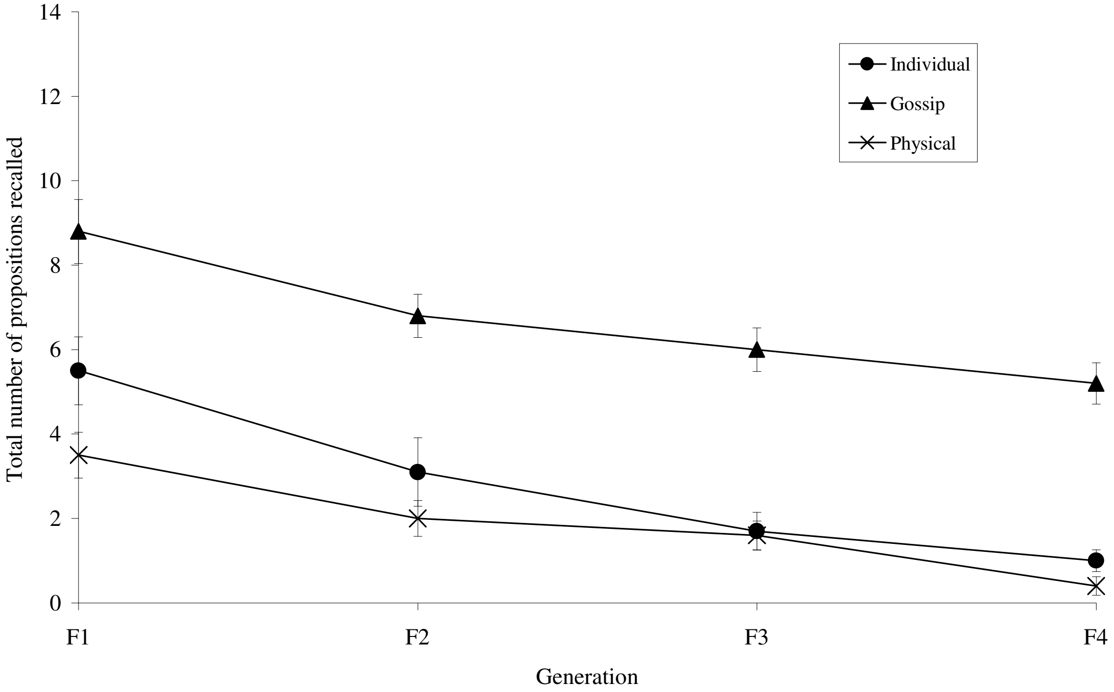

Figure 5.2 - The total number of propositions recalled by each generation of Experiment 5a (irrespective of accuracy). Error bars show standard errors.

5.3.2.2 Recall accuracy

Fig. 5.3 suggests a similar pattern for the measure of recall accuracy to that shown in Fig. 5.2 for recall quantity. A mixed 2x3x4 ANOVA with sex as a between-groups factor and material and generation as within-groups factors showed an overall effect of material ($F_{(2,16)} = 73.55$, $p < 0.01$) and of generation ($F_{(3,24)} = 26.91$, $p < 0.01$) but no effect of sex ($F_{(1,8)} = 2.90$, ns). There was a significant material x generation interaction ($F_{(6,48)} = 2.81$, $p < 0.05$), probably due to the levelling off at base level shown by the Individual and Physical material, while the Gossip was still degrading at a steady rate. Planned comparisons showed significant differences between Gossip and Individual ($F_{(1,9)} = 151.22$, $p < 0.01$) and between Gossip and Physical ($F_{(1,9)} = 117.36$, $p < 0.01$), and no significant difference between

Individual and Physical ($F_{(1,9)} = 8.05$, ns). The prediction that Gossip is transmitted with greater accuracy than the other material is therefore supported.

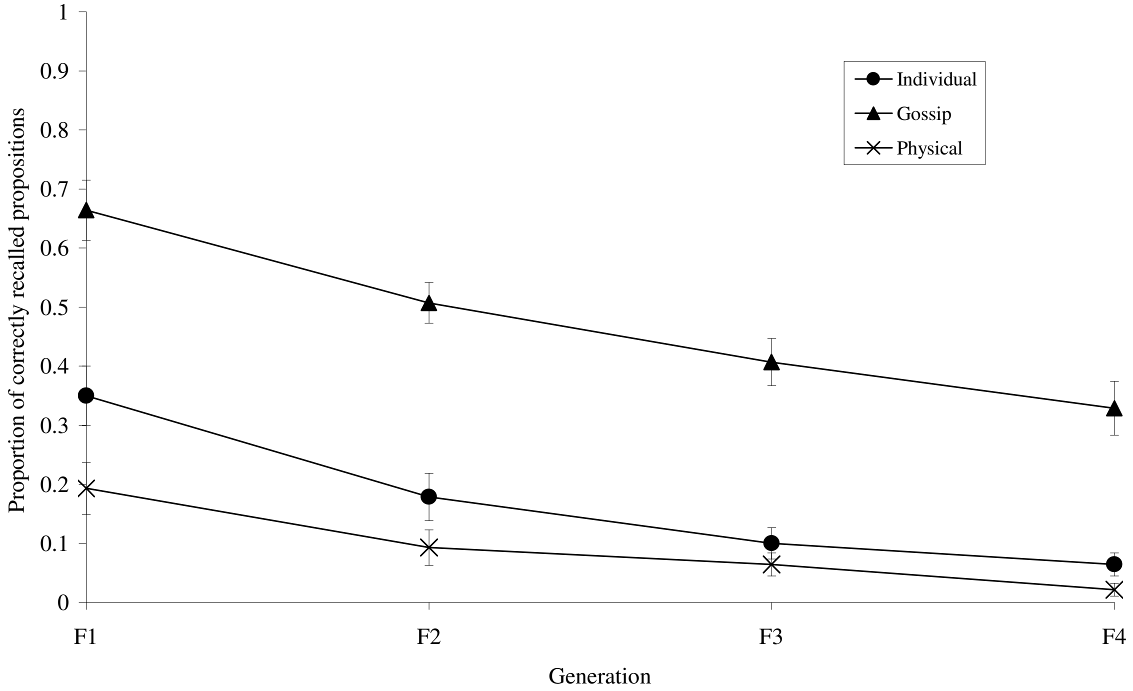

Figure 5.3 - The proportion of propositions that were correctly recalled by each generation of Experiment 5a. Error bars show standard errors.

The Gossip vs. Physical comparison additionally showed a significant material x generation interaction ($F_{(3,27)} = 4.38$, $p < 0.017$). Given that the Gossip material shows the steepest decline and the Physical material the shallowest, this supports the explanation given above for the overall material x generation interaction, i.e. that Physical is at base level while Gossip is steadily declining. Partial correlation coefficients showed no effect of age on overall recall ($r_p=0.09$, $n=40$, ns), controlling for generation, and none of the tests above violated the assumption of sphericity.

5.3.3 Discussion

The results of Experiment 5a support the hypothesis that the Gossip material would be transmitted in greater quantity and with greater accuracy than the non-social material (either Individual or Physical). However, a concern is that as well as differing in informational content, the three paragraphs could also be seen as differing in coherence. That is, the Gossip material may form a coherent narrative, with the character's affair and pregnancy integrating the entire paragraph. The other two paragraphs perhaps showed a less coherent narrative, lacking an integrating theme and reading more like a list of unconnected facts. The reason that the Gossip was transmitted with greater accuracy than the other two types of material could therefore have been due to its coherence, rather than the fact that it had gossip-like content. This issue was addressed in Experiment 5b.

5.4 EXPERIMENT 5B

The aim of Experiment 5b was to equate conditions with respect to the integrating theme or coherent narrative. What, however, should count as an 'integrating theme' or 'coherent narrative'? Mandler and Johnson (1977), Thorndyke (1977) and Rumelhart (1977) developed the idea, originally put forward by Bartlett (1932), that stories are particularly easy to remember because they form coherent narratives that can be represented by a hierarchical schema structure. It is unlikely, however, that a paragraph of approximately sixty words would have such a complex hierarchical structure, beyond a simple linear chain of events linked causally and temporally. For example, the pregnancy causes the professor to refuse to see Nancy, which then causes Nancy to threaten to tell his wife about the affair. In contrast, a chain that is linked temporally but not causally would simply be a list of unconnected events and lack coherence, while a chain that is linked causally but not temporally would not form a narrative. Each type of material used in Experiment 5b was therefore designed to constitute a comparable linear chain of events linked causally and temporally, so that superior recall of the Gossip material can be more definitely attributed to its gossip-like content rather than its greater structural coherence, as was possible in Experiment 5a.

Experiment 5b also featured the fourth type of material from Table 5.1, distinguished as Social Non-Gossip information (henceforth simply *'Social'*). This material contained the same number of social interactions and social agents as the Gossip but with interactions that would not be considered as intense or salient. So Experiment 5b tested firstly the prediction of the broad Machiavellian intelligence hypothesis that both the Social and Gossip material would be transmitted in greater quantity and with greater accuracy than the non-social Individual and Physical material, and secondly the additional prediction of the strong Machiavellian intelligence hypothesis that the Gossip material would be transmitted better than the Social material.

5.4.1 Materials and Methods

The design of Experiment 5b was largely identical to that of Experiment 5a, with ten chains each comprising four participants again transmitting all types of material. There were three minor differences: first, there were now four types of material (Gossip, Social, Individual and Physical) rather than three; second, the order in which this material was presented was now counterbalanced; and third, five of the chains were now female, and five were male. None of the participants tested here took part in, or had any knowledge of, Experiment 5a. All forty participants were students, participated voluntarily, were unpaid and had normal reading and writing ability. Their mean age was 21.40 years (standard deviation = 3.83).

The original material given to the first participant in each chain is reproduced in Appendix A.2. The *Gossip* information again featured an affair and pregnancy as its theme, although the information that Nancy is lying to her friends did not fit into the single linear chain, so was replaced with extra information at the end concerning the professor's wife leaving him. The *Social* (non-gossip) information comprised a causal and temporal chain consisting of a series of social interactions and containing the same number of agents as the Gossip, but without gossip-like content such as deception, infidelity and pregnancy. *Individual* information featured a chain consisting of interactions between a single character and the inanimate world. Finally, *Physical* information contained no intentional agents in the chain, consisting entirely of interactions within a physical system.

To test whether each of the four types of material were comparable on dimensions other than the desired experimental manipulation of social content, ten additional participants not involved in the experiment proper were given the four paragraphs (Gossip, Social, Individual and Physical) and asked to rate each of them on a 7-point scale for 'coherence', 'familiarity' and 'realism'. No significant differences were found between the paragraphs on any of these dimensions, suggesting that any differences found in Experiment 5b are unlikely to be due to differences in coherence, familiarity or realism, which had been a concern in Experiment 5a.

5.4.2 Results and Discussion

5.4.2.1 Recall quantity

A mixed 2x4x4 ANOVA with sex as a between-groups factor and material and generation as within-groups factors showed an overall effect of material ($F_{(3,24)} = 15.29$, $p < 0.01$) and of generation ($F_{(2,15)} = 36.76$, $p < 0.01$, Greenhouse-Geisser corrected) but no effect of sex ($F_{(1,8)} = 0.11$, ns). Planned comparisons were again made between the pairs of material types predicted to differ, using 2x4 within-groups ANOVAs at a Bonferroni corrected significance level of $\alpha^* = \alpha / n$ where n = no. of comparisons (there are now five comparisons, hence $\alpha^* = 0.05 / 5 = 0.01$). There were significant differences between Gossip and Individual ($F_{(1,9)} = 25.72$, $p < 0.01$) and Gossip and Physical ($F_{(1,9)} = 28.23$, $p < 0.01$), demonstrating that a larger quantity of Gossip material was transmitted than of either the Individual or the Physical material, as was predicted. Also as predicted, a significantly larger quantity of the Social material was transmitted than of the non-social materials, as shown by significant differences between Social and Individual ($F_{(1,9)} = 15.43$, $p < 0.01$) and Social and Physical ($F_{(1,9)} = 21.49$, $p < 0.01$). There was, however, no significant difference between Gossip and Social ($F_{(1,9)} = 0.16$, ns). These effects are illustrated in Fig. 5.4.

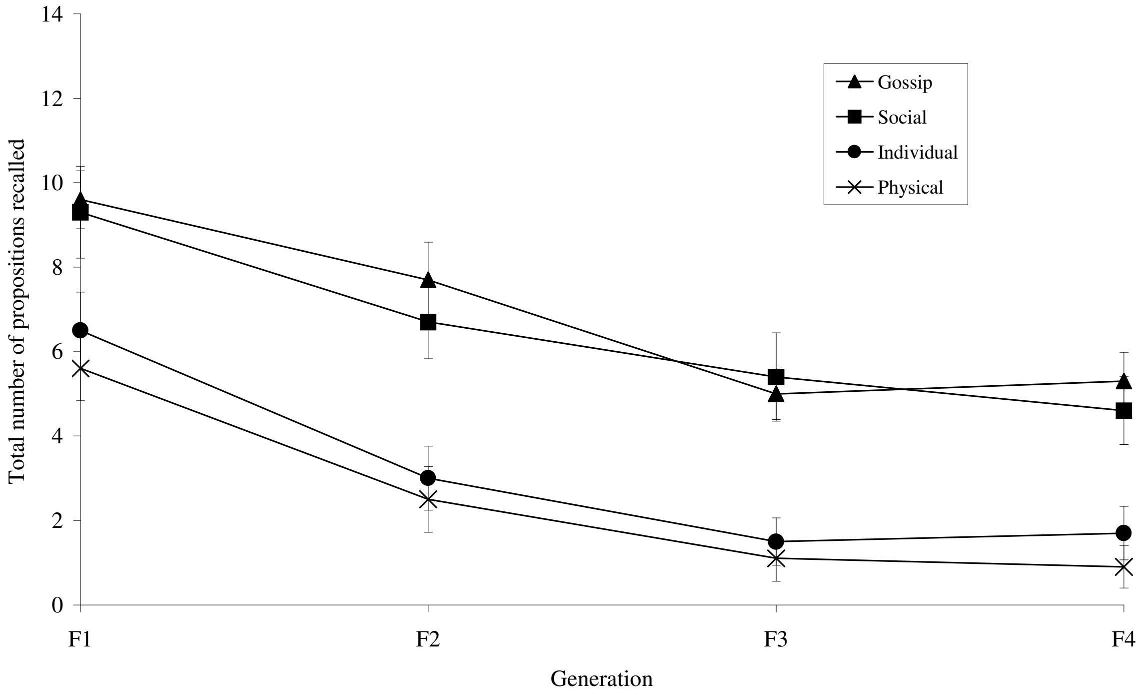

Figure 5.4 - The total number of propositions recalled by each generation of Experiment 5b (irrespective of accuracy). Error bars show standard error.

5.4.2.2 Recall accuracy

Fig. 5.5 suggests that the Gossip and the Social material were likewise transmitted with greater accuracy than the Individual and Physical material. Compared with the measure of quantity shown in Fig. 5.4, however, there is a larger difference between Gossip and Social, with the latter transmitted with slightly poorer accuracy than the former, especially at generations F2 and F4. A mixed 2x4x4 ANOVA with sex as a between-groups factor and material and generation as within-groups factors showed an overall effect of material ($F_{(3,24)} = 12.99$, $p < 0.01$) and of generation ($F_{(2,15)} = 38.78$, $p < 0.01$, Greenhouse-Geisser corrected) but no effect of sex ($F_{(1,8)} = 0.08$, ns).

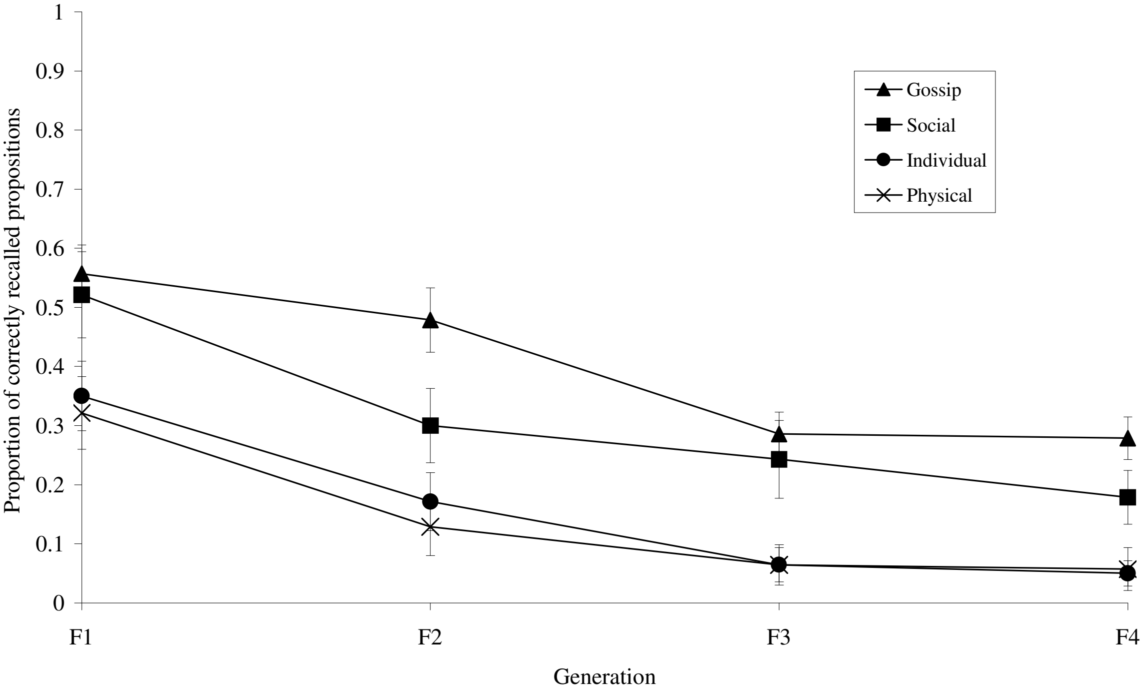

Figure 5.5 - The proportion of propositions that were correctly recalled by each generation of Experiment 5b. Error bars show standard errors.

Planned comparisons showed significant differences between Gossip and Individual ($F_{(1,9)} = 43.34$, $p < 0.01$) and Gossip and Physical ($F_{(1,9)} = 18.89$, $p < 0.01$). The Gossip material was therefore transmitted with greater accuracy than the two non-social types of material, as was predicted. The comparisons between Social and Individual ($F_{(1,9)} = 10.19$, $p = 0.011$) and Social and Physical ($F_{(1,9)} = 10.30$, $p=0.011$) were both extremely close to significance at the Bonferroni corrected significance level of 0.01, and so will be treated as such. This confirms the second part of the hypothesis that the Social material would also be transmitted with greater accuracy than the two non-social material types (Individual and Physical).

The additional prediction that the Gossip would be transmitted with greater accuracy than the Social was not supported. There was no significant difference between the Gossip material and the Social material ($F_{(1,9)} = 2.40$, ns). However, as can be seen in Fig. 5.5, there is a trend toward the Gossip being transmitted with greater accuracy than the Social material, and at generation F2 this difference is indeed significant ($F_{(1,9)} = 7.98$, $p<0.05$). This difference is not strong, however, and there is no theoretical reason why generation F2 would be any more likely to show a difference than the other generations. Thus, while there seems to be a trend for the Gossip to be transmitted with greater accuracy than the Social, with the results certainly not as clear cut as for the measure of recall quantity, the hypothesis that the Gossip material is transmitted with greater accuracy than the Social material cannot be accepted.

Partial correlation coefficients showed no effect of age on overall recall ($r_p = 0.08$, $n=40$, ns), controlling for generation. None of the statistical tests described above featured any interactions, and none violated the assumption of sphericity (except where the Greenhouse-Geisser corrected significance level is given).

5.5 CONCLUSIONS

The aim of Chapter 5 was to investigate whether there is a bias for social information in human cultural transmission, as predicted by evolutionary theories that posit a social origin for human intelligence. Experiment 5a found evidence that gossip-like social information is transmitted with significantly greater accuracy and in greater quantity than non-social information. Experiment 5b replicated the finding of

Experiment 5a using material equivalent in narrative coherence, demonstrating that coherence was not responsible for the superior recall of the gossip. Experiment 5b also found that information concerning social interactions that would not be described as gossip was transmitted with an accuracy and in a quantity not significantly different from the gossip itself. That is, the gossip-like content of infidelity, deception and pregnancy was relatively unimportant; what mattered for superior transmission was that there were a number of third party social agents interacting with one another.

These results are therefore consistent with the Machiavellian intelligence (Byrne & Whiten, 1988; Whiten, 1999b; Whiten & Byrne, 1997) or social brain (Dunbar, 1998, 2003) hypothesis, that primate intelligence evolved primarily to deal with social, rather than ecological, information. Here, this is reflected in a social bias in cultural transmission. The results are also consistent with Dunbar's (1993, 1996) social gossip theory of language evolution, that language evolved to exchange social information. A stronger form of the Machiavellian intelligence hypothesis, and theories which argue for a more negative, exploitative function of language, such as the control of free-riders (Enquist & Leimar, 1993) or the promotion of group interests (Wilson *et al.*, 2000), were not supported, in that information commonly considered gossip-like in content was transmitted no better than equivalent non-gossip social information. Theories which argue that primate intelligence is the result of ecological selection pressures were also not supported, with information concerning the non-social environment transmitted poorly. Before considering the wider theoretical implications of these findings and possible directions for future research, we must examine a number of potential objections to this interpretation of the results.

One possible objection might be that the Social material used in Experiment 5b (asking directions from strangers) was not ‘social’ in the sense of the Machiavellian intelligence hypothesis. That is, the relationships between the characters were not very meaningful and the characters were not exchanging information about themselves or other people. However, it should be recognised that the broad Machiavellian intelligence hypothesis might predict that *any* social interactions should be memorable, whatever their content or quality. Even though the characters are exchanging non-social information, there are still many potentially important social cues that are present, such as the personality of the character (e.g. their helpfulness) or the reliability of the information they give. This information might then be stored and used to negotiate future social interactions, which may be more complex. In any case, information which is intermediate between the Social and the Gossip material, featuring interactions more strongly Machiavellian than the Social material (but not as strong or negative as the Gossip material), would presumably be transmitted just as well as these two were in Experiment 5b, hence still supporting the Machiavellian intelligence hypothesis.

It might be argued that rather than being the result of a biologically evolved predisposition, the social bias seen here is the result of some related property of the material, such as its emotional impact or attentional salience. Various findings from the social psychological literature concerning memory might also be used to account for some of the findings presented here, such as that people have better recall for descriptions of behaviour that violates social norms (Wyer, Budesheim, Lambert, & Swan, 1994), for information that is incongruent with social expectations (Stangor &

McMillan, 1992), and for negative self-discrepant in-group behaviour (Gramzow, Gaertner, & Sedikides, 2001). These two types of explanation should not, however, be seen as in opposition. Properties such as ‘arousing’, ‘salient’ or ‘memorable’ represent the proximate mechanisms by which an evolved bias may operate. The two levels of explanation, ultimate and proximate, should be seen as separate and complementary (Tinbergen, 1963). Indeed, a full account of human cognition and behaviour requires empirical evidence from all explanatory levels.

As well as ultimate and proximate explanations, Tinbergen (1963) also specified a developmental level of explanation. From this perspective it could be argued that information about social relationships becomes particularly salient during a child’s development, causing such a bias to be learned. Again, however, the likelihood that such learning might take place does not contradict an ultimate evolutionary argument for a biologically evolved predisposition or bias to learn and transmit certain types of information. To the contrary, the comparative evidence for the social brain hypothesis (R. I. M. Dunbar, 1995; Joffe, 1997) makes it likely that such a bias does indeed have an evolutionary basis at some stage of development. Nevertheless, developmental investigations would be useful in further clarifying the nature and origin of the social bias observed here.

It might be argued that the transmission aspect of this study adds little to the findings of Owens *et al.* (1979) concerning recall at the individual level. Such an effect was already apparent in the first generation recall, where single participants recalled social information better than non-social information. However, a bias in memory or recall and a bias in transmission should not be seen as alternative or opposing phenomena. The long-term transmission bias does of course reflect a memory bias, but its significance is that it uniquely documents the cumulative operation of that memory bias in successive participants, providing an experimental microcosm for the study of cultural, as opposed to merely cognitive (memory) processes. Furthermore, the assumption that a consistent effect will be observed along an extended chain is just that: an assumption. In fact, other transmission chain studies (e.g. Kashima, 2000a; Chapter 6) have demonstrated cross-over effects in which later generations reverse a trend exhibited by earlier generations. Hence the assumption of persistence needs to be empirically tested, as was done here, rather than assumed *a priori*.

Data on persistence consequently allow us to draw conclusions regarding the wider effect of a social bias on human culture in general. As noted by Kashima (2000b), Bartlett (1932) was interested not only in cultural *transmission* but also large-scale cultural *change*, and Kashima (2000b) suggests that the transmission chain method "provides one way of examining how micro-processes contribute to a macro-phenomenon such as the maintenance of culture" (p. 394). We may speculate that the bias for social information found here can be extrapolated to the population level to explain the popularity of socially oriented mass media such as gossip magazines and television soap operas over non-social or factual journals and television documentaries. There are a number of theoretical frameworks that might be used to make this link more formally, such as Moscovici's (1984) social representation theory, Sperber's (1996) epidemiological model of cultural change, and theories of cultural evolution (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Mesoudi *et al.*, 2004).

As noted by Emler (2001), there has been very little experimental work on gossip in the past. Hence this study was intended to be an initial investigation of the phenomenon under very simplified conditions. There are undoubtedly a number of factors not examined here that likely play an important role in the transmission of social information in the real world, and it is hoped that this study will provide the foundation for future work systematically examining such factors. For example, the participants in the present study were not instructed that the experiment was a memory test, that the material had come from another participant, or that their recall would be passed on to another participant. The third parties described in the material were also not known to the participants. Given that it is well established that people often tailor their messages to suit the intended receiver (Sperber & Wilson, 1986), providing such knowledge to the participants may well affect the content or accuracy of the recall. Similarly, having the participants transmit the material face-to-face rather than via anonymous written text would allow the investigation of interpersonal factors such as intonation of voice or non-verbal cues. More naturalistic methods, such as those used to study rumour transmission (Rosnow, 1980, 1991), might also be used to investigate such factors.

The conclusions drawn here are of course dependent on the specific material used, and there is a need to replicate the study with alternative examples of the different types of information. In Experiment 5b an effort was made to ensure that the four material types contained equivalent underlying causal and temporal chains so that differences in transmission could be more confidently attributed to differences in content. However, this underlying structure was still somewhat informal, and future studies might use more advanced models of causal links in narratives (e.g. Trabasso & Sperry's (1985) causal network representation or Trabasso & van den Broek's (1985) recursive transition network model) to more precisely equate the underlying structure of the different material.

There may also be an effect of varying the number of social agents or interactions. The Gossip and Social material in Experiment 5b featured three people (Nancy, the professor and his wife for the Gossip material; Nancy, the old man and the bus driver for the Social material), which is within the typical upper bound of four found in natural conversational groups (Dunbar, Duncan, & Nettle, 1995). Perhaps material featuring interactions between more than four people would be transmitted less well.

There is also a need to replicate the study cross-culturally. Although condition-dependent biases might modulate outcomes according to ecological variations, the evolutionary theories outlined above would predict that people in many different societies would show the social bias found here. However, it should also be noted that the sample used in the present study is particularly useful in one respect in challenging the stereotypical and historical view of a 'gossip' as poorly educated, of low intelligence, and female (Emler, 2001, pp. 318-319). The present study found that highly educated and intelligent young people of both sexes exhibit a bias for gossip over non-social ('factual') information.

In summary, Chapter 5 has experimentally demonstrated the operation of a bias in human cultural transmission toward social information, defined as information concerning social interactions between a number of people. Such information was transmitted with greater accuracy and in greater quantity than both information about an individual person's behaviour and non-human physical interactions. It was found that the quality of the social interactions was largely unimportant, insofar as information featuring gossip-like interactions was transmitted no better than information featuring commonplace everyday interactions. This social bias is argued to have evolutionary origins, consistent with theories positing emphasis on the social functions of human intelligence.

CHAPTER 6 - THE HIERARCHICAL TRANSFORMATION OF EVENT KNOWLEDGE[5]

6.1 ABSTRACT

There is extensive evidence that adults, children, and some non-human species represent routine events in the form of hierarchically structured ‘action scripts’, and show superior recall and imitation of information at relatively high-levels of this hierarchy. Chapter 6 investigated the hypothesis that a ‘hierarchical bias’ operates in human cultural transmission, acting to impose a hierarchical structure onto descriptions of everyday events, and to increasingly describe those events in terms of higher hierarchical levels. Descriptions of three everyday events (going to a restaurant, getting up and going shopping) expressed entirely in terms of basic low-level actions were transmitted along ten chains each containing four adult human participants. It was found that the proportion of low-level information showed a significant linear decrease with transmission generation, while the proportions of medium- and high-level information showed significant linear increases, consistent with the operation of a hierarchical bias. The findings additionally provide support for script theory in general, and are discussed in relation to hierarchical imitation in non-human primates.

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[5] Reproduced with minor revisions from Mesoudi, A. and Whiten, A. (2004). The hierarchical transformation of event knowledge in human cultural transmission. *Journal of Cognition and Culture*, 4(1), 1-24.

6.2 INTRODUCTION

Cultural transmission is the process by which learned information passes from individual to individual. This is contrasted with the transmission of information genetically, or information acquired through individual learning. The earliest experimental investigations into cultural transmission were carried out by Bartlett (1932) using his ‘method of serial reproduction’, in which a participant reads some stimulus material, then after a short delay recalls it. This recall is then presented to a second participant to recall, whose output is given to the third participant, and so on along a transmission chain. Bartlett (1932) was thus able to study the changes that occurred to the material as it passed along the chain, and compare the differential degradation rates of different types of material.

One of the key findings of Bartlett’s (1932) original studies was that folk tales were transmitted with greater fidelity than any other text, such as a newspaper article, a description of a scene or a scientific argument. Bartlett (1932) argued that folk tales were more amenable to transmission because people possess ‘story schemas’, which represent the underlying structure of generic stories such as folk tales, around which the specific details of that particular story may be reconstructed. Cognitive psychologists such as Mandler and Johnson (1977), Rumelhart (1977) and Thorndyke (1977) later expanded this concept of a ‘story schema’, characterising its structure as *hierarchical*, drawing on Chomsky’s (1957) argument that the grammatical structure of language is organised hierarchically (indeed, some of these were called ‘story grammars’). Specifically, folk stories are organised in branching tree-like structures, with the general theme or gist at the highest level of the hierarchy, which branches out into separate events, each of which in turn contain sub-goals, and finally down to the low-level constituent actions that are performed to achieve those sub-goals[6]. Consistent with this theory, Thorndyke (1977) found that stories with such an underlying hierarchical organisation were rated as easier to comprehend and recalled better than stories similar in content but without a hierarchical organisation. Furthermore, the higher a fact was in the hierarchy, the more likely it was to be recalled.

Schank and Abelson (1977) similarly invoked the concept of an underlying hierarchical structure in their script theory. A *script* is defined as a stereotypical knowledge structure for an everyday routine event, such as going to a restaurant or visiting the doctor, around which specific instances of that event are built. For example, going to a restaurant would contain several sub-goals, such as being seated, ordering food, eating, and paying the bill. Each of these in turn contains a series of actions that must be performed in order to achieve the sub-goal. 'Ordering', for example, contains actions such as reading the menu, deciding what to have, signalling to the waitress and so on. Ultimately, each sub-goal must be completed before the

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[6] This is, therefore, a *partonomic* hierarchy, based on 'part-of' relations (i.e. each action forms 'part of' a sub-goal, which in turn is 'part of' the gist), rather than a *taxonomic* hierarchy, such as taxonomies of species, which are based on 'kind-of' relations (Zacks & Tversky, 2001). Henceforth, discussion of hierarchies concerns partonomies rather than taxonomies.

overall goal of eating at a restaurant can be achieved. An example of this hierarchical structure is displayed in Figure 6.1.

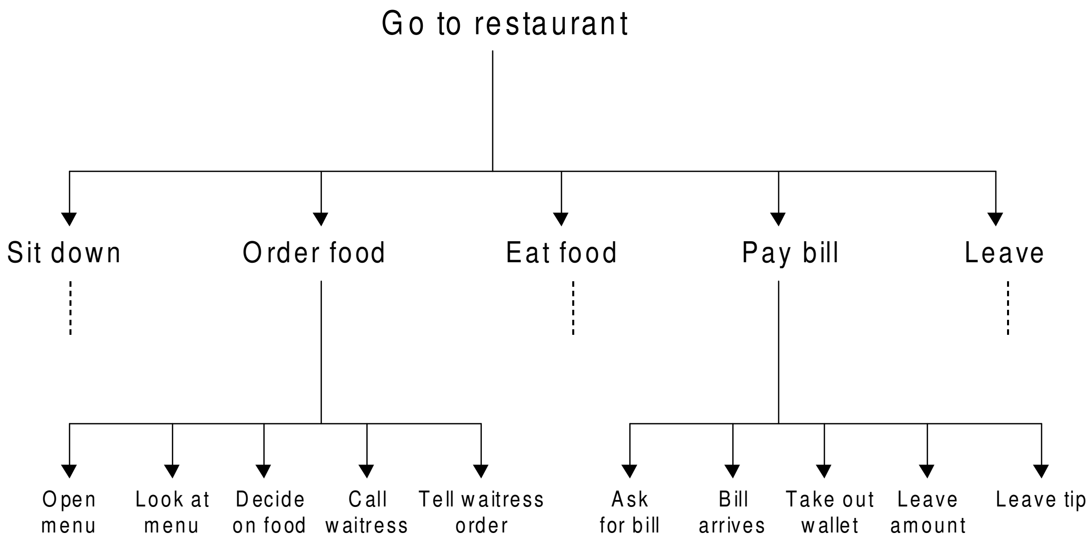

Figure 6.1 – An action script for going to a restaurant. The three levels correspond to the high-, medium- and low-levels used in this study. Not all of the low-level actions are displayed.

Consistent with script theory, Bower, Black, and Turner (1979) found that when presented with a series of actions forming a script event, participants agreed on how to group those actions into higher level segments. Furthermore, when the usual order of a script was scrambled, participants tended to spontaneously reintroduce the original order, and in subsequent memory recognition tests, participants claimed to have read actions that were not in the original stimulus material but which could be inferred from higher levels of the script. Abbott, Black and Smith (1985) expanded upon this latter finding by showing that participants falsely inferred the presence of higher level sub-goals (e.g. 'They ordered their meal') when presented with lower level constituent actions (e.g. 'They discussed what they wanted to eat'), but not vice versa. This asymmetry suggests the existence of a hierarchical organisation with increasing levels of abstraction.

More recently, Zacks, Tversky and Iyer (2001) found further evidence for the hierarchical structure of scripts using a slightly different methodology. Participants were shown videotapes of models performing routine activities, such as washing the dishes or making the bed, and were asked to segment these activities into either the smallest or the largest meaningful units. It was found that the large unit boundaries were significantly likely also to be small unit boundaries, suggesting an underlying hierarchical structure. This was observed when segmentation was performed both while watching the video (by pressing a key when a segment boundary occurred) and when recalling the video from memory. An important point from this study is that it demonstrates that the hierarchical organisation of script events is not simply an artifact of representing such events linguistically, and so dispels the criticism that the effects described above may simply be a by-product of the hierarchical organisation of linguistic grammar.

That the hierarchical nature of event knowledge is independent of language is reinforced by studies of preverbal children and non-human species. Developmental psychologists have shown that children also possess well organised and stable knowledge about familiar events that resembles action scripts, suggesting that scripts are a fundamental component of cognition. Nelson and Gruendel (1986) interviewed 2½ to 6 year old children for their verbal descriptions of everyday events such as eating lunch, getting dressed and going shopping. It was found firstly that there was general agreement across children on the acts that constituted each event, secondly that these acts resembled the sub-goals of an action script (e.g. sitting down, ordering, eating), and thirdly that these acts were produced more often than more specific low-level actions. Slackman, Hudson and Fivush (1986) reported that upon further prompting, children readily produced the constituent actions of each sub-goal, indicating an understanding of the lower levels of the hierarchy. Slackman *et al.* (1986) also reported the use of increasingly more elaborate hierarchical organisation between the ages of 4 to 6 years, with both the number of elements (e.g. sub-goals and actions), and the children's understanding of how those elements can be placed in the hierarchy (e.g. whether they are necessary or optional, or conditional upon another element), increasing with age and experience. More recently, van den Broek, Lorch and Thurlow (1996) similarly found that 4 and 6 year olds showed better memory for events at a higher hierarchical level than at a lower level when recalling stories from television programmes.

There is also evidence that a precursor to hierarchical action scripts is present in children under two years of age. Bauer and Mandler (1989) modelled a series of causally related actions resembling a simple script (such as 'remove bear's shirt, put bear in bath, wash bear') for 16 and 20 month olds. When subsequently encouraged to imitate these actions, sequences with causal (or enabling[7]) relations were reproduced more accurately than arbitrarily connected sequences lacking causal relations. Bauer and Mandler (1989) also found that irrelevant actions within otherwise causally connected action sequences tended to be displaced or omitted, resembling the spontaneous reintroduction of order found by Bower *et al.* (1979). Evidence from developmental psychology, therefore, shows that from a very early age children understand and use causal relations to organise their recall of events, an ability that may act as a precursor to fully formed hierarchically organised scripts that emerge around three years of age.

The concept of hierarchical organisation has also been used in the study of animal behaviour. Dawkins (1976a) has argued that hierarchical structure constitutes ‘good design’, and so would be expected to have been favoured by natural selection. Indeed, one example of hierarchically organised behaviour given by Dawkins (1976a, pp. 42-43), that of a predator catching prey, bears a striking resemblance to Schank and Abelson’s (1977) restaurant script: the overall goal of ‘catching prey’ is broken down into lower level components (‘searching’, ‘pursuit’, ‘killing’ and ‘eating’), each of which contain further lower level action rules. While this example was

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[7] Strictly, many of the links described here are enabling rather than causal. For example, the act of opening a door *enables*, but does not in itself *cause*, the subsequent act of passing through the door. For simplicity of expression, however, further references to ‘causal connections’ imply either causal or enabling relations.

hypothetical, Dawkins (1976a) presents in more detail analyses of blowfly grooming and fish behaviour that demonstrate hierarchical organisation.

Recent work on social learning in primates has also focused on the hierarchical nature of what is learned. Byrne and Russon (1998) have argued that imitation can occur at two levels: the action level, which contains the basic constituent acts; and the program level, which constitutes the higher-level hierarchical organisation of those constituent acts. For example, the process by which mountain gorillas prepare the herb galium for consumption could potentially be imitated at any of several hierarchical levels, from the overall goal ('eat galium'), to more detailed sub-goals ('repeatedly pick green strands of galium with one hand…'), down to the fine motor details of the actions ('pick out a strand of green galium from the mass with any precision grip of the left hand…'). In Byrne and Russon's (1998) terminology, program level imitation involves copying the second of these, at the sub-goal level. Using observational data concerning gorillas and orang-utans, they go on to argue that imitation in great apes is primarily at the program level, with occasional action level imitation occurring for social functions (although see Stoinksi, Wrate, Ure, & Whiten, 2001 for experimental evidence that failed to find program level imitation in gorillas).

Whiten (2002), meanwhile, has investigated imitation of similar hierarchical structures experimentally. Three-year-old children observed an adult opening an artificial fruit in one of two hierarchically different ways, row-wise or column-wise. The children were statistically more likely to adopt the hierarchical organisation that they observed, while the sequential order within the subroutines of that hierarchy (within-rows or within-columns) was not copied. This thus represents an extension of Bauer and Mandler's (1989) work on imitation in younger infants, demonstrating that by three years of age children can imitate high-level hierarchical information. Although these studies of primates and preverbal children are investigating the behavioural *execution* of script events rather than the knowledge of such events represented in memory, script theory would predict the two should match, insofar as the script knowledge is built up from previous behavioural experiences of events.

To summarise, the evidence outlined above suggests that humans and some other species represent knowledge of routine events or stereotypical action sequences hierarchically, and tend to show better memory for, and imitation of, actions that are represented at a relatively high level of that hierarchy. Chapter 6 was designed to systematically test for such a 'hierarchical bias' in human cultural transmission, by passing descriptions of events entirely in terms of their low-level constituent actions along chains of participants. It was predicted that these low-level descriptions would gradually 'move up the hierarchy', that is, the low-level actions would be subsumed into their higher level sub-goals, which would in turn be subsumed into the highest level overall goal. In essence, then, this study is coming full circle, updating Bartlett's (1932) original transmission chain studies, from which the concept of the 'schema' first emerged, with the past seventy years of schema research, the main contribution of which has been the concept of the hierarchy.

6.3 METHODS

6.3.1 Design

The transmission chain design was adopted, in which the first participant in each chain recalls the original stimulus material, the output of which is then given to the second participant to recall, whose recall is in turn given to the third participant, and so on down the chain. Ten chains each containing four participants were run, with the first participant in each chain given the material reproduced in Table 6.1 constituting just the low-level actions of the hierarchy. The overall design is illustrated in Figure 6.2. Each chain transmitted all three scripts, with the order in which they were presented on the page counterbalanced.

The independent variable was the transmission generation, of which there were five: the original (F0) stimulus material and four recall generations (F1-F4). The dependent variable was the proportion of the total number of propositions recalled at each generation that was categorised at each hierarchical level (low, medium, high or none). It was predicted that, as the material is transmitted along the chain, the proportion of propositions classed as at the low-level in the hierarchy would significantly decrease, while the proportions classed as at the medium- and high-levels would significantly increase.

Going to a restaurant
Low-level (given to the first generation): John and Nancy entered the restaurant and were shown to a table by the waitress. They sat down on the chairs and placed napkins on their laps. Then they looked at the menu and decided what food to have. They signalled to the waitress and told her their order, which the waitress wrote down. John and Nancy drank wine and talked until their food arrived. They ate the main course, then they had dessert. John asked for the bill, and the waitress brought it over. John took out his wallet and left money, as well as a tip. Then they both stood up and went to the cloakroom to fetch their coats. John and Nancy put on their coats and walked outside. (122 words, 10 sentences, 25 propositions)
Medium-level: John and Nancy sat down (1), ordered their food (2), ate their food (3), paid the bill (4) and left (5).
High-level: John and Nancy went to a restaurant.
Grocery shopping
Low-level (given to the first generation): Rachel parked her car outside the supermarket. She got out of her car, collected a trolley and wheeled it inside. She checked her list and went down the aisles. She put the items that were on her list into her trolley until she had them all. Then Rachel went to the checkout where she joined the fastest queue. She waited in the queue, and then unloaded her items onto the belt. The cashier rang up the items on the till and told Rachel the total. Rachel gave the cashier some money and the cashier gave Rachel her change. Rachel put the shopping into the bags and put the bags into the trolley. She wheeled the trolley out to her car and put the bags into the boot before driving away. (130 words, 10 sentences, 25 propositions)
Medium-level: Rachel arrived at the supermarket (1), got items (2), queued (3), paid (4) and left (5).
High-level: Rachel went shopping.
Getting up
Low-level (given to the first generation): Ian woke up and switched off the alarm. He lay in bed and stretched, then stood up. Ian went into the bathroom and turned on the shower. He washed himself then dried off with a towel. Then Ian went back into the bedroom and picked out some clothes from his wardrobe. He put on the clothes and checked himself in the mirror. Ian went downstairs and made some tea and some toast. He ate the toast while reading the newspaper. Then Ian got the books that he needed, put on his shoes and his coat and went outside. (98 words, 9 sentences, 25 propositions)
Medium-level: Ian got out of bed (1), had a shower (2), got dressed (3), had breakfast (4) and left the house (5).
High-level: Ian got up.

Table 6.1 – Descriptions of the action scripts at each hierarchical level. Only the low-level descriptions were given to the first participant in each chain.

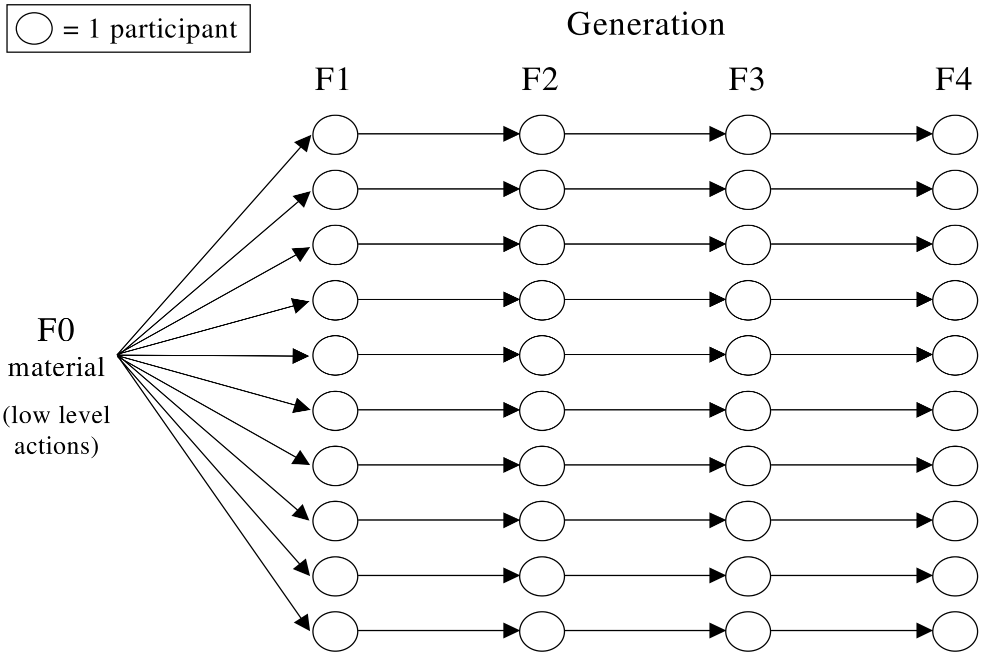

Figure 6.2 – The transmission chain design of Chapter 6

6.3.2 Materials

The material was derived from Bower *et al.*'s (1979) Experiment 1, in which 161 participants were asked to generate a sequence of actions that best describe a routine everyday event, specifically going to a restaurant, attending a lecture, getting up, grocery shopping and visiting a doctor. Table 2 in Bower *et al.* (1979) lists every action mentioned by at least 25% of participants, and these actions were used to construct the hierarchical descriptions shown in Table 6.1 here, concerning three of those action scripts: going to a restaurant, getting up, and going shopping.

The descriptions in Table 6.1 were designed to contain identical hierarchical structures in terms of their underlying propositions (see Coding section 6.3.3 below for details of propositions). Each script contained a single high-level proposition which branched out into five medium-level propositions, each of which in turn branched out into five low-level propositions (giving 25 low-level propositions in total), similar to the structure shown in Figure 6.1. The low-level propositions roughly correspond to those actions generated by 25-50% of Bower *et al.*'s (1979) participants, the medium-level to actions generated by 50-75% of Bower *et al.*'s (1979) participants, and the high-level proposition to the overall heading originally presented by Bower *et al.* (1979) to their participants. No proposition was present at more than one level of the hierarchy. Note that the structure does not correspond exactly with every one of the actions in Bower *et al.*'s (1979) Table 2 as it was necessary that each of the three scripts contained the same number of propositions at each hierarchical level. Minor changes were also made to make the text more easily understood by modern day British participants.

6.3.3 Coding

A propositional analysis (Kintsch, 1974) was performed on each participant's recall, where the text is divided into separate propositions (see Chapter 4). In the present analysis, the names of the characters and the tense were considered unimportant to the hypothesis, and so were ignored. The couple in the restaurant script was also considered as a single unit, rather than two separate people, in order to match the other two scripts. Once the propositional analysis had been performed, the recall was then compared to the structure presented in Table 6.1, with each proposition classed as either low-, medium- or high-level (or 'none' if not present at any level of the hierarchy).

To assess inter-rater reliability, an independent coder blind to the nature and hypotheses of the study performed the entire coding procedure for three of the ten chains. That is, the second coder divided each recall into propositions and classed each as low, medium, high or none, although the terms low, medium and high were replaced with the nondescript labels A, B and C. The coding of the blind second coder and myself were highly correlated, with a Pearson's correlation coefficient of 0.93.

A problem that arose during coding concerned the high-level Getting Up proposition. While this proposition ('Ian got up') was frequently produced by the participants, it was obvious from the context that the intended meaning was closer to the first medium-level proposition ('Ian got out of bed'), rather than the entire act of getting out of bed, showering, dressing, having breakfast and leaving the house. It was therefore decided to code each of these propositions as medium-level, in effect eliminating the Getting Up high-level proposition.

6.3.4 Participants

Nineteen male and twenty-one female participants, of mean age 20.59 years, were assigned randomly to one of the ten chains. All were students of the University of St. Andrews and were unpaid. All participants spoke English as their first language (or had passed entry examinations demonstrating that their English was of a sufficient standard to study at a British university). All participants had normal reading and writing skills.

6.3.5 Procedure

Each participant was given a four-page booklet. The front page instructed the participant to read the passage printed on the second page once at a comfortable reading speed. The second page contained the material to be recalled, as appropriate to that chain and generation. At no point in the printed instructions or by the experimenter were the participants informed that they would have to recall this material later. The third page contained the instructions:

> ‘In the space below, please write out the text you just read as best you can. Try to be as accurate as possible, but don’t worry if you can’t remember it all. Spelling is not important. When you have finished, turn the page.”

This was followed by a blank space for recall, for which no time limit was given. The final page solicited the participant’s age and gender, and thanked them for taking part. The experimenter then debriefed them as to the nature of the study. Their recall was then typed up, correcting for spelling and grammar, and inserted into the next generation’s booklet as appropriate.

6.4 RESULTS

6.4.1 General findings

As predicted for the transmission chain design, the total number of propositions and words decreased with generation. One-way repeated-measures ANOVAs confirmed significant effects of generation on the total number of words ($F_{(1,13)} = 282.67$, $p < 0.01$) and propositions ($F_{(1,11)} = 217.37$, $p < 0.01$) contained in each recall (both of these tests violated the assumption of sphericity, therefore the Greenhouse-

Geisser corrected significance level is reported). Figure 6.3 shows the more meaningful of these two measures of recall, the number of propositions, broken down into the three scripts. A 3 x 5 (story x generation) repeated measures ANOVA showed no significant differences between the three scripts ($F_{(2,18)}$ = 0.85, ns). Data for the three scripts were therefore combined in subsequent analyses.

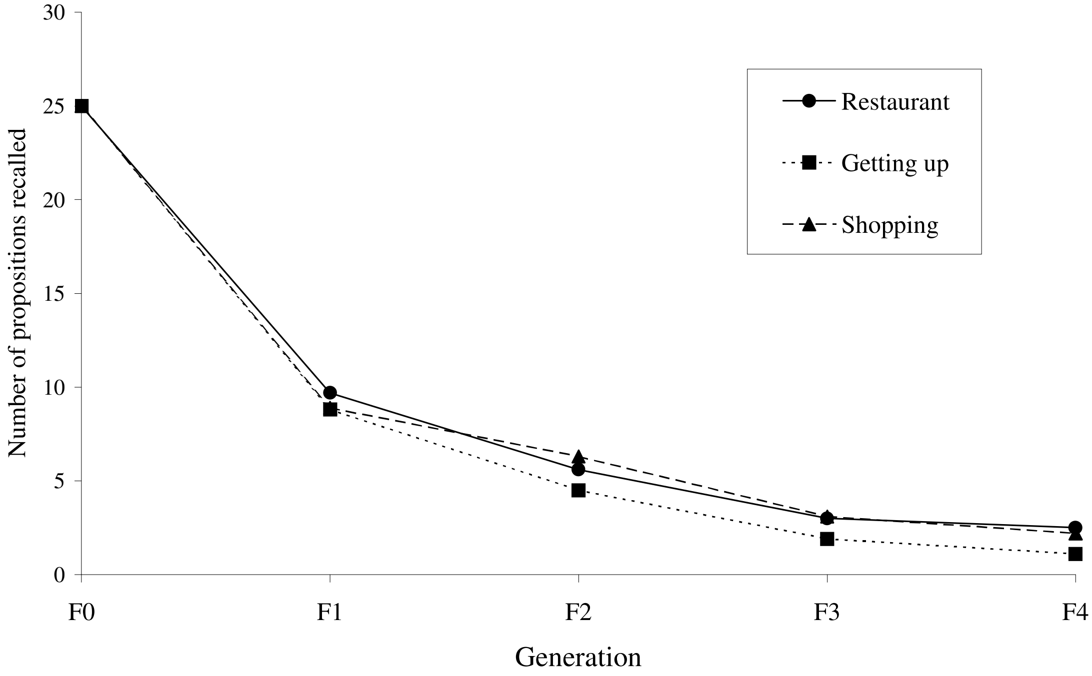

Figure 6.3 – The total number of propositions recalled by each generation, broken down into the three scripts.

Figure 6.4 shows the proportion of the recall of each generation that was classified as either low-, medium- or high-level in the script hierarchy, or 'none' if the proposition was not present at any level. Inspection of Figure 6.4 appears to confirm the prediction that the proportion of low-level information would decrease with generation and the proportion of medium- and high-level information would increase.

Information not present at any level ('none') initially increased to around 0.2 of the total propositions recalled, then neither increased nor decreased in a linear fashion. To test these trends statistically, linear trend analyses were performed on each hierarchical category separately.

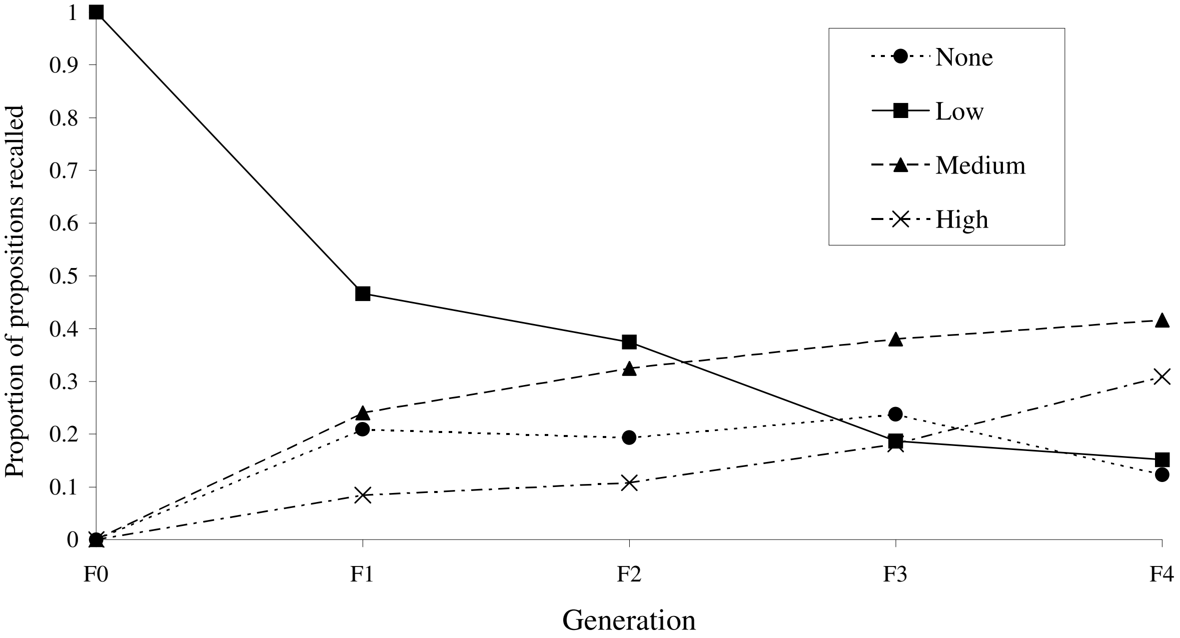

Figure 6.4 – The proportion of the total propositions recalled by each generation that was classed at each hierarchical level. Data from the three scripts are combined. 'None' refers to propositions not contained anywhere in the script hierarchy.

6.4.2 Trend analyses

Trend analyses were performed first including the original F0 stimulus material (i.e. five generations F0-F4) and second excluding F0, including just the four recall generations (F1-F4). On the one hand, it was felt that excluding F0 would lose the contribution of the first (F1) participant in each chain in initially transforming the F0 material. On the other hand, it was also of interest whether the four recall generations (F1-F4) would alone show the predicted trends, as F0 was in a sense engineered by the experimenter with the hypothesis in mind.

The following analyses were performed on all five generations, including the original F0 stimulus material. Four separate one-way repeated measures ANOVAs were performed, one for each hierarchical category (low, medium, high and none). Where the assumption of sphericity is violated, Greenhouse-Geisser corrected significance levels are reported. The ANOVAs revealed significant effects of generation at each of the four levels (Low: $F_{(4,36)} = 78.05$, $p < 0.01$; Medium: $F_{(1,11)} = 7.96$, $p < 0.05$, Greenhouse-Geisser corrected; High: $F_{(1,11)} = 7.40$, $p < 0.05$, Greenhouse-Geisser corrected; None: $F_{(2,21)} = 4.18$, $p < 0.05$, Greenhouse-Geisser corrected). The trend analyses revealed that the low-level proportion showed a significant linear decrease with generation ($F_{(1,9)} = 175.92$, $p < 0.01$), while the medium-level proportion ($F_{(1,9)} = 10.41$, $p < 0.01$) and the high-level proportion ($F_{(1,9)} = 11.82$, $p < 0.01$) showed separate significant linear increases with generation. The 'none' proportion showed no significant linear trend ($F_{(1,9)} = 3.30$, ns). These trend analyses therefore confirm the prediction that low-level information would significantly decrease with generation, and medium- and high-level information would significantly increase.

The following analyses were performed after excluding the original F0 stimulus material, leaving the four recall generations (F1-F4). The low-level proportion again showed a significant effect of generation ($F_{(3,27)} = 13.68$, $p < 0.01$), and a trend analysis again revealed a significant linear decrease with generation ($F_{(1,9)} = 22.30$, $p < 0.01$). The medium-level proportion, however, showed no significant effect of generation ($F_{(1,11)} = 1.55$, ns, Greenhouse-Geisser corrected) and thus no significant trend. The high-level proportion showed no significant effect of generation using the Greenhouse-Geisser correction ($F_{(1,11)} = 4.60$, ns), although this became significant with the less conservative Huynh-Feldt correction ($F_{(1,11)} = 4.60$, $p < 0.05$). If the latter correction is accepted, then there was a significant linear increase with generation ($F_{(1,9)} = 5.55$, $p < 0.05$). Finally, there was no effect of generation for the 'none' proportion ($F_{(3, 27)} = 0.87$, ns).

One reason for the lack of a significant trend for the medium-level after the first generation may have been that while low-level propositions were being converted into medium-level propositions, medium-level propositions were in turn being converted into high-level propositions, with the net change at the medium-level being zero. An analysis was therefore performed on the combined proportion of medium- and high-level propositions, resulting in a significant effect of generation ($F_{(2,16)} = 7.84$, $p < 0.01$, Greenhouse-Geisser corrected) and a significant linear increase with generation ($F_{(1, 9)} = 13.75$, $p < 0.01$).

In summary, the trend analyses support the hypothesis that information moves up the hierarchy as it is passed along the transmission chain. Including the original F0 stimulus material in the analyses, there was a significant decrease in low-level information and separate significant increases in both medium- and high-level information. As might be expected given that the F0 material was specifically designed with the hypothesis in mind, excluding the F0 material gave a somewhat less robust effect, although the hypothesis was still supported. There was again a significant decrease in low-level information, and a significant increase in medium- and high-level information combined, although not separately. The fact that there was a significant effect despite removing the contribution of the first generation confirms the value of the transmission chain method over and above a standard single generation memory experiment. Finally, information not contained within the hierarchy showed no linear increase or decrease with generation, both with and without F0.

6.4.3 Deviations of order

Abelson (1981) has argued that ‘strong’ scripts, such as the ones used in this study, contain implicit information on the correct order of sub-goals, often dictated by causal or enabling relations between those sub-goals. For example, eating food in a restaurant can only be achieved once ordering is completed: ordering *enables* eating. The finding by Bower *et al.* (1979) that scrambled scripts were corrected into their canonical order supports this assertion.

In line with this, the order of both medium- and low-level propositions was transmitted almost entirely intact in the present study. Only one of the 163 medium-level propositions recalled by all forty participants deviated from the original medium-level order in the stimulus F0 material. This single violation occurred in a first generation recall of the Getting Up script, where the character was described as having a shower *after* getting dressed. Although this is possible, it is highly improbable, and a closer inspection revealed that the recall in fact reads more like a list of actions with no temporal or causal connections: 'He gets dressed *and* he has a shower" (italics added), rather than a temporally connected narrative (which might use 'then' rather than 'and'). It may be no coincidence, then, that the next generation in this chain lost the Getting Up script entirely, given that script-like narratives should be more likely to be remembered than unconnected lists of events.

Similarly, only three of the 241 low-level propositions that were recalled deviated from the original low-level order. The first consisted of the couple in the restaurant drinking wine after eating their meal, rather than before. Such a deviation might be expected, as wine can be, and usually is, drunk before, during and after a meal. The other two deviations were identical but from different chains (a possible instance of 'convergent cultural evolution'), and consisted of the Getting Up character going downstairs before having a shower, rather than after. However, it should be noted that the student residences in which all of the participants lived have showers on the ground floor, perhaps explaining this change in order. If this is indeed the reason, then this is an interesting example of how recent experience shapes underlying scripts, and hence also shapes immediate recall of script-like descriptions.

6.4.4 Illustrative examples

A representative chain illustrating the 'hierarchisation' of the original low-level material is reproduced in Table 6.2. Although the script shows a drastic reduction in length, there is an intuitive sense that the 'gist' or 'core' of the story has been preserved through every step of the chain. In terms of the theory presented here, this is the result of the script being described at progressively higher hierarchical levels. This can also be observed, with low-level actions (e.g. giving money to the cashier and receiving change in return) gradually being subsumed into higher order sub-goals (e.g. ‘paying’).

Generation F0 (original material):
Rachel parked her car outside the supermarket. She got out of her car, collected a trolley and wheeled it inside. She checked her list and went down the aisles. She put the items that were on her list into her trolley until she had them all. Then Rachel went to the checkout where she joined the fastest queue. She waited in the queue, and then unloaded her items onto the belt. The cashier rang up the items on the till and told Rachel the total. Rachel gave the cashier some money and the cashier gave Rachel her change. Rachel put the shopping into the bags and put the bags into the trolley. She wheeled the trolley out to her car and put the bags into the boot before driving away.
Generation F1:
Rachel went shopping, parked her car at the supermarket, got out of the car, got a trolley, went into the supermarket and collected the food she wanted. She went to pay for the goods, gave the cashier the money, he gave her change and a receipt. Then she took the trolley back and then drove off in her car.
Generation F2:
Rachel drove to a supermarket, parked her car, got a trolley and chose some food. Then she went to the cashier to pay for her food. The cashier gave her some change. Then she put back the trolley and drove away.
Generation F3:
Rachel drove to the supermarket, parked her car, got a trolley and chose some food. She paid the cashier and drove home.
Generation F4:
Rachel went to the supermarket, got some food and went home.

Table 6.2 - An illustrative example showing the changes in one of the episodes during transmission

Two more specific examples illustrate the hierarchical bias further. First, in one of the chains the three separate scripts merged to form a single narrative. For example, one fourth generation recall stated:

> "Ian woke up and ate breakfast. Nancy went to the supermarket for shopping. Afterwards they both met up and had lunch."

Here, the two originally different characters from the Getting Up and Shopping scripts became the two characters in the Restaurant script, creating a single narrative of their day. Details of the restaurant are also lost, becoming 'having lunch'. The second example comes from another fourth generation recall, in which a participant forgets one of the stories (Getting Up) and invents a completely new one. While the content is forgotten, however, the hierarchical level of description, roughly corresponding to the medium-level of the other scripts, is perfectly preserved:

> "Peter went to the cinema and watched a movie and went home."

These two phenomena – imposing links to turn three fragments into a single narrative, and preserving the script-like structure despite entirely forgetting the content – illustrate a seeming compulsion to describe actions and events in terms of highly structured script-like representations, and provide additional evidence for the psychological reality of script theory.

6.5 DISCUSSION

The aim of Chapter 6 was to investigate the possible operation of a 'hierarchical bias' in the cultural transmission of event knowledge. This bias is hypothesised to impose a script-like hierarchical structure onto descriptions of such events, and progressively subsume low-level actions into their higher level goals as the descriptions are passed from person to person. This was tested by passing short descriptions of three scripts (going to a restaurant, getting up and going shopping) consisting entirely of information at a relatively low hierarchical level along multiple chains of participants. The results confirmed that as these low-level descriptions were passed along the chains, there was a significant linear decrease in low-level information, and a significant linear increase in medium- and high-level information.

These significant linear trends, demonstrating a cumulative increase or decrease in information with generation at specific hierarchical levels, illustrate the value of the transmission chain method over standard single generation memory experiments, and confirm that the effect is genuinely ‘cultural’. It can be hypothesised that this experimental finding of a hierarchical bias using the transmission chain method can be extrapolated to human cultural transmission more generally, and a similar process would be observed whenever information concerning everyday events is passed from person to person in the population as a whole.

As well as elucidating a particular aspect of cultural transmission, this result also provides support for the psychological reality of script theory (Schank & Abelson, 1977), complementing studies such as Bower *et al.* (1979) and Zacks *et al.* (2001). In addition to the main finding, it was also found that the canonical order of the medium- and low-level actions was preserved in the vast majority of recalls, as predicted by Abelson (1981). It was further found that causal connections were imposed on script fragments to form a single narrative, and that even where the content of a script was entirely forgotten the high-level hierarchical structure was retained, both of which suggest that events are represented in a highly structured fashion.

The demonstration of a hierarchical bias in human cultural transmission also adds plausibility to the prediction made by Byrne and Russon (1998) that non-human primates are most likely to successfully imitate actions at a relatively high ('program') level of the hierarchy. Although the present study examined verbally-expressed knowledge of events rather than the behavioural execution of such acts, script theory predicts that the two would be matched, given that script knowledge is shaped by past behavioural experience of such events. Furthermore, Whiten (2002) has demonstrated hierarchical imitation in human children, suggesting that the hierarchical bias can be extrapolated to the perception of actions, and this begs testing in other primate species. Although initially it would be desirable to experimentally demonstrate the one-to-one imitation of hierarchical structure as suggested by Whiten (2002), ultimately it may be fruitful to adapt the method used in the present study, to see whether hierarchical structure can be transmitted along chains of non-human primates. Indeed, based on the results reported here, marked effects may not be observed for several generations.

The identification of hierarchical structure in human cultural transmission is also relevant to memetics, which argues that human culture evolves through the differential transmission of discrete 'cultural replicators', or 'memes', loosely analogous to genes (Dawkins, 1976b; see Aunger, 2000 and Part A for further discussion of cultural evolution and memes). One major criticism of the memetics literature is that memes are too ephemeral to function as replicators, because the mutation rate is too high to provide sufficient copying fidelity (e.g. Dennett, 1995). However, Plotkin (1996; 2000) has suggested that if culturally transmitted information is hierarchically structured, then although information at the low or surface level of the hierarchy may not have sufficient copying fidelity, information higher up the hierarchy at a deeper level may change slowly enough to constitute genuine cultural replicators. The results of the present study suggest that this may be the case, with the core high-level information (e.g. going to a restaurant) showing much greater copying fidelity than the low-level details. Memeticists looking to identify memes might therefore be advised to start with such high-level structures.

Extensive evidence was presented in the Introduction (Section 6.2) for the tendency of adults, children and non-human species to represent events hierarchically, and show superior recall and imitation of information at relatively high-levels of that hierarchy. The present study confirmed the operation of a hierarchical bias in human cultural transmission. What, however, is the functional significance of this hierarchical bias to cultural transmission? The answer may lie in Bartlett's (1932) explanation for his finding that folk tales, even unfamiliar folk tales, were transmitted with far greater fidelity than any other material, such as newspaper reports and scientific arguments. Bartlett (1932) argued that this occurred because people already possessed story schemas, around which they could reconstruct the particular story they had read. In the present case of action scripts, an even stronger argument can be made. As well as possessing the hierarchical structure of everyday events, the participants studied here would also possess the *content* of scripts such as going to a restaurant or getting up. Given that everyone in a society shares the same implicit script knowledge, then it is more efficient to transmit only the high-level goals or medium-level sub-goals, as it can be assumed that people can reconstruct for themselves the constituent low-level actions. In other words, the low-level information is redundant, and so can be removed without any loss in the intended message.

The evidence presented in the Introduction (Section 6.2) suggests that the key assumption upon which this explanation rests – that everyone in a society shares the implicit structure and content of action scripts – is a good one. Bower *et al.* (1979) and Nelson and Gruendel (1986) found substantial agreement amongst adults and children respectively on the actions that make up common scripts and their hierarchical structure, while Bauer and Mandler (1989) found evidence for very early development of an understanding of causally linked script-like sequences of actions.

Two predictions follow from this explanation. First, if the low-level information is indeed redundant, then it should be possible for new participants to reconstruct an approximation of the original F0 material from just the final F4 recalls produced in this study (given appropriate instructions such as 'make up a typical story based around the following sentence'). Second, if the low-level information is made non-redundant, i.e. it cannot be reconstructed just from the high-level sub-goals, then it should be preserved as well as the higher levels. This would occur if the low-level information were not part of the usual script. Just such an effect was observed by Bower *et al.* (1979), who found that unexpected intrusions to the script were more likely to be recalled than routine script actions. However, this only occurred for intrusions that constituted interruptions in the causal structure of the script, such as an obstacle to a sub-goal (e.g. the menu is in French) or a distraction that sets up a new goal (e.g. the waitress spills soup on the customer, requiring a trip to the bathroom). Intrusions that constituted simple errors that did not affect the causal structure were recalled less well than routine script actions. This resembles the finding by Bauer and Mandler (1989) that infants omitted causally-irrelevant actions when imitating sequences of actions. Causally-relevant intrusions should, therefore, be preserved during transmission.

Alternatively, the participant could be instructed to write out the story for an imaginary recipient who they know does *not* possess the implicit script, such as a hunter gatherer unfamiliar with restaurants or supermarkets. This latter test assumes, however, that the hierarchical bias is under conscious or intentional control, rather than an unconscious constraint on memory, in itself an interesting question that further experiments could investigate.

As well as altering the material, it may also be of interest to repeat the present study with different populations. Although non-Western populations might not possess the scripts that have been studied by Western psychologists, such as visiting a restaurant or going shopping, they should possess just as highly structured scripts for stereotyped routine events in their own societies, for which the hierarchical bias should operate. There is also evidence that autistic individuals show a difficulty in generating scripts (Trillingsgaard, 1999), suggesting that they would not show a hierarchical bias. Indeed, this deficit might be predicted from the theory outlined above. Autistic individuals, who have difficulty representing other people's mental states, might not be able to make the assumption that other people possess implicit knowledge of script events, in which case the low-level information would not be redundant.

One final point concerns the relation between the hierarchical bias found here and what is colloquially known as ‘summarising’. Many of the fourth generation recalls obtained in the present study resemble summaries of the original F0 stimulus material (see, for example, Table 6.2), suggesting that the act of summarising a text entails the same process as hierarchisation during transmission, i.e. the retention of the high-level information and the discarding of low-level details (see also Kintsch & van Dijk, 1978, who describe similar constructive and reproductive processes in both recall and summarization of texts in general). Indeed, it might be that if a single person is asked to summarise the material used here, the result would look similar to the cumulative product of asking four people to copy the material exactly. A specific instance of this might even be found at the beginning of this chapter: the abstract of a scientific paper represents the high-level hierarchical content of the entire report, containing the main rationale, findings and implications, and discarding the intricate methodological details (Kintsch & van Dijk, 1978). Intriguingly, the results of the present study suggest that a summary in terms of high-level hierarchical information, such as a scientific abstract, should be highly conducive to cultural transmission. Given that a successful scientist is partly one whose ideas are disseminated the most widely, perhaps the role of abstract writing in science is being greatly underestimated.

CHAPTER 7 - INDIRECT BIAS AND THE EFFECT OF STATUS

7.1 ABSTRACT

Boyd and Richerson (1985) have proposed that human cultural transmission may exhibit what they call ‘indirect bias’, where cultural traits are preferentially copied from people who are of high social status. Two experiments used the transmission chain method to test whether the transmission of written arguments concerning contentious contemporary issues were affected by the status of the stated source, irrespective of the content of those arguments. In Experiment 7a the issue was whether fluoride should be added to the water supply and the high-status source was an academic expert. In Experiment 7b the issue was whether the UK should adopt the euro and the high-status source was a famous celebrity. Neither experiment found any effect of status on the accuracy or quantity of transmission, and so failed to show evidence for an indirect bias. This implies that simply reporting that written information originated from a high-status source is not sufficient to elicit an indirect bias favouring that information. Indirect bias may instead be restricted to the transmission of behaviour in the presence of the high-status source.

7.2 INTRODUCTION

Boyd and Richerson (1985) have argued that human culture exhibits transmission biases which are not present in biological inheritance but nevertheless have the potential to significantly affect the large scale dynamics of cultural change. Such biases would therefore necessitate the development of novel evolutionary models of cultural inheritance. One such transmission bias is an *indirect bias*. Boyd and Richerson (1985) argued that when choosing between potential models from whom to copy a cultural trait, people often use indicator traits, or measures of success or status that are not directly related to the copied trait. Examples they give of indicator traits are "number of cows, number of children, or number of publications" (p. 243). A more specific example of indirect bias might be the adoption of the haircut of a famous and successful footballer, despite that haircut having no connection with their ability to play football. Such a bias could represent a useful rule of thumb, especially when it is difficult or costly to personally evaluate different cultural variants.

Boyd and Richerson (1985) also went on to demonstrate mathematically how indirectly biased cultural transmission can lead to the spread of biologically non-adaptive or maladaptive cultural traits through a population as a result of a runaway selection process. The existence of an indirect bias is, therefore, of considerable theoretical interest, first in demonstrating that cultural inheritance differs in important ways from biological inheritance and hence merits its own methods of analysis, and second in the argument over whether culture is held on a 'genetic leash' (Lumsden & Wilson, 1981), or whether it can promote the spread of biologically maladaptive behaviour. More recently, Henrich and Gil-White (2001) have extended Boyd and Richerson's (1985) argument, proposing that an indirect bias will lead to the development of prestige hierarchies and deference displays, drawing on ethnographic data to support their case.

To support their hypothesised transmission bias, Boyd and Richerson (1985) cited three sources of evidence. First, social learning studies show that observers prefer to copy the behaviour of models who exhibited certain other characteristics. For example, Bandura, Ross and Ross (1963) found that children imitated incidental behaviours exhibited by powerful, controlling adults more frequently than behaviours exhibited by more passive adults. Boyd and Richerson (1985) themselves, however, admitted that such studies are 'only suggestive' of indirect bias (p. 245), with very few indicator traits and transmission parameters investigated. Second, studies of the diffusion of innovations (Rogers, 1995) have found that people report preferentially adopting innovations such as new technologies or health practices from high-status 'opinion leaders'. Third, evidence from socio-linguistics (e.g. Labov, 1972) suggests that dialect change is driven by people of high-status in the community. These latter two sources of evidence, however, are both observational, and so lack the degree of control over other variables available in experimental studies.

The studies cited above examined the transmission of *behaviour* in the *direct presence* of sources of different status. The children in Bandura, Ross and Ross (1963), for example, acquired a series of behaviours such as hand gestures acquired directly from a source experienced as being of high-status (having access to quality toys). The aim of Chapter 7 was to extend the hypothesis of an indirect bias to the transmission of *verbal information reported to have originated* from sources of different status.

In order to test this, two experiments used Bartlett's (1932) transmission chain method to experimentally simulate the transmission of two arguments attributed to a source of either high- or low-status. If the transmission of verbal information is guided by an indirect bias, then the argument stated as originating from a high-status source should be transmitted with greater accuracy and in greater quantity than the argument from a low-status source, irrespective of the content of the arguments.

This study represents a novel and important extension of the indirect bias hypothesis. First, most of the evidence cited above is observational, and the social learning experiments are limited in scope. It is important to verify such effects experimentally using an explicitly transmission-based paradigm. Second, whether information originating from a high-status source continues to be preferentially transmitted in the absence of that source, as is hypothesised here, or whether it loses its preferential advantage when the source is no longer immediately present, may well affect the population-level dynamics of an indirectly biased trait. Third, much of human cultural transmission, perhaps the majority, involves either written or spoken verbal information rather than behaviour. Hence the overall impact of an indirect bias on human culture is likely to be much greater if it extends to verbal information such as that used in this study.

7.3 EXPERIMENT 7A

Experiment 7a involved the transmission of arguments for and against a health issue: whether fluoride should be added to the water supply. The high-status source was a (fictional) university professor with particular expertise in this issue.

7.3.1 Methods

7.3.1.1 Participants

Four chains each comprising four participants were run, giving a total of 16 participants. All participants were students at the University of St. Andrews and were unpaid volunteers. Their mean age was 22.79 years and 44% were female.

7.3.1.2 Materials

A booklet was produced with the relevant material printed on the front sheet, followed by a blank sheet for recall, and a final debriefing sheet. All material in all generations was prefaced with the following text:

> "Following last Thursday's announcement by the government of a review of whether fluoride should be added to Scotland's water supply, The Herald has received the following letters."

There were then two arguments, each prefaced with a fictional source. The high-status source was "Alan Peters, professor of dental health at Oxford University for over 20 years, and chair of the British Dental Council", while the low-status source was "Herald reader Brian Phillips from East Fife". Again, these did not change with generation, and if not reproduced in later generations were reintroduced.

Following each of these sources, there followed the transmitted material that was passed from generation to generation. The original arguments presented to the first generation concerned a topic of much recent debate - whether fluoride should be added to the public water supply. Several local and national newspapers were searched for articles on this topic, and a list made of all arguments for and against. These were used to construct two generic arguments, matched for number of words, arguments and propositions, that were presented to the first participant of each chain. These passages are reproduced in Appendix B.1.

7.3.1.3 Design

The independent variable was the status of the source, either high or low. All participants recalled both high- and low-status material, making this a within-groups factor. A second within-groups factor was generation, with four levels. The dependent variables were three measures of recall. Word count represented a gross measure that was independent of actual content. The number of arguments from the original material that was recalled at each generation represented a gross measure but one that was based on content. The original material contained five arguments for and five arguments against, with an argument roughly defined as a single reason why fluoride should or should not be added to the water. Finally, the number of propositions (Kintsch, 1974) contained in the original material recalled by each generation was a more sensitive meaning-based measure (see Chapter 4). The original material contained 21 propositions for and 21 against. It should be noted that each recall is scored against the arguments or propositions contained in the *original* material, rather than the previous generation’s material, as it is the cumulative ‘cultural’ effects that we are interested in here rather than any single participant’s performance.

7.3.1.4 Procedure

Participants were told they would be participating in a psychology experiment (not a memory test) that would last approximately five minutes. They were seated and presented with the booklet and a pen. The front sheet instructed them to ‘Please read the following extract from a local newspaper. When you have finished turn the page.” After reading the material, the next page contained the following instructions:

> ‘Now, without turning back, please write out as best you can the two letters you just read. Be as accurate as possible, but don’t worry if you can’t remember it all. When you have finished turn the page.”

After a blank space for recall, the final page solicited their age, sex and whether they were personally for or against the presented argument. They were then thanked and debriefed by the experimenter. After each participant had finished, their recall was taken by the experimenter, typed up (correcting for spelling and grammar) and inserted as the material in the next generation’s booklet as appropriate.

7.3.1.5 Analyses

Two-within-factor ANOVAs were performed on each measure of recall, with status as the first repeated measure (with two levels: high and low) and generation as a second repeated measure (with four levels: F1, F2, F3 and F4). A power analysis was performed using Potvin and Schutz’s (2000) Monte Carlo-derived formula for calculating the non-centrality parameter ë and hence power of an ANOVA with two repeated measures (see Appendix B.2 for this formula and more details of the power analysis).

7.3.2 Results

A two-within-factor ANOVA showed no effect of status on word count ($F_{(1,3)} = 0.37$, ns), although there was an effect of generation ($F_{(3,9)} = 25.45$, $p < 0.001$). That is, all of the material showed significant degradation over the four generations, as expected, but the high- and low-status material did not differ in the rate of that degradation, against the experimental hypothesis. A second two-within-factors ANOVA showed an identical result for the number of arguments correctly recalled, with no effect of status ($F_{(1,3)} = 4.86$, ns) and a significant effect of generation ($F_{(3,9)} = 15.40$, $p<0.001$). A final ANOVA on the proportion of correctly recalled propositions again found no effect of status ($F_{(1,3)} = 0.66$, ns) and a significant effect of generation ($F_{(3,9)} = 14.81$, $p < 0.001$). Figures 7.1, 7.2 and 7.3 illustrate these effects graphically, and show that if there is any trend, it is for the *low*-status material to be recalled better than the high-status material.

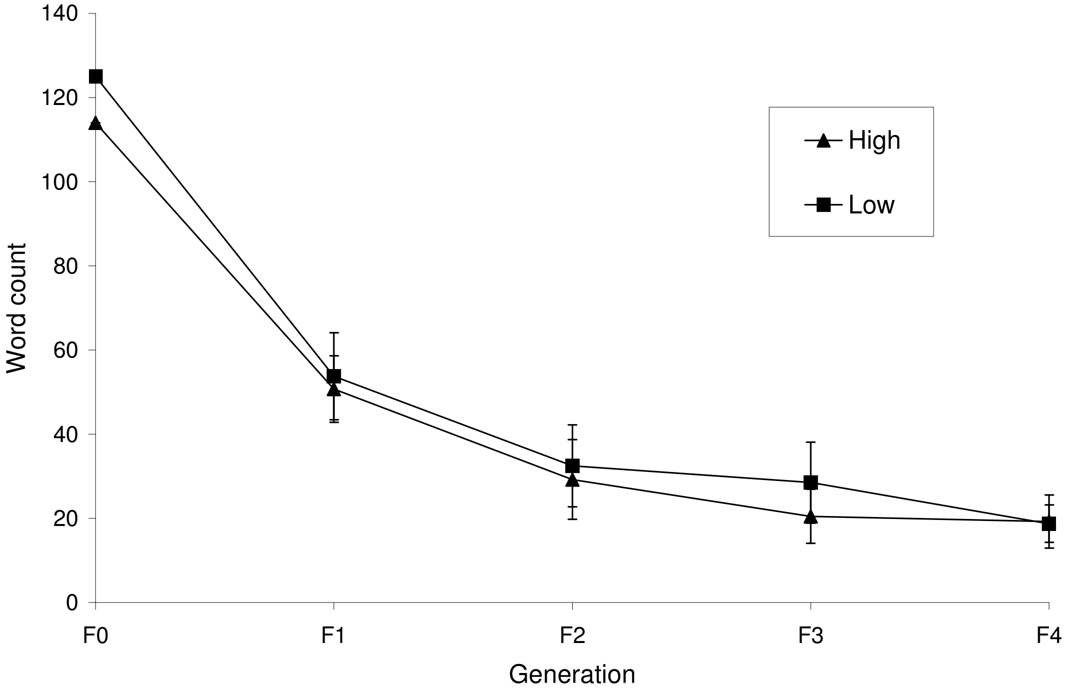

Figure 7.1 - Transmission of high- and low-status material by each generation of Experiment 7a, as measured by word count. Error bars show standard error.

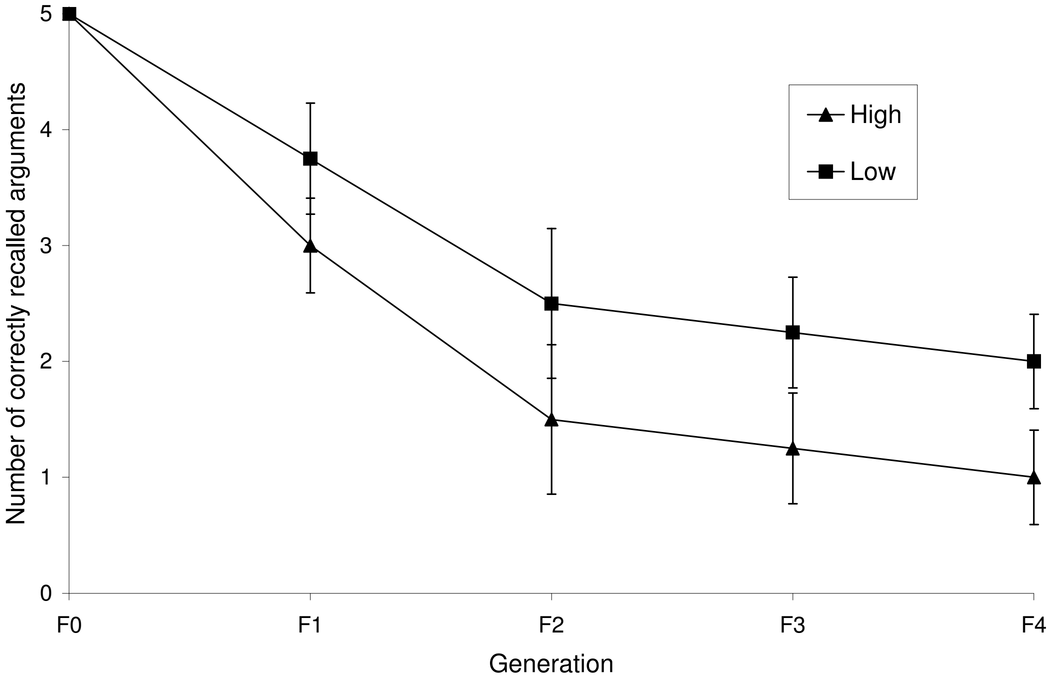

Figure 7.2 - Transmission of high- and low-status material by each generation of Experiment 7a, as measured by the number of arguments from the original material correctly recalled (out of 5). Error bars show standard errors.

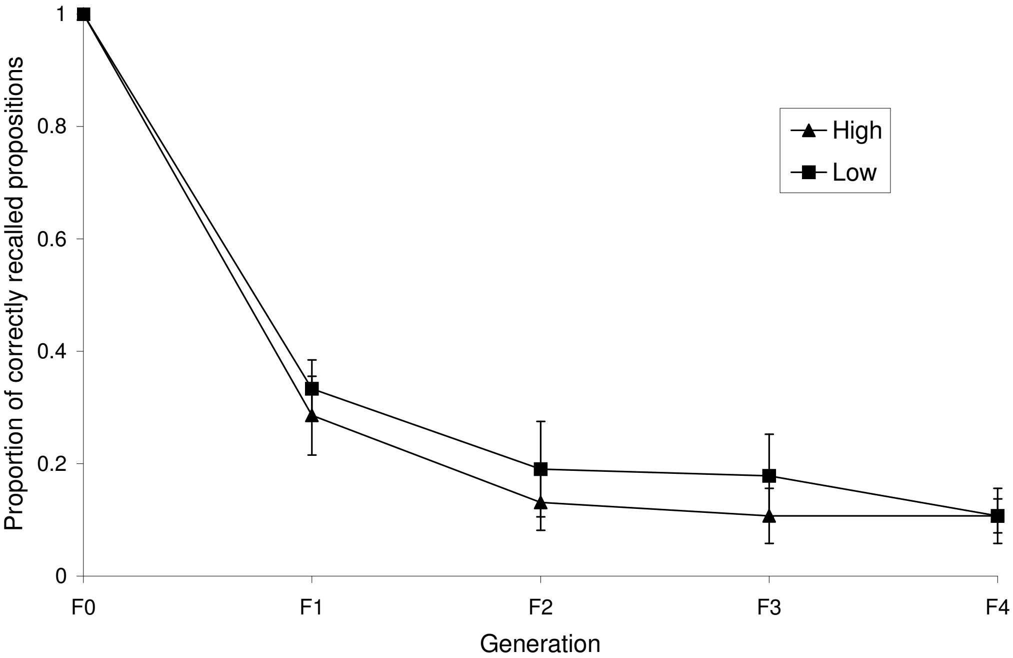

Figure 7.3 - Transmission of high- and low-status material by each generation of Experiment 7a, as measured by the proportion of propositions contained in the original material correctly recalled. Error bars show standard errors.

A power analysis for the measure of propositions (the data presented in Figure 7.3) gave a non-centrality parameter of ë = 0.75, giving a very low estimate of power (<0.17). It is therefore likely that this non-significant result was due to a small sample size. No effect was found of the order of presentation on propositions correctly recalled ($F_{(1,3)}$ = 0.12, ns), suggesting that primacy or recency effects were not responsible for the findings reported above. There was also no effect of whether the argument was for or against fluoridation on propositions correctly recalled ($F_{(1,3)}$ = 2.22, ns). 68.7% of participants stated that they personally were against fluoridation, although given the small sample size it was not possible to correlate a participant's personal opinion with which argument they recalled better. Finally, 62.5% of participants reproduced the status label in their recall (either 'professor' or 'member of public') despite not being told to, suggesting that the status labels were not forgotten, they simply had no effect on recall.

7.3.3 Discussion

Experiment 7a failed to find evidence for an indirect bias operating on verbal material using the transmission chain method. There was no significant difference in the copying fidelity of arguments stated as originating from a high- or a low-status source. Although a power analysis revealed that the sample size was too small to detect a significant difference, the fact that there was a trend in the *opposite* direction, i.e. low-status arguments were transmitted slightly better than high-status arguments, suggests that the hypothesis would not have been supported even if the sample size was increased. Indeed, previous experiments (Chapters 5 and 6) that featured the same within-groups design found a significant difference with just three or four chains.

There are a number of other possibilities aside from sample size for the failure to find an effect. First, the material was health-based, with the arguments concerning the health benefits or risks of consuming fluoride. It may be that people do not trust high-status authorities over health issues, as attested by recent public health scares over BSE, GM foods and the MMR vaccine.

Second, people may not in general view university professors as having high status. It may be that in today's materialistic and media-driven society status is better indicated by wealth or fame, particularly for the young people who participated here.

Perhaps a rich and famous film actor or sports-person would be more likely to elicit an indirect bias.

Third, it may be that although the status of the source had no effect on *recall* of the material, there may have been an undetected effect on people's beliefs or opinions, with high-status material seen as more reliable and having a greater effect on underlying beliefs than low-status material. In Experiment 7a the participants were asked after recalling the material for their personal opinion as to whether fluoride should be added to the water supply (yes or no), and although the sample size was too small to detect a significant effect, no effect of status on this opinion was apparent. However, perhaps a more accurate test of this prediction could be made if more sensitive and sophisticated methods are used to assess people's underlying beliefs.

7.4 EXPERIMENT 7B

Experiment 7b addressed the four concerns outlined above. First, the sample size was increased from four to twelve separate chains. The power analysis of the data obtained in Experiment 7a suggested that a sample of n=12 would afford a modest power of approximately 0.6. Second, the material is no longer health-based, so will hopefully not be affected by a general public mistrust of sources over health issues. The material now concerns the debate over whether the UK should join the single European currency, the euro, which has gained significance since the government announced a potential referendum on joining. Despite this, however, most people in Britain seem to feel uninformed and undecided on this issue.

Third, the high-status source was now the actor Sean Connery. He was chosen because he has several potential indicator traits signalling his high-status: he is internationally well known, rich, has received awards for his acting including an Oscar and a Knighthood, and he is Scottish so should have added identification for most of the participants here. The low-status source was an unknown person with a low-status job in the same field (a cameraman) to ensure that the comparison is plausible.

Fourth, more sensitive methods were used to measure participants' opinions and representations of the arguments, to test more effectively the hypothesis that the status of the source affects underlying causal representations as well as (or instead of) recall. Rather than simply asking the participants whether they agree or disagree with the adoption of the euro, participants are now asked to rate their opinion on a 7-point scale, where 1 is 'highly disagree' and 7 is 'highly agree'.

Participants were also asked to draw a network diagram of their opinions. This is based on the proposal by Green (1996; 2000) that the decisions that people reach and the beliefs that they hold result from a process of argumentation, both internally and with others. A person's beliefs and opinions can therefore be represented in the form of an 'argument model', which is derived from the more general concept of a mental model (Johnson-Laird, 1983), in which mental tokens correspond to actual entities in the world. An argument model therefore comprises a number of claims made on the basis of certain data.

Green and McManus (1995) measured people's argument models by asking participants to draw a network diagram to represent their beliefs concerning the risk factors of coronary heart disease. The target issue, 'coronary heart disease', was placed in the centre of the diagram, and around this the participants wrote a number of relevant risk factors (e.g. 'fatty foods', 'smoking', 'exercise'). Lines were then drawn between each factor and the target phenomenon (e.g. fatty foods -> CHD), and also between factors (e.g. fatty foods -> cholesterol), according to whether the participant believed that the factor affected the target. The connections could be either positive or negative, and the strength of each connection was rated on a scale of 0-100. The total path strengths in these diagrams were found by Green and McManus (1995) to strongly correlate with the participants' subsequent ratings of the effectiveness of modifying each factor in reducing coronary heart disease. Later studies used the same network diagram method to predict people's beliefs concerning unemployment (Green, McManus, & Derrick, 1998) and whether the UK should join a single European currency (Green, 2000), similar to the present study.

Such a method seems suitable for measuring people's mental representations of arguments which contribute to their overt beliefs and opinions. Following recall of the material the participants were therefore asked to draw a network diagram containing the arguments they just recalled, and to rate the strength of each connection.

7.4.1 Methods

7.4.1.1 Participants

Twelve chains each comprising three participants were run, giving a total of 36 participants. All participants were students at the University of St. Andrews and were unpaid volunteers. Their mean age was 19.89 years and 58.3% were female.

7.4.1.2 Materials

The material concerns the debate over whether the UK should join the single European currency, the euro. The introductory text below established the context of the argument and was intended to make the material more believable and plausible to the participants.

> "Following the recent announcement of a possible referendum on whether the UK should adopt the single European currency (the euro), a leading newspaper asked 100 people connected to the Scottish film and television industry to give their opinion on the issue. Two of the responses are reprinted below: one from Sir Sean Connery, the Oscar-winning film actor, and the other from a cameraman from the local Edinburgh news. Please read them through once at a comfortable reading speed. When you have finished reading turn the page."

The two arguments were then printed, labelled as to the source: 'Sir Sean Connery, Oscar-winning film actor' or 'Michael Jones, cameraman for the local Edinburgh news'. The original arguments given to the first participant in each chain are reproduced in Appendix B.3. These were constructed from the website www.theeurodebate.co.uk. Each side contains four constituent arguments (e.g. 'increase political unity' or 'lose economic control'), twenty propositions (each argument comprising one sentence and five propositions) and approximately 85 words.

7.4.1.3 Design

The design of Experiment 7b was identical to Experiment 7a. Hence the source (high or low) and argument (for or against) were counterbalanced so that in half of the chains the ‘for’ argument was attributed to the high-status source and the ‘against’ argument to the low-status source, and in the other half of the chains the high-status source was attributed to the ‘against’ argument and the low-status to the ‘for’ argument. It was again predicted that the arguments attributed to the high-status source would be transmitted with greater accuracy and in greater quantity than the arguments attributed to the low-status source, irrespective of the nature of those arguments (for or against). It was additionally predicted that, in the network diagrams, the arguments attributed to the high-status source would have more connections and stronger connections to the target (adopting the euro) than the low-status arguments.

Twelve chains were run, three for each permutation of high/low-status, for/against the euro and first/second order of presentation. Note that the chains in Experiment 7b only comprised three generations rather than four, as the material very quickly degraded to an average of less than two propositions after three generations.

7.4.1.4 Procedure

The procedure of Experiment 7b was identical to that of Experiment 7a, with the addition of an extra sheet in the booklet asking the participant to list all of the constituent arguments in their recall, then to draw an argument diagram. This sheet comprised a box with 'euro' printed inside, and the following instructions:

> 'The box printed below represents the UK adopting the euro. Write all of the arguments you listed on the previous page (from both sources) in the space around this box. Then draw a line from each argument to the 'euro' box if, in your opinion, you think that the argument is relevant to whether the UK should adopt the euro.
>
> If you think the argument is a reason for adopting the euro, place a '+' sign on the line. If, on the other hand, you think the argument is a reason against adopting the euro, place a '–' sign on the line.
>
> Then write a number on each line representing how strong or convincing you personally find that argument out of 100. For example, if you think that a particular argument is a very strong reason for adopting the euro, you might write '+ 90' on the line.
>
> Ensure you have a sign and a number on every line. When you have finished your diagram, turn the page."

7.4.2 Results

Three separate two-within-factor ANOVAs were again performed on the measures of word count, correctly recalled propositions and correctly recalled arguments. For word count, there was no effect of status ($F_{(1,11)} = 0.01$, ns) and a significant effect of generation ($F_{(2,22)} = 16.50$, $p < 0.001$). For propositions, there was no effect of status ($F_{(1,11)} = 0.53$, ns) and a significant effect of generation ($F_{(2,22)} = 27.68$, $p < 0.001$). For arguments, there was no effect of status ($F_{(1,11)} = 0.70$, ns) and a significant effect of generation ($F_{(2,22)} = 13.73$, $p < 0.001$). Figures 7.4, 7.5 and 7.6 illustrate how the measures of word count, correctly recalled arguments and correctly recalled propositions change with generation in each case, showing little difference between the high- and low-status material. Experiment 7b therefore replicated the findings of Experiment 7a, finding that the status of the source had no effect on either the quantity or accuracy of transmission.

Further analyses revealed no significant effect on the measure of propositions of whether the argument was for or against the euro ($F_{(1,11)} = 1.79$, $p > 0.05$), nor whether the argument was presented first or second on the page ($F_{(1,11)} = 0.85$, $p > 0.05$). A power analysis performed on the measure of propositions gave similarly low values of noncentrality (ë = 0.52) and power (<0.17) to those of Experiment 7a, despite the threefold increase in sample size.

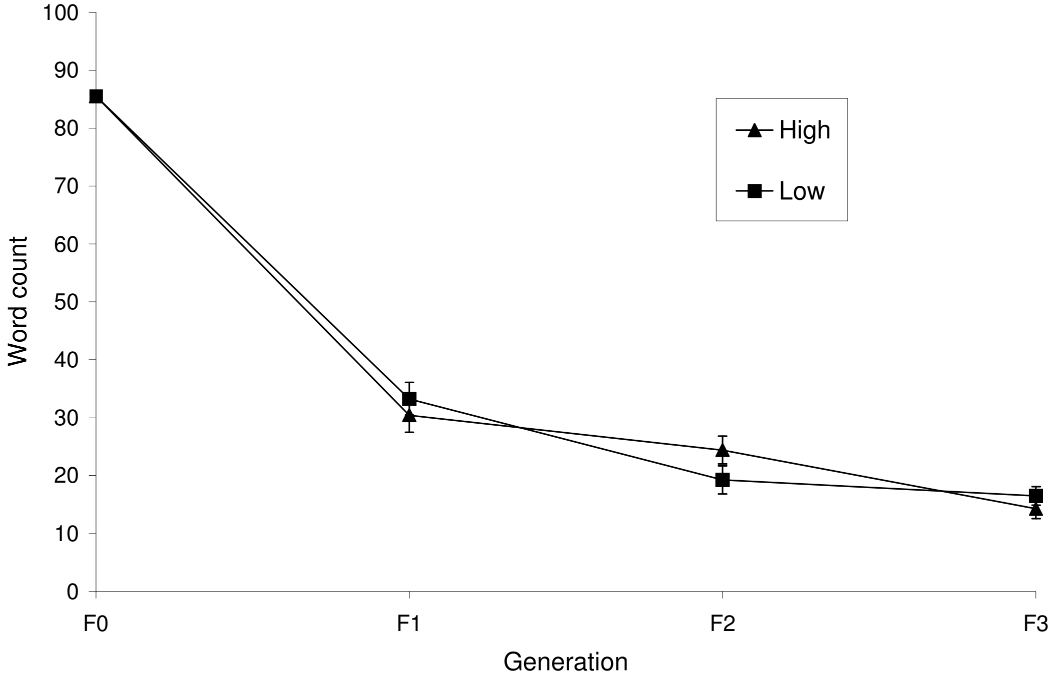

Figure 7.4 - Transmission of high- and low-status material by each generation of Experiment 7b, as measured by word count. Error bars show standard error.

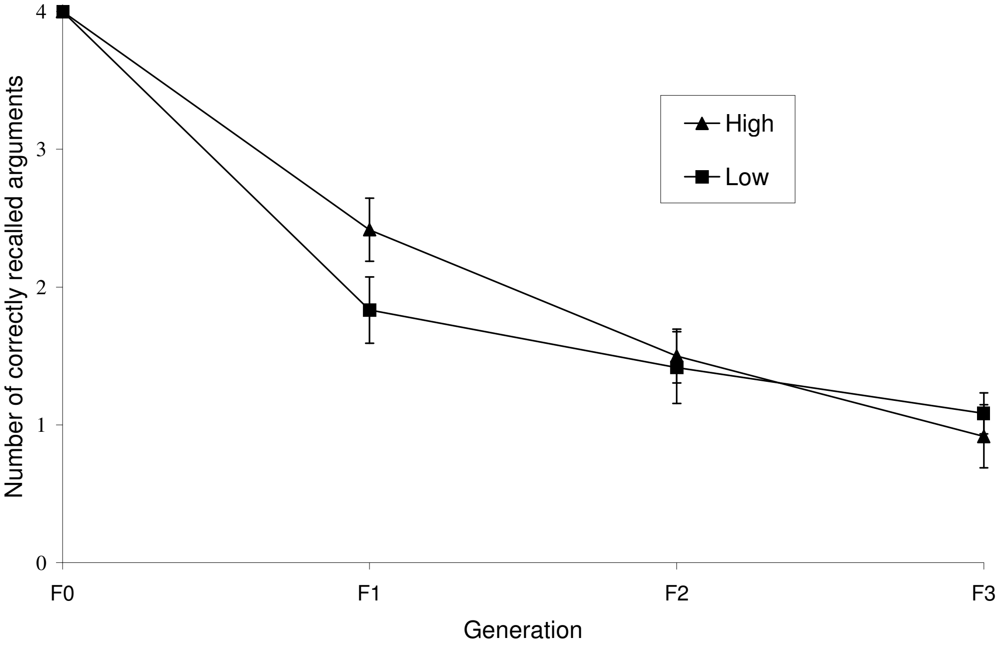

Figure 7.5 - Transmission of high- and low-status material by each generation of Experiment 7b, as measured by the number of arguments from the original material correctly recalled (out of 4). Error bars show standard errors.

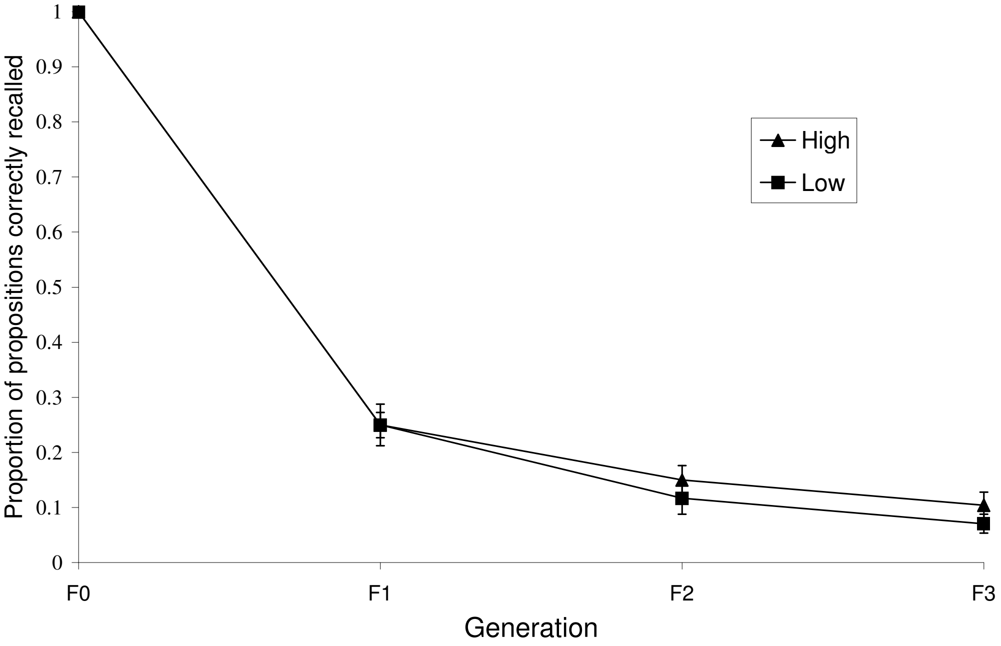

Figure 7.6 - Transmission of high- and low-status material by each generation of Experiment 7b, as measured by the proportion of propositions contained in the original material correctly recalled. Error bars show standard errors.

There was also no effect of status on the personal opinion of the participant regarding the euro (on a seven-point scale), with an equal number of participants agreeing and disagreeing with the high-status source. After transforming these data so that positive values indicate agreement with the high-status model and negative values indicate disagreement, a one sample t-test showed that the opinions did not significantly differ from zero ($t_{(35)} = 0.79$, mean = 0.25, $p > 0.05$), indicating that the participants neither systematically agreed nor disagreed with the argument presented as originating from the high-status source. The same was found for the summed weights in the argument diagrams: these also did not significantly differ from zero according to a one-sample t-test ($t_{(35)} = 0.86$, mean = 15.14, $p > 0.05$), although the weights did correlate with the direct measure of opinion ($r = 0.41$, $p < 0.015$) supporting the validity of the diagram method.

7.5 GENERAL DISCUSSION

Boyd and Richerson's (1985) proposed indirect bias in human cultural transmission implies that information from sources of high status is copied more reliably than information from low-status sources. Experiments 7a and 7b both failed to find any evidence that arguments attributed to high-status sources are transmitted with any greater accuracy or quantity than arguments attributed to low-status sources. Before discussing the implications of this negative result for the theoretical status of the indirect bias, we must first consider possible methodological problems.

Experiment 7b addressed a number of potential problems with Experiment 7a, which can now be reconsidered as to their influence on the non-significant findings.

First, the estimated power of Experiment 7b was still very low. However, the fact that the sample size was increased threefold from Experiment 7a yet the difference between the high- and low-status material decreased, and the fact that the test for an effect of status was not approaching significance, suggest that increasing the sample size further would not reveal a significant difference. Furthermore, previous studies (Chapters 5 and 6) have yielded significant results with fewer chains. There are a number of reasons, then, for suspecting that the non-significant result was not due to a small sample size.

Second, the health arguments were replaced with economic arguments about whether the UK should adopt the euro. Although economic arguments might be considered less emotive than health issues, they were perhaps not emotive or interesting enough, and the material very quickly degraded to an average of less than two propositions after only the third generation. Consequently only three generations were run, rather than the four that were planned. If the participants found it difficult to recall this kind of material, then any effect of source status may have been obscured by a floor effect.

Third, the high-status source was changed from an academic expert to a rich and famous celebrity, with no discernible effect. This is consistent with the lack of an effect of source on transmission. However, future studies might systematically vary variables such as fame, wealth and expertise, as well as similarity to the participants. Both the diffusion of innovations literature (Rogers, 1995) and the literature on rumour transmission (Rosnow, 1991) have found that models who are too dissimilar to the recipient are unlikely to be copied. It may be that the high status of the Oxford professor and the international film star is counteracted by their dissimilarity to the participants. The low-status source, meanwhile, despite being of low status, benefits from his similarity to the participants. Future studies might systematically vary the similarity of the source, perhaps comparing the transmission of information originating with fellow students and non-students.

If, on the other hand, this negative finding is assumed to be valid, it implies that an indirect bias does not operate when written verbal information is transmitted in the direct absence of the high- or low-status source. Given that much of human culture in post-industrial societies is transmitted as verbal information through very large populations where direct first-hand experience of high-status individuals (e.g. Oxford professors or Oscar-winning film actors) is rare, this finding implies a more limited role of status in human culture than perhaps envisaged by Boyd and Richerson (1985).

However, two factors might counteract this limitation. First, if transmission is one-to-many rather than one-to-one (Cavalli-Sforza & Feldman, 1981) then a high-status source can be directly experienced simultaneously by a large number of individuals. Second, mass media such as television can amplify this one-to-many transmission, greatly increasing the number of individuals than is possible with face-to-face transmission. In any case, the potency of indirect bias and whether it operates in the absence of the source are likely to be important factors in determining its large-scale population-level effects, factors which future mathematical models might explore.

It is not possible to infer from the present results whether the failure to observe an indirect bias is because the stimulus was second-hand, or verbal, or both. Future studies might employ more complex experimental designs to explore this further. For example, a group of participants could be asked to perform a task for which they are rewarded by access to resources. The participant who shows the best performance (the 'high-status' participant) and the participant who shows the worst performance (the 'low-status' participant) would then both transmit verbal information to the other members along chains similar to those used here. If the indirect bias only operates in the presence of the source, then the first generation should exhibit a preference for the information from the high-status participant, and this preference would diminish with generation in the absence of the high-status participant. Information from the low-status participant would not show such a preference. A second version of the experiment might use behaviour rather than verbal information.

In conclusion, Chapter 7 failed to find evidence that verbal material is indirectly biased when it is reported to have originated from sources of different status. This implies that Boyd and Richerson's (1985) hypothesised indirect bias in cultural transmission may be more limited in its effect than originally assumed, although a number of modifications to the methodology and material of the present study would be needed to state this conclusively.

CHAPTER 8 - ANTHROPOMORPHISM AND THE ATTRIBUTION OF INTENTIONALITY

8.1 ABSTRACT

There is extensive evidence that people attribute human mental states and human psychological or emotional dispositions to non-intentional, non-human behaviour. It is hypothesised in Chapter 8 that this tendency translates into an 'anthropomorphic bias' in human cultural transmission, which is predicted to cause non-intentional animal behaviour to be increasingly described in terms of mental state terms and human attributions. Two experiments used the transmission chain method to test this hypothesis. Descriptions of animal behaviour initially expressed entirely in non-intentional terms were passed along multiple chains of participants. Very few mental state terms or human attributions were introduced during the course of transmission, failing to demonstrate the operation of an anthropomorphic bias.

8.2 INTRODUCTION

Several researchers from a number of disciplines have proposed that people have a tendency to attribute human intentions and human mental states to non-human animals and inanimate objects, a tendency variously described as *folk psychology*, *anthropomorphism* (Kennedy, 1992), *mind-reading* (Baron Cohen, 1995) and *adopting an intentional stance* (Dennett, 1987). It is hypothesised that this tendency, here labelled an ‘anthropomorphic bias’, operates in human cultural transmission to cause information concerning the behaviour of non-human animals to be increasingly described in terms of human mental states as it is transmitted through a population.

Coming from a philosophical standpoint, Dennett (1987) described the intentional stance as the attribution of human beliefs and desires to an object and the use of these attributions to predict its behaviour. This was contrasted with the ‘physical stance’, in which behaviour is interpreted in terms of the internal workings of the object, and the ‘design stance’, in which an object’s behaviour is explained by appealing to the assumed function for which it was designed. Dennett (1987) argued that people predominantly adopt the intentional stance because in many cases the physical causes of a system are unknown, and its function is unclear. In other words, the intentional stance is simply easier to use (although this does not really explain *why* it is easier, or why it is not also easier for other species). Psychologists have used the terms ‘theory of mind’ (Baron Cohen, Leslie, & Frith, 1985) or ‘mind-reading’ (Baron Cohen, 1995) to describe the same phenomenon.

In the scientific study of animal behaviour, the term anthropomorphism is used to mean "the ascription of human mental experiences to animals" (Asquith, 1984, p. 138). It is often used as a derogative term for unscientific and inaccurate writing (e.g. Kennedy, 1992); indeed, the APA publication manual specifically instructs that authors "do not attribute human characteristics to non-human animals or to inanimate sources." Others such as Asquith (1984) and Fisher (1996), however, argue the opposite, that anthropomorphism is a valuable heuristic for the understanding of animal behaviour. This study makes no judgement with regards to the validity of anthropomorphism in the study of animal behaviour, beyond simply noting that the existence of anthropomorphism, right or wrong, supports the presence of an intentionality bias. The fact that safeguards are needed *against* anthropomorphism in the study of animal behaviour, even amongst highly intelligent researchers, suggests that the attribution of human mental states is in fact the norm.

Indeed, some authors have claimed that attributing mental states is an evolved feature of human cognition. Within the framework of his social function of intellect hypothesis (that primate intelligence evolved in response to complex social problems: see also Byrne & Whiten, 1988; Whiten & Byrne, 1997), Humphrey (1976) argued that there was consequently a "predisposition among men to try to fit non-social material into a social mould" (p. 312). More recently, Mithen (1996) has argued that anthropomorphism is the result of an interaction between the once separate domains of natural history intelligence, concerning animal behaviour, and social intelligence, in which human behaviour is understood in terms of mental states and intentions. Reviewing evidence which suggests that anthropomorphic thinking is widespread in modern humans and appeared somewhat abruptly in the archaeological record around 40-30,000 years ago, Mithen (1996) proposed that this breakdown in the barrier between natural history and social intelligence marked a significant transition in human cognitive evolution. In particular, anthropomorphic thinking allowed more accurate prediction of animal behaviour, resulting in an improved ability to track the movement of prey and allowing the development of more advanced hunting techniques. As such, Mithen (1996) argued that anthropomorphism represents a fundamental cognitive feature of the modern human mind.

Similarly, Whiten (1999a) has proposed that mind-reading evolved as part of a suite of cognitive abilities that can be described as ‘deeply social’, where social cognition deals not only with complexities of the social world but is so well cognitively integrated that it impinges onto analysis of the non-social aspects also. These claims are supported by evidence that mind-reading is universal (Avis & Harris, 1991; Brown, 1991) and exhibits a specific pattern of breakdown (autism, or ‘mind-blindness’: Baron-Cohen, 1995).

Early experimental evidence for a tendency to attribute mental states to inanimate objects came from a classic study by Heider and Simmel (1944), who found that participants interpreted the movement of simple geometric shapes in terms of human intentions (e.g. one shape ‘bullying’ another). More recently, Mitchell and Hamm (1997) presented brief descriptions of animal behaviour to undergraduates, and then asked them to evaluate to what degree various psychological states described that behaviour. One of these descriptions is reproduced below.

> ‘Patricia Ekman studies nonverbal behavior of chimpanzees. She observed the following interaction in a nature park:
>
> B, a male, is with S, a female, comfortably stroking her. G, another male, moves to S, and begins to stroke her. B turns away from S and looks intently at his hand.”
>
> (Mitchell and Hamm 1997; p. 187)

Mitchell and Hamm (1997) found that participants who read descriptions of animal behaviour suggestive of jealousy or deception (but containing no mental state terms) later rated that behaviour as evidence of those human psychological states. For the passage reproduced above, the chimpanzee staring at his hand was described as ‘upset’, ‘jealous’, ‘thinking about what to do next’ and ‘angry’. Similar ratings were given when different species were used in the description, with chimpanzees, elephants, bears, otters and dogs all yielding results comparable to humans. This indicates that it is the *behavioural* similarity to humans, rather than the phylogenetic or physical similarity, or familiarity with the species, which provokes anthropomorphism. That is, people tend to explain the human-like behaviour of a range of species in terms of human mental states.

There is also non-experimental evidence directly addressing the transmission of information concerning mental states. Studies of the orally transmitted stories of hunter-gatherer societies show that animal behaviour is frequently described in terms of human mental states and characteristics (see Scalise Sugiyama (2001) for a review). Such reports support the above argument that taking the intentional stance is adaptive, as attributing mental states to animals makes their behaviour easier to predict and hence easier to hunt or avoid. For example, personifying snakes as crafty and devious (as with the serpent in Genesis) highlights the fact that they are often well concealed and attack without warning. Experimental evidence for an anthropomorphic bias in human cultural transmission comes from Bangerter (2000), who found that as a description of conception was transmitted along a chain of subjects the sex cells tended to move from the object position to the subject position of the sentences. While Bangerter (2000) argued that this anthropomorphism was a result of sex-role stereotyping, further experiments using the transmission chain method might reveal a more general anthropomorphic bias. Experiments 8a and 8b therefore combined the material from Mitchell and Hamm (1997) with the methodology of Bangerter (2000), transmitting a number of behavioural episodes along multiple chains of participants.

8.3 EXPERIMENT 8A

In Experiment 8a the brief descriptions of animal behaviour found by Mitchell and Hamm (1997) to elicit anthropomorphic attributions were transmitted along multiple chains of participants, with the prediction that the behaviour would be increasingly described in terms of human mental states and human emotions.

8.3.1 Methods

8.3.1.1 Design

The transmission chain design was adopted, in which the first participant in each chain recalls the original stimulus material, the output of which is then given to the second participant to recall, whose recall is in turn given to the third participant, and so on down the chain.

Four chains each comprising four participants (or four ‘generations’) were run. The first participant in each chain was given five paragraphs similar to those used by Mitchell and Hamm (1997), featuring a description of behaviour containing no mental state terms, but that could potentially be described in terms of human mental states and intentions. Each chain transmitted the same five descriptions for a single species, although the species was varied between chains. The species varied in terms of their physical similarity and familiarity to humans: chimpanzees are similar but relatively unfamiliar; dogs are familiar but dissimilar; newts are neither familiar nor similar. Human behaviour was used as a control.

The independent variables were therefore transmission generation, with five levels (F0-F4), and species, with four levels (human, chimp, dog and newt). The dependent variables were measures of intentionality, specifically the frequency of mental state terms and psychological attributions (see Analysis section 8.3.1.4 below). It was predicted that the frequency of such terms would increase with generation. Measures of recall quantity and accuracy were also assessed.

8.3.1.2 Participants

Four chains each comprising four participants were run, giving a total of 16 participants. All participants were students of the University of St. Andrews and were unpaid volunteers. Their mean age was 18.73 years and 60% were female. Students of biology, zoology and psychology who may have been explicitly taught not to anthropomorphise when describing animal behaviour were excluded from this study.

8.3.1.3 Materials

The first participant in each chain was presented with five descriptions of a single species' behaviour, although the species was varied between chains. The species were human children, chimpanzees, dogs and newts, with the same five behavioural descriptions adapted for each species. The descriptions were designed to contain no mental state terms such as 'want' or 'know', and to be as impersonal as possible, hence each animal was given a letter rather than a name. The five descriptions concerned deception, reconciliation, problem-solving, emotional concealment and jealousy (although these labels were not given to the subjects). The full descriptions are reproduced in Appendix C.1.

8.3.1.4 Analysis

It was predicted that as the descriptions of behaviour were passed along the chains, they would be increasingly described in terms of human mental states and emotional dispositions. That is, the frequencies of mental state terms would show a significant effect of generation and trend analyses would show a significant increase with generation. Such an analysis is similar to that performed by Bartsch and Wellman (1995) on the conversations of children in order to assess theory of mind development, the methods of which can be adapted for use here. Bartsch and Wellman (1995) examined eleven mental state terms, concerning either desires (want, hope, wish, care (about), afraid (that)) or beliefs (think, know, believe, expect, wonder, dream), although the vast majority concerned only three of these: *want*, *think* and *know*. A term was also only counted if it referred to a genuine psychological state rather than a reference to overt behaviour. In addition to these mental state terms, the use of human psychological attributes, such as jealousy or anger, were also recorded, following Mitchell and Hamm (1997).

Additional measures of quantity and accuracy were also calculated for each participant's recall. The number of words represents a gross content-independent measure of recall. In order to measure accuracy, it was determined whether each of the five behavioural episodes (deception, reconciliation, problem-solving, emotional concealment and jealousy) was recalled *and* retained the gist of the original behaviour. For example, the 'deception' episode would require one individual to find a desirable item, a second individual to appear, and the first to ignore the item until the second leaves. This measure gives the total number of episodes that retained the gist (out of five) for each recall.

8.3.1.5 Procedure

Each participant performed the experiment on their own. They were presented with a booklet containing the material appropriate to their chain and generation on the first page, with written instructions to read the text through at a comfortable reading speed. The second page contained a blank space with the instructions:

> "In the space below, please write out the descriptions you just read as best you can. Try to be as accurate as possible, but don't worry if you can't remember it all. When you have finished, turn the page"

The final page of the booklet solicited their age, sex and study subject, after which they were debriefed by the experimenter. The recall they produced was then typed up and inserted as the first page of the next booklet, and given to the next participant in the chain as appropriate. No time limit was given for recall.

8.3.2 Results and Discussion

Table 8.1 shows the dependent variables (word count, the number of accurately recalled episodes and the number of human attributions) for each of the four chains. The main variable of interest, the number of human attributions (either mental state terms or human emotional attributions), showed very little increase with generation. The final three generations of the human chain contained the following phrase with a mental state term:

‘Child A *wanted* some biscuits…’ (italics added)

while all four recall generations of the dog chain contained variations on the phrase:

‘Dog A *talks* to Dog C’ (italics added)

Only two human attributions in four chains each containing five episodes constitutes little evidence for an anthropomorphic bias in these participants. As such, a within-groups ANOVA showed no significant effect of generation on this measure ($F_{(4,12)} = 2.00$, ns). Word count and accuracy both decreased with generation as would be expected, although there are too few chains in this initial study to meaningfully compare species.

		Generation				
Measure	**Chain**	**F0**	**F1**	**F2**	**F3**	**F4**
Attributions	Human	0	0	1	1	1
	Chimp	0	0	0	0	0
	Dog	0	1	1	1	1
	Newt	0	0	0	0	0
Word count	Human	209	91	75	82	70
	Chimp	218	130	121	94	58
	Dog	210	98	85	59	51
	Newt	200	161	60	35	29
Accuracy	Human	5	3	3	3	1
	Chimp	5	4	3	3	2
	Dog	5	3	3	3	2
	Newt	5	5	2	0	0

Table 8.1 – The number of human attributions (mental state terms or emotional attributions), the word count, and the number of descriptions in which the gist was retained (out of 5) for each of the four species chains of Experiment 8a.

8.4 EXPERIMENT 8B

8.4.1 Introduction and Methods

Following the initial exploration of the anthropomorphism hypothesis in Experiment 8a, three changes were made to the material and methodology in Experiment 8b in order to provide a better test of the hypothesis. First, several of the participants in Experiment 8a reported difficulty keeping track of the letters used to label the individuals (e.g. "Chimp A" or "Newt B"). The material in Experiment 8b therefore removed the letters and used verbal descriptions (e.g. "a female chimp" or "a second male newt"). This new material is reproduced in Appendix C.2. Second, it is possible that the participants in Experiment 8a *were* in fact using human intentional states to understand and remember the behaviour that they read, but when writing out their recall they converted it back to the behaviourist style of the original. Hence in Experiment 8b the instructions were changed from "Please write out the descriptions you just read as best you can. Try to be as accurate as possible" (Experiment 8a) to "Please write in your own words the descriptions you just read as best you can" (Experiment 8b). The addition of the phrase 'in your own words' was intended to encourage the participants to reproduce the material as they understood it, rather than as they thought it should be reported (without biasing their recall to conform to the experimental hypothesis). Finally, the number of chains was increased to twelve, three for each species. In all other respects the method of Experiment 8b was identical to that of Experiment 8a. Forty-eight students of the University of St. Andrews participated in Experiment 8b, none of whom had participated in Experiment 8a. Their mean age was 20.94 years and 87.5% were female.

8.4.2 Results

Table 8.2 shows the mean values of the three dependent measures for the four species, averaged across all three chains. Each dependent variable was analysed using a mixed 5 x 4 ANOVA with generation as a within-groups factor and species as a between-groups factor. The variable directly related to the experimental hypothesis, the number of human attributions, again showed little increase with generation. None of the participants in Experiment 8b introduced mental state terms. A small number of human psychological or emotional attributions were made: children were stated to be "jealous" of one another, one chimp was stated to "tell" another chimp something, and dogs got "angry", "apologised" and "became friends". However, these frequencies were very low given the total number of words produced, and thus there was no significant effect of generation on this measure ($F_{(1,10)} = 1.67$, ns, Greenhouse-Geisser corrected). There was also no effect of generation on the number of attributions when the data from Experiments 8a and 8b were combined ($F_{(1,16)} = 2.72$, ns, Greenhouse-Geisser corrected).

		Generation				
Measure	**Chain**	**F0**	**F1**	**F2**	**F3**	**F4**
Attributions	Human	0	0.67	0.67	0.67	0.67
	Chimp	0	0	0	0	0.33
	Dog	0	0	1.00	1.00	1.67
	Newt	0	0	0	0	0
Word count	Human	224.00	113.00	97.33	63.00	64.00
	Chimp	233.00	171.33	152.33	115.67	103.00
	Dog	227.00	120.67	81.67	72.00	75.33
	Newt	226.00	102.67	74.00	58.00	45.33
Accuracy	Human	5.00	3.33	3.00	2.67	2.33
	Chimp	5.00	3.33	2.67	1.33	1.33
	Dog	5.00	3.33	2.00	2.00	2.00
	Newt	5.00	2.33	1.00	0.67	0.33

Table 8.2 – The number of human attributions (mental state terms or emotional attributions), the word count, and the number of descriptions in which the gist was retained (out of 5) for each of the chains of Experiment 8b. Each value is the mean of three replicate chains.

As before, both word count ($F_{(4,32)} = 67.81$, $p < 0.001$) and accuracy ($F_{(4,32)} = 70.52$, $p < 0.001$) showed significant overall decreases with generation. The increased sample size now allows comparisons between species on these measures. Word count showed a significant effect of species ($F_{(3,8)} = 4.62$, $p < 0.05$), with Tukey's HSD post-hoc test showing that this was due to a significant difference between the chimp chains and the newt chains, with no other comparisons significant at $p < 0.05$. The change in word count with generation is shown in Figure 8.1.

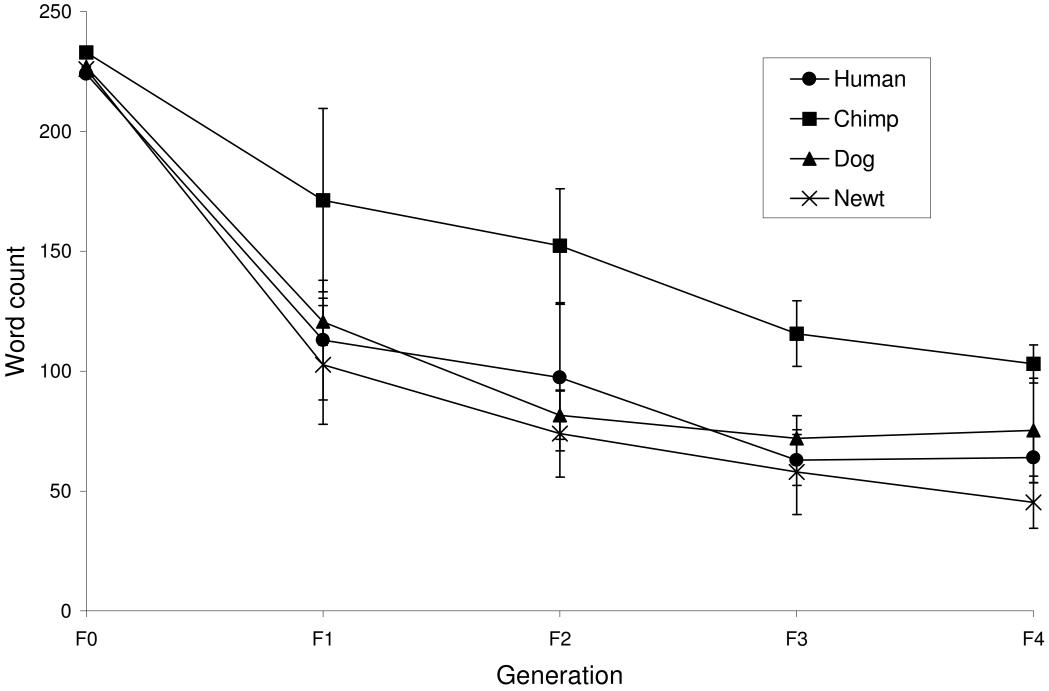

Figure 8.1 – Change in word count with generation in Experiment 8b, according to species. Error bars show standard errors.

The accuracy measure (the number of behavioural episodes correctly recalled and with their gist preserved) also showed a significant effect of species ($F_{(3,8)} = 6.80$, $p < 0.015$). Because the material from both Experiments 8a and 8b started with the same five behavioural episodes, these data can be combined (unlike the word count measure, which had a greater F0 starting value in Experiment 8b). For the combined data there was a significant effect of species on accuracy ($F_{(3,12)} = 6.93$, $p < 0.01$), with Tukey's HSD post-hoc test showing that the newt chains had significantly lower accuracy than each of the other three species chains at the 0.05 level of significance. The change in accuracy with generation is shown in Figure 8.2.

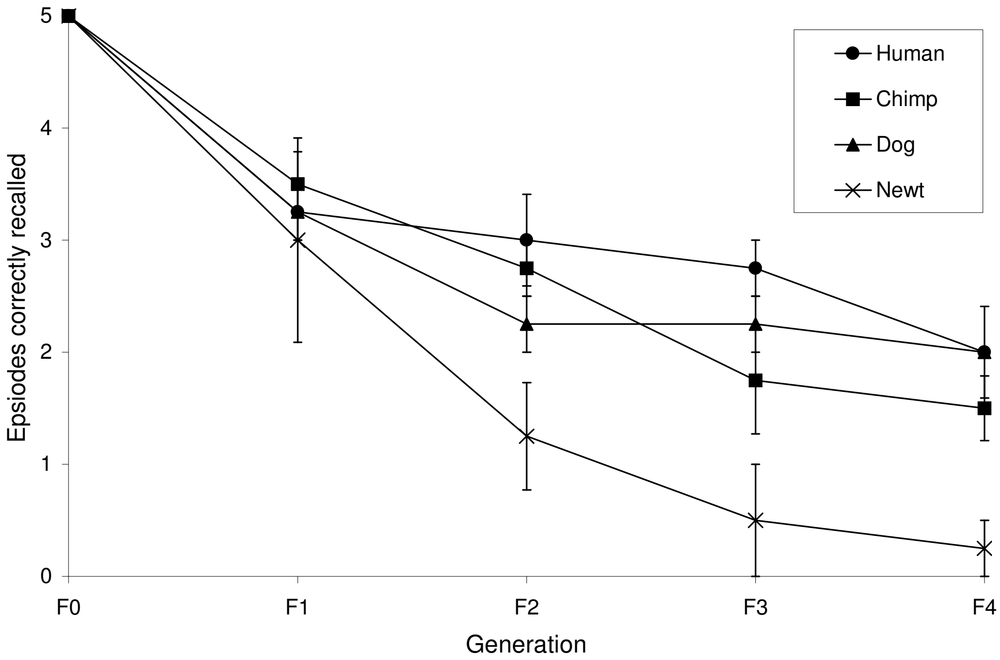

Figure 8.2 – Change in accuracy with generation in Experiments 8a and 8b combined, according to species. Error bars show standard errors.

8.5 GENERAL DISCUSSION

Experiments 8a and 8b combined failed to find experimental evidence for an anthropomorphic bias in human cultural transmission. There were isolated and very infrequent instances of mental state terms and human psychological or emotional attributions, with no cumulative increase in frequency with generation.

This result is surprising given the extensive evidence cited in the Introduction (Section 8.2) that people see non-intentional animal behaviour in intentional or anthropomorphic terms. Mitchell and Hamm (1997) found evidence for anthropomorphism using very similar material to that used here, while Bangerter (2000) found evidence for anthropomorphism using the same transmission chain methodology.

The only significant finding from the present study was that newt behaviour was transmitted with poorer accuracy than the same behaviour attributed to humans, chimpanzees and dogs. It could be that the participants simply found newt behaviour less interesting and harder to recall than the behaviour of more familiar or similar species. However, this finding might also be consistent with the operation of an anthropomorphic bias. If the participants were in fact using human intentions and dispositions to understand and recall the behavioural episodes, and the participants found it easier to attribute those intentions and dispositions to humans, chimpanzees and dogs, then the newt behaviour would be recalled with poorer accuracy. The fact that not one of the four newt chains featured any human attributions (Tables 8.1 and 8.2) supports this contention, although it remains speculative. It might be tested by encouraging the participants to report the behaviour as they understood it rather than in the style in which they originally read it, for example by asking them to write the material out as they would tell a friend, or by using a face-to-face rather than written version of the methodology.

Another aspect of the data suggestive of an anthropomorphic bias is that, although very few anthropomorphic terms were introduced, those that *were* introduced remained in the chain until the experiment was stopped. That is, an anthropomorphic bias might not act to spontaneously *generate* anthropomorphic terms, but it might act to *preserve* anthropomorphic terms once they are introduced. This could be tested by presenting the first participant in the chain with a mixture of anthropomorphic and non-anthropomorphic descriptions and comparing the persistence of each. It might also be useful to extend the number of generations that the material is transmitted through to obtain a better measure of persistence.

CHAPTER 9 - A PREFERENCE FOR NEOTENY AND THE EVOLUTION OF THE TEDDY BEAR

9.1 ABSTRACT

Hinde and Barden (1985) documented how teddy bears became steadily more neotenous, or baby-like, over an 80 year period. Chapter 9 used the transmission chain method to experimentally simulate this process of cultural evolution. In Experiment 9a, multiple chains of participants transmitted pictures of a non-neotenous bear in a lecture theatre setting. Experiment 9b repeated this method controlling for overall face size and using a stimulus bear that was easier to draw. Finally, Experiment 9c adopted a more controlled, laboratory-based method. No convincing evidence for a trend toward neoteny was found in any of the three experiments. The most likely explanation for these negative results is that the passive perceptual preference for neotenous faces does not operate during the active reproduction of drawings from memory.

9.2 INTRODUCTION

A fascinating example of cultural evolution was provided by Hinde and Barden (1985), who documented how the teddy bear has become steadily more neotenous[8], or baby-like, since its invention at the turn of the 20th century. Hinde and Barden (1985) measured the facial dimensions of teddy bears of various ages, dating from 1903 to 1984, finding that the forehead became progressively larger and the snout became progressively shorter over this period. Such features (large forehead, small nose) are characteristic of neotenous faces. To explain this trend, Hinde and Barden (1985) appealed to Lorenz's (1950) suggestion that neotenous features act as innate releasing mechanisms which elicit a reaction of nurturing and affection in adults. With respect to the bears, this innate preference for neotenous facial features would cause consumers to select and purchase the most neotenous bear available at any particular time, with teddy bear makers responding by continuing production only of these best-selling neotenous lines. The teddy bear population would thus gradually become more neotenous due to this artificial selection by successive consumers. Independent support for the cultural evolution of artifacts in response to artificial selection for neoteny was provided by Gould (1980), who documented how the cartoon character Mickey Mouse has similarly evolved to be increasingly neotenous over roughly the same period as the bears.

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[8] Strictly, the correct term should be 'paedomorphic', meaning baby-like (Gould, 1977). 'Neoteny' refers to one of several quite different heterochronous processes that can produce paedomorphosis (Gould, 1977). The term 'neotenous' is used here to be consistent with other studies in this field.

Support for the existence of a preference for neotenous facial features has been found by numerous studies examining what makes human faces attractive (Berry & McArthur, 1985; Cunningham, Roberts, Barbee, Druen, & Wu, 1995; Fullard & Reiling, 1976; Gardner & Wallach, 1965; Gross, 1997; Jones, 1995; Perrett *et al.*, 1998; Sternglanz, Gray, & Murakami, 1977). These studies found that a number of neotenous features increased the attractiveness of human faces, including a large forehead, large eyes, full lips, a small nose and a small chin. Several studies reported cross-cultural evidence for a preference for neoteny, finding significant effects with participants from the US, Brazil, Russia, and the isolated Ache and Hiwi groups of South America (Jones, 1995), as well as Taiwan (Cunningham *et al.*, 1995) and Japan (Perrett *et al.*, 1998), lending support to Lorenz's (1950) suggestion that such a preference is innate.

Other studies found that very young children show a reduced or absent preference for neoteny (e.g. Fullard & Reiling, 1976; Gross, 1997). This was confirmed by Morris, Reddy and Bunting (1995), who found that a preference for neotenous teddy bear faces only emerges at around five years of age. This suggests that it is parents and other adults who are driving the evolution of the teddy bear when they buy bears for infants, rather than the infants themselves selecting neotenous bears. This is consistent with Lorenz's (1950) argument that the preference for neoteny evolved because it encouraged nurturing and care-taking behaviour by parents towards their offspring, thereby increasing the offspring's chances of survival.

The present study used the transmission chain method to experimentally simulate the process of cultural evolution documented by Hinde and Barden (1985). An experimental simulation affords greater control over the transmission process, and can overcome the limitations of an historical data set. For example, the majority of Hinde and Barden's (1985) bears were taken from a museum exhibit, which constitute a tiny subset of the total number of bears in the hypothesised evolutionary lineage, a subset that furthermore may have been biased in some way. An experimental simulation would ensure the direct transmission of bears along chains of a determined length, and allows every step in the transmission chain to be examined.

The first participant in each chain was shown a picture of a non-neotenous bear (roughly equivalent in facial dimensions to a 1903 teddy bear) and then instructed to draw it from memory. Their drawing was then passed to the second participant in the chain, who viewed it and drew it from memory, with their drawing in turn acting as the stimulus for the third participant, and so on down the chain. It was predicted that the sequence of drawings would show a similar increase in neoteny to that found by Hinde and Barden (1985) for teddy bears over an 80 year period. That is, the same innate human preference for neotenous facial features that caused consumers to buy neotenous bears was also predicted to cause participants in the present study to distort their drawings in a neotenous manner. Experiment 9a constituted an initial test of this hypothesis using a face-to-face method of transmission. Experiment 9b repeated this method correcting for two potential methodological problems that arose from Experiment 9a. Finally, Experiment 9c adopted a more controlled, lab-based method of transmission.

9.3 EXPERIMENT 9A

9.3.1 Materials and Methods

The transmission chain design was adopted, in which the first participant in each chain views the original stimulus material and reproduces it from memory, the output of which is then given to the second participant to reproduce. This reproduction is in turn given to the third participant, and so on down the chain. Four separate chains were run each comprising 13 participants, giving 52 participants in total. All were undergraduate students of the University of St Andrews. The experiment was run as part of a practical class in Evolutionary Psychology, although at the time the participants were blind to the precise experimental aims and hypotheses.

The independent variable was the transmission generation, of which there were 13, or 14 if the original stimulus bear is included. The dependent variables were measures of neoteny drawn from previous studies. From Hinde and Barden (1985) only forehead size could be calculated, as snout length was inapplicable to the two dimensional drawings obtained here. Forehead size (FS) was defined as the vertical distance between the top of the face (not including the ears) and the eyes, divided by the vertical distance between the eyes and the base of the head, to obtain a ratio controlling for overall face size. Where the eyes were large or lopsided, eye level was taken as the point equidistant between the centres of the two eyes. Early teddy bears in Hinde and Barden's (1985) sequence had an FS of around 0.6 to 1.0, increasing to around 1.6 in 1984 (with the FS of some 1984 bears exceeding 2.2).

Four further measures of neoteny were used which have been shown both to be typical of neotenous (human) faces and to significantly correlate with judgements of attractiveness. From Jones (1995), eye width (EW) was defined as the mean width of the two eyes, and nose height (NH) was defined as the vertical distance from the top to the bottom of the nose. An additional measure specific to the bear face was added, snout height (SH), defined as the vertical distance from the top to the bottom of the snout. From Cunningham *et al.* (1995), distance between eyes (DE) was defined as the distance between the centre of each eye. Each of these measures (EW, NH, SH and DE) were divided by the face height to obtain a ratio controlling for the overall size of the face. Based on the results of these and the other studies listed in the Introduction (Section 9.2), neoteny is indicated by large values of FS, EW and DE, and low values of NH and SH. It was therefore predicted that FS, EW and DE would increase with generation, and NH and SH would decrease.

The first teddy bears were originally made to resemble actual bears, so the original stimulus material given to the first participant in each chain was a schematic outline of an actual adult bear. A photograph was obtained from the internet showing an adult brown bear (*Ursus arctos*) looking directly at the camera. Photo-imaging software was then used to trace around the salient facial features of this photograph (the face outline, nose, snout, ears, eyes and mouth) to produce a schematic bear face, as shown in Figure 9.1. This image was presented to the first participant in each chain printed on an otherwise blank sheet of A4 paper, with an actual face height of 17 cm. As expected if the early teddy bears were modelled after actual bears, the FS of this picture (0.83) falls within the range of FS given by Hinde and Barden (1985) for their earliest bears (0.6 – 1.0).

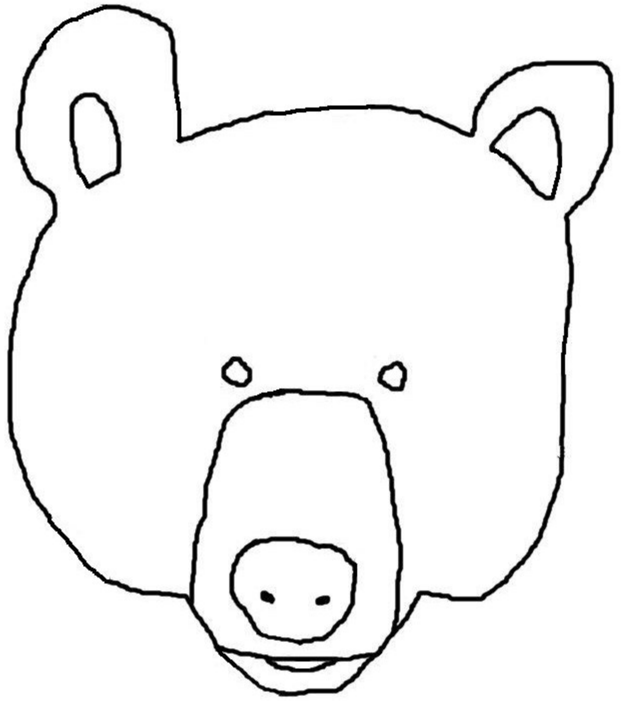

Figure 9.1 – The original stimulus material given to the first participant in each chain of Experiment 9a.

Participants were seated in four rows of a lecture theatre, with an equal number of participants in each row. Each row constituted one transmission chain. The first participant in each chain, that is, the four participants seated at one end of each row, were given the original stimulus bear shown in Figure 9.1 and given 10s to examine the picture. After 10s they were instructed to turn the picture face down and were given 30s to reproduce on a blank sheet of paper the stimulus bear from memory. They then passed their drawing to the person sitting next to them, who went through the same procedure (viewing the drawing for 10s and reproducing it from memory for 30s) with the first participant's drawing as their stimulus. The second participant's drawing was given to the third participant in the row, who did the same, and so on along each row/chain. Participants were instructed not to look at any drawing other than the one they were supposed to see.

9.3.2 Results

Figure 9.2 shows how the various measures of neoteny changed with generation. There was little systematic change, with much seemingly random fluctuation. Indeed, what change there was did not conform to the predicted effects. For example, forehead size showed an initial decrease from 0.83 to values that fluctuated between 0.4 and 0.5, against the predicted increase that would indicate a tendency towards neoteny. A series of repeated measures ANOVAs with generation as a within-groups factor (with 13 levels after excluding the original F0 stimulus bear) confirmed this observation, showing that for none of the measures was there a significant effect of generation.

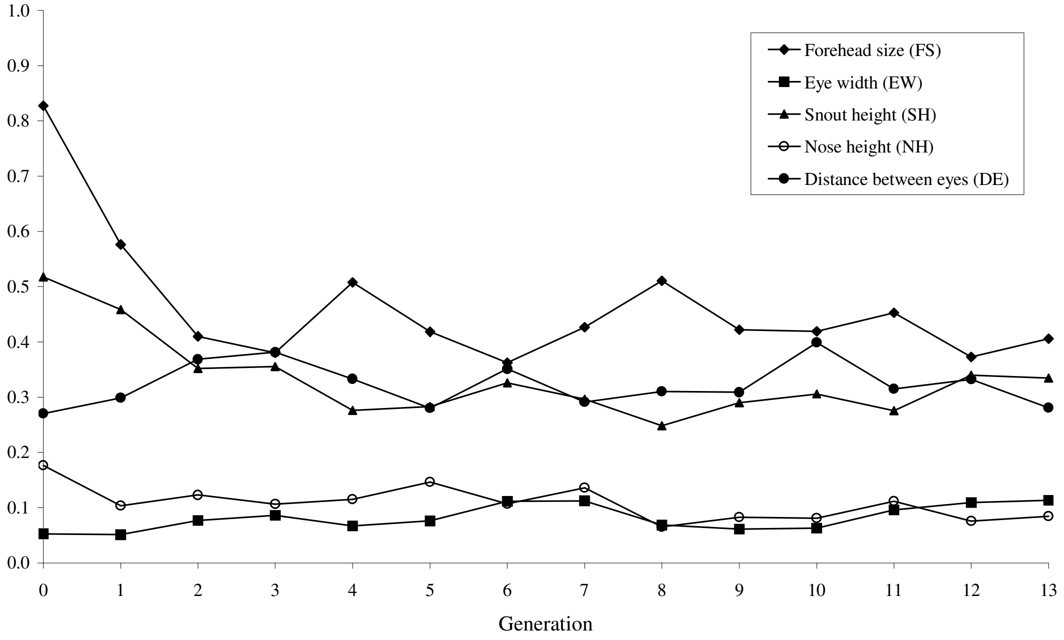

Figure 9.2 – Changes in various measures of neoteny with generation (Experiment 9a). Each data point is the mean measurement of all four chains.

The only clear effect that was observed is demonstrated in Figure 9.3, which shows the overall face height decreasing steadily with generation. This was confirmed by a repeated measures ANOVA showing a significant effect of generation ($F_{(3,8)}=16.47$, $p<0.001$, Greenhouse-Geisser corrected) and a significant linear downward trend ($F_{(1,3)}=56.51$, $p<0.005$). To summarise, the bears in Experiment 9a showed no evidence of increasing in neoteny, the only significant effect being a decrease in overall face size.

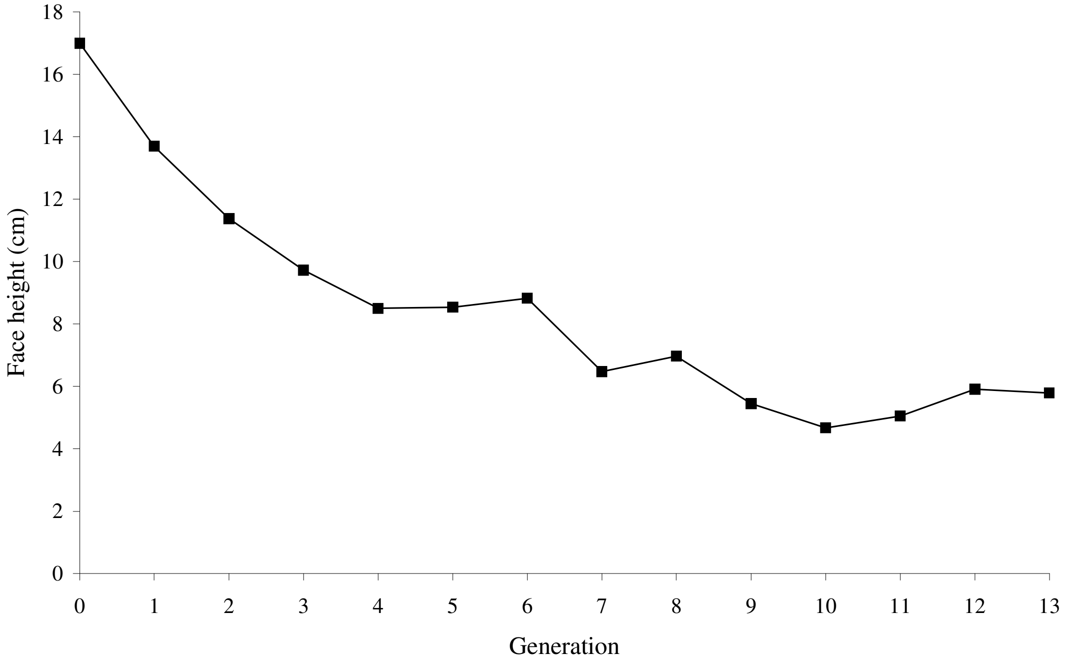

Figure 9.3 – The decrease in face height with generation (Experiment 9a). Each data point is the mean measurement of all four chains.

9.3.3 Discussion

One obvious factor that may have obscured any effect of neoteny is the significant reduction in overall face size. Although all of the neoteny measures were expressed as ratios to control for face size, there may not be a linear relationship between the overall face size and the positions of the facial features (similar to allometric growth patterns). A second problem was that many participants had difficulty reproducing the three-dimensional protruding snout, owing to the fact that the original stimulus bear was derived from a photograph. Indeed, the snout would often become entirely detached from the face, and in two of the four chains did not survive past the fifth generation. These two problems – reduction in overall face size and difficulty in drawing a three-dimensional image – were addressed in Experiment 9b.

9.4 EXPERIMENT 9B

9.4.1 Materials and Methods

Experiment 9b repeated the basic design of Experiment 9a but with two improvements to address the methodological problems discussed above. First, the overall face size was kept constant throughout each generation by giving every participant a blank outline of the face shape and instructing them to reproduce only the internal facial features. Second, the stimulus bear given to the first participant in each chain was made easier to draw, to prevent the difficulty with the three dimensional snout shown by the participants of Experiment 9a. The stimulus bear for Experiment 9b was drawn by hand using an early teddy bear as a model, and is shown in Figure 9.4. The actual face height of this image as presented to participants was 10.7 cm, and the FS was 0.61. This was even less neotenous than the bear from Experiment 9a, although again fell within the range of FS given by Hinde and Barden (1985) for their earliest bears (0.6 – 1.0).

The procedure was identical to that of Experiment 9a except that before the experiment began each participant was given a blank outline of the stimulus bear with the internal features missing. Six chains each comprising eight participants were run, giving a total of 48 participants. Although all of the 48 participants performed the experiment, nine of the reproductions were not returned to the experimenter, giving data from only 39 participants. The overall design is shown in Figure 9.5. The participants were undergraduate students of the University of Gloucestershire who performed the experiment as part of a course on Evolutionary Psychology. None of the participants who took part in Experiment 9b had any knowledge of Experiment 9a.

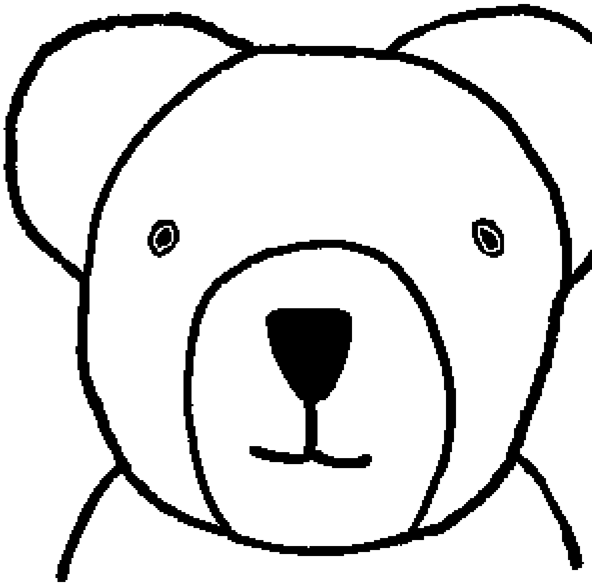

Figure 9.4 – The original stimulus material given to the first participant in each chain of Experiment 9b.

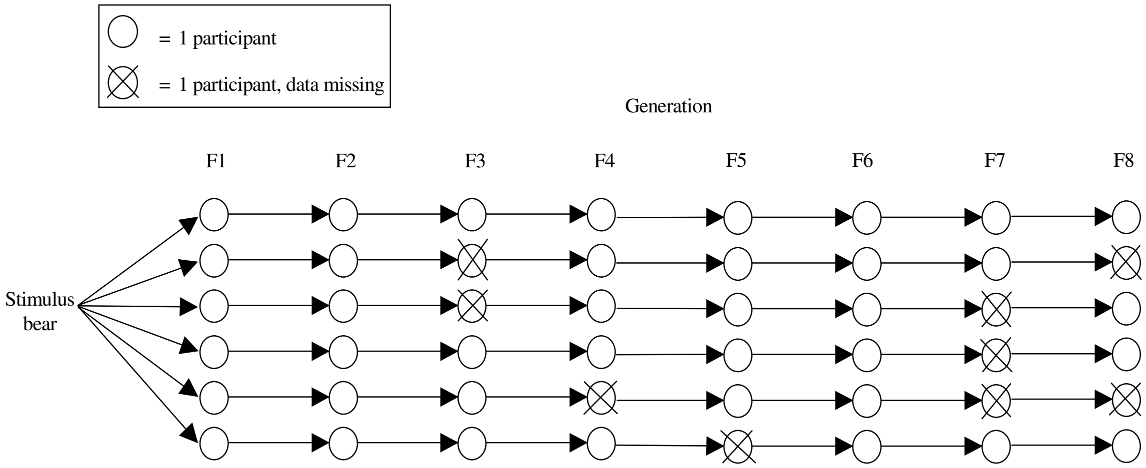

Figure 9.5 – Design of Experiment 9b

9.4.2 Results and Discussion

Figure 9.6 shows how the various measures of neoteny changed with generation. The results are roughly comparable to those from Experiment 9a (illustrated in Figure 9.1). FS again fluctuated around 0.5, indicating no increase in neoteny. DE showed a slight decrease, again indicating a decrease in neoteny, while NE and EW showed little change. The attempt to make the snout easier to draw seemed to be successful, as the snout no longer detached itself from the rest of the face. Despite this, the snout still disappeared from four of the six chains (after the first, second, fourth and sixth generations respectively). The steady decrease in SH, which would indicate an increase in neoteny, should therefore be treated with caution.

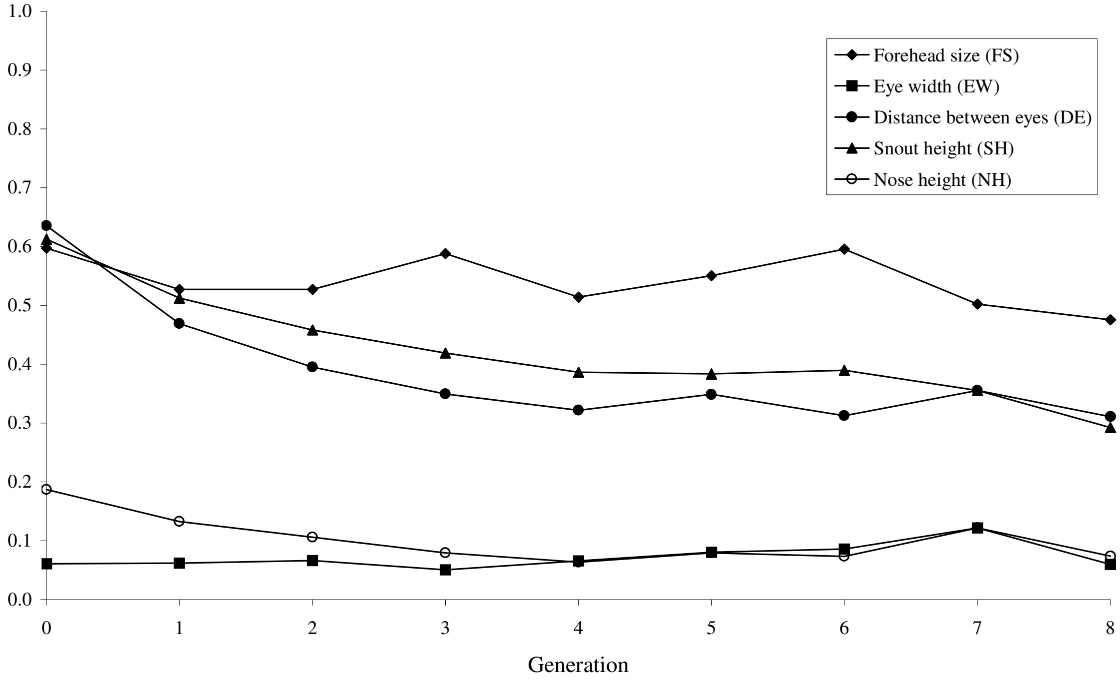

Figure 9.6 – Changes in various measures of neoteny with generation (Experiment 9b). Each data point is the mean measurement of all six chains.

Repeated measures ANOVAs were performed on all measures with generation as a within-groups factor, now with 8 levels. As can be seen in Figure 9.5, only one chain contained complete data for all eight generations. Excluding chains with missing values would therefore leave a sample size of n = 1 (where n = number of chains), so mean substitution was used to estimate the missing values, giving sample sizes of n = 6 (except SH, as noted above, for which n = 2).

FS, EW, DE and SH all showed no significant effect of generation. NH showed a significant effect of generation ($F_{(3,13)}=8.28$, $p<0.005$, Greenhouse-Geisser corrected) and a significant linear decrease according to a trend analysis ($F_{(1,5)}=11.96$, $p<0.05$), indicating an increase in neoteny as predicted. However, given the negative findings on the majority of the measures, including the measure used by Hinde and Barden (1985), the conclusion from Experiment 9b must be that there was no general tendency towards neoteny with generation in these teddy bear faces.

Figure 9.7 shows a bear whose facial dimensions (FS, EW, DE and NH) match the mean values of the final (eighth) generation reproductions. As the majority of chains lost the snout, the snout has been omitted in this composite bear. A comparison with the original stimulus bear in Figure 9.4 gives the impression that the eyes have moved closer together and the nose has become smaller, as would be expected if DE and NH both significantly decreased.

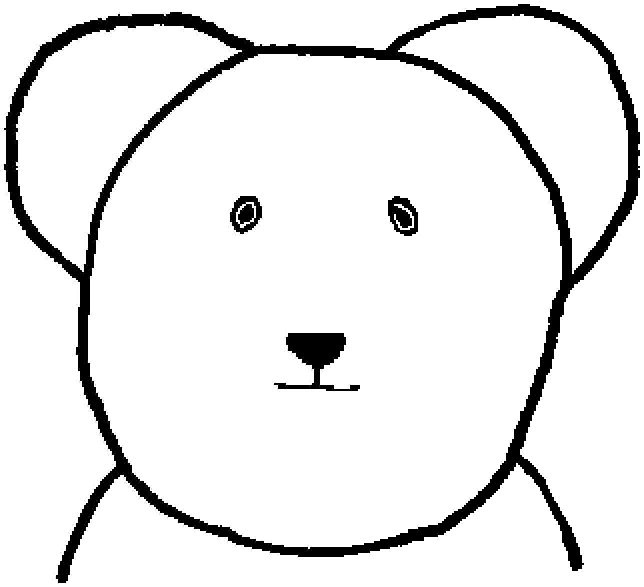

Figure 9.7 – Composite bear whose facial dimensions match the mean dimensions of the final (eighth) generation bears of Experiment 9b.

9.5 EXPERIMENT 9C

One remaining criticism of Experiments 9a and 9b might be that the experimental setting, a lecture theatre, is not conducive to transmission. It is possible that performing the procedure in front of fellow students in some way inhibited or distracted the participants. Experiment 9c therefore repeated the basic design of Experiments 9a and 9b but in a more controlled laboratory setting. This opportunity was also taken to alter the stimulus bear again, to make the image easier still to draw and to make the face as un-neotenous as possible, to maximise the chances of detecting any neotenous tendency.

9.5.1 Materials and Methods

The standard transmission chain design was adopted, as originally employed by Bartlett (1932). Hence participants were tested one at a time, with the experimenter passing the material from generation to generation. Participants carried out the present study after participating in an unrelated transmission chain study involving verbal material (the anthropomorphism study of Chapter 8). Following completion of that study, participants were instructed that they would then go through the same procedure but with a picture instead of a text. The stimulus bear was then shown to the participant for approximately 5s and then removed, after which the participant was instructed to reproduce the picture from memory in the blank outline provided. The resulting image was then taken by the experimenter and presented to the next participant in the chain at a later time.

Five separate chains each containing six generations were run. Four chains comprised all female participants, and one chain comprised all male participants. The mean age of all 30 participants was 21.34 years (standard deviation = 3.91), and all were students of the University of St. Andrews. Each participant was paid £2 to complete both this and the anthropomorphism study.

The original stimulus bear face given to the first participant in each chain is shown in Figure 9.8, and was designed to be as low in neoteny as possible in order to maximise the chances of detecting a preference for neoteny. Hence this bear has a small forehead, small eyes close together, a large nose and a small chin. Given that several of the participants in Experiments 9a and 9b omitted the snout or had difficulty integrating it with the other facial features, a snout was not included in the stimulus bear for Experiment 9c. Removing the snout now allows a new measure of chin height (CH), defined as the vertical distance from the base of the face to the lowest part of the mouth, which is predicted to increase with generation. The FS of this bear is 0.29, much lower (i.e. less neotenous) than the original bears used in Experiments 9a and 9b and also the bears measured by Hinde and Barden (1985).

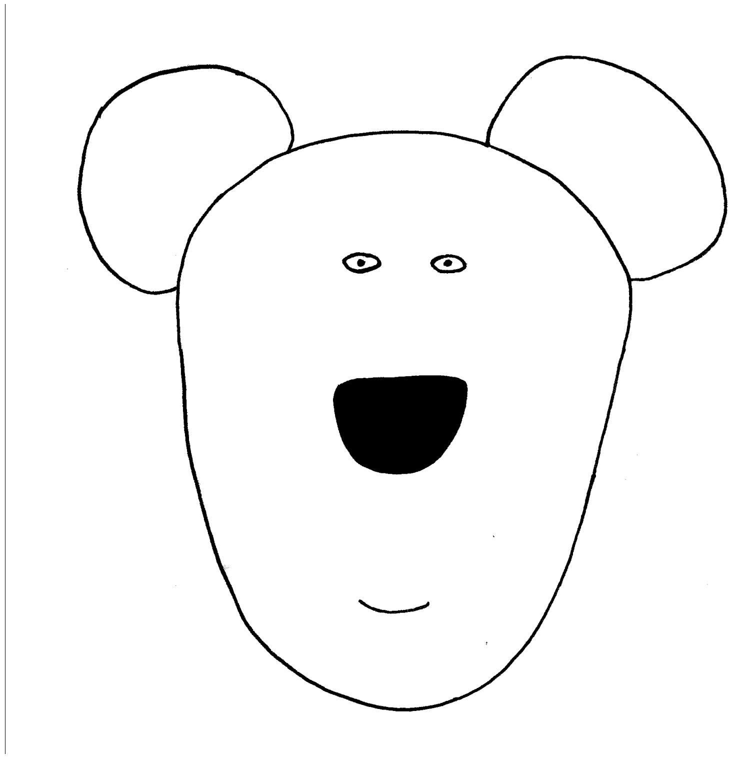

Figure 9.8 – The original stimulus bear given to the first participant in each chain of Experiment 9c.

9.5.2 Results and Discussion

Figure 9.9 shows how the various measures of neoteny changed with generation. FS showed a slight increase, which would indicate a tendency toward neoteny, but the final generation value of around 0.5 is still not even at the least neotenous value of FS recorded by Hinde and Barden (1985) of 0.6. The other measures also showed little change with generation, although there were very small movements in the neotenous direction. Figure 9.10 shows a composite bear constructed with the facial dimensions (FS, DE, EW, NH, and CH) matching the mean values of the final (sixth) generation reproductions. This composite bear appears slightly more neotenous than the original bear (Figure 9.8), with slightly larger eyes further apart, a larger forehead and a smaller nose.

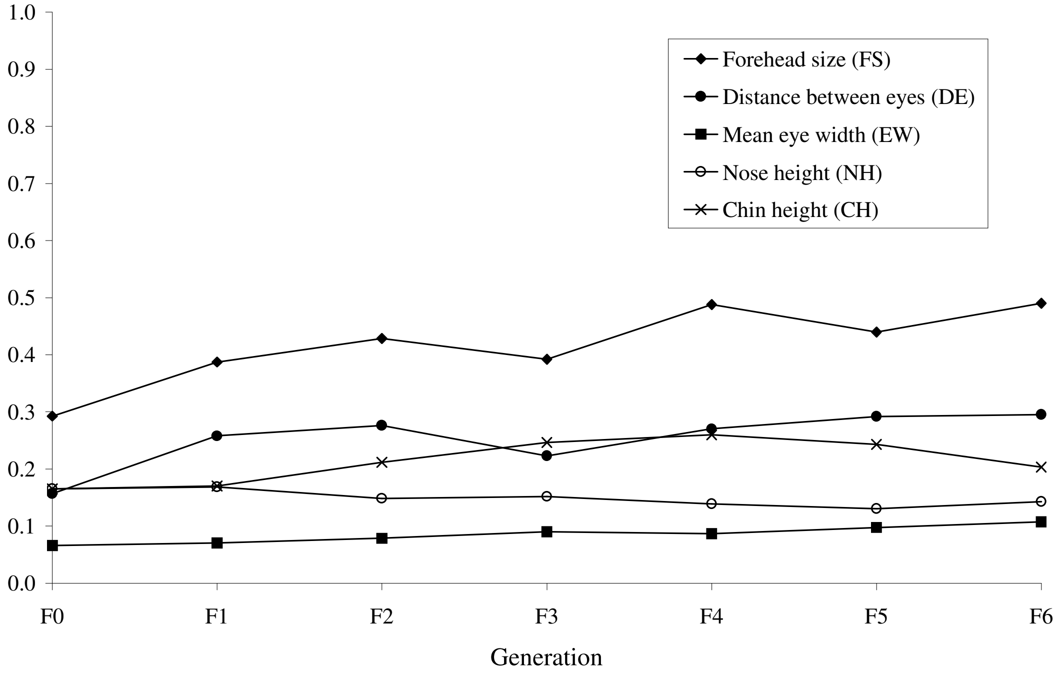

Figure 9.9 – Changes in various measures of neoteny with generation (Experiment 9c). Each data point is the mean measurement of all five chains.

Repeated measures ANOVAs with generation as a 6-level within-groups factor showed no significant effect of generation for any of the five measures of neoteny. Given that there was a certain amount of fluctuation in the measures with generation, it may be that although there is no progressive trend toward neoteny, there is a significant difference between the first and final generations in the direction predicted. A paired-samples t-test indeed showed that for the FS measure the final (F6) generation values were significantly greater than the first (F1) generation values ($t_{(4)}=2.91$, $p<0.05$), suggesting an increase in neoteny. This effect was not strong, however, and equivalent t-tests for the other measures of neoteny were not significant. The overall conclusion from Experiment 9c must therefore echo that of Experiments 9a and 9b in finding no significant overall tendency toward neoteny in the transmission of these bear faces.

Figure 9.10 – Composite bear whose facial dimensions match the mean dimensions of the final (sixth) generation bears of Experiment 9c.

9.6 GENERAL DISCUSSION

Chapter 9 used the transmission chain method to experimentally simulate the cultural evolution of the teddy bear, as documented by Hinde and Barden (1985). It was predicted that bear faces would become more neotenous as they are transmitted along chains of participants, just as teddy bears have become more neotenous over an 80 year period. However, neither Experiments 9a or 9b, which used a face-to-face method of transmission, nor Experiment 9c, which adopted a more controlled Bartlett-style laboratory method of transmission, found any robust evidence of an increase in neoteny with generation. Making the drawing task easier by removing the three dimensional snout, presenting a blank outline to keep the face size constant, and making the stimulus bear as un-neotenous as possible all failed to elicit the predicted effect.

At least four potential explanations can be suggested for this negative result. First, the participants in this study might not possess a preference for neotenous facial features. However, given the large number of studies listed in the Introduction (Section 9.2) that found significant correlations between measures of neoteny and judgements of attractiveness, across various cultures, stimuli and ages, this would seem unlikely. There is no reason to suspect that the participants who took part in this study are any different to the participants of those studies, or indeed to the teddy bear consumers responsible for Hinde and Barden's (1985) data.

Second, it may be that the transmission chain method is in some general sense not suitable for studying the cultural transmission of pictorial stimuli, and no significant changes can be expected regardless of the theoretical preference or bias in question. However, the fact that some of the measures *did* show significant linear trends in Experiment 9b, albeit not in the manner that was predicted, suggests that the method is indeed potentially useful. Bartlett (1932), Allport and Postman (1947) and Hall (1951) also presented several successful transmission chain results using pictorial stimuli (see Chapter 4).

Third, it may be that the participants were attempting to exhibit a preference for neoteny in their reproductions, but their lack of skill at drawing prevented the preference from being expressed. However, it is hard to see how the stimulus bear used in Experiment 9c (shown in Figure 9.8) could be made any easier to draw.

A final possibility is that although the participants do indeed possess a preference for neoteny, this particular preference does not affect the reproduction of pictures from memory. Perhaps the preference is exclusively perceptual, and is only exhibited when perceptual judgements are made, such as selecting a teddy bear or rating the attractiveness of a face. The active reconstruction of an image from memory, on the other hand, may be too far removed from this perceptual preference for any significant effect of neoteny to have been observed here.

These last two possibilities might be investigated by making the experimental procedure more passive and less reliant on actively drawing the faces. A computer program could generate a number of bear faces randomly varying in the dimensions measured above (FS, EW, NH, SH and DE), with the participant asked to select their favourite. The next participant in the chain would then be presented with a selection of bear faces with mean dimensions moved towards the values chosen by the previous participant. Repeating this process of artificial selection would allow the experimenter to test whether the mean dimensions of the bears gradually become more neotenous with generation, without relying on the drawing skills of the participants and more closely resembling the neotenous selection of real teddy bears as investigated by Hinde and Barden (1985). This design resembles the ‘artificial selection’ paradigm used by evolutionary biologists to detect the selection of biological traits (see Chapter 3).

CHAPTER 10 - DISCUSSION OF PART B

One of the main conclusions that was drawn from the literature review regarding work on cultural transmission in Chapter 4 was that Bartlett's (1932) transmission chain method constitutes an easily-implemented, potentially fruitful yet under-used means of empirically studying human cultural transmission. Hence the general aim of the following Chapters 5-9 was to demonstrate that this methodology can be successfully used for this purpose.

The specific aim of each chapter was to experimentally test for a different hypothesised bias in cultural transmission. Chapter 5 found evidence that social information is transmitted with greater accuracy and in greater quantity than equivalent non-social information, in line with evolutionary theories positing a social origin for human intelligence. Chapter 6 found evidence for a 'hierarchical bias' that acts to convert knowledge of everyday events from a low hierarchical level to increasingly higher hierarchical levels. Chapter 7 failed to find evidence for an indirect bias in which information from high status sources is transmitted with greater accuracy than the same information from low status sources. Chapter 8 failed to find evidence for an 'anthropomorphic bias' which predicts that animal behaviour is increasingly described in terms of human mental states and intentions. Finally, Chapter 9 failed to demonstrate that teddy bear faces are made increasingly neotenous during transmission, hence failing to reproduce the equivalent historical trend in actual teddy bears.

Overall, I feel that the general aim of Section B has been achieved, and the transmission chain method has been shown to be an effective means of experimentally studying human cultural transmission. Chapters 5 and 6 both demonstrated significant effects predicted by the respective hypothesised transmission biases. An important finding was the cumulative multiple-generation effect observed in Chapter 6, where only after a number of generations did the transformation from low- to high-levels of the hierarchy become evident. This effect would therefore not have been observed in a standard single-generation memory experiment, and illustrates the contribution of the transmission chain method in comparison to these more traditional methods. Although only two of the five hypotheses were upheld, a negative result does not mean that the methodology was invalid. In some cases there was perhaps a limitation of the precise design used, such as the reliance on drawing skill in Chapter 9 or the use of 'second-hand' verbal information in Chapter 7, although these limitations may be overcome by using a different form of the transmission chain method (see below). Hopefully future work using the transmission chain method will produce evidence of more biases and result in a rich body of empirical data concerning human cultural transmission.

The results of these empirical studies can be used to inform the wider theory of cultural evolution outlined in Part A. Indeed, Chapter 3 identified the experimental study of cultural transmission as an area which has been particularly neglected compared with the more well-developed theoretical work involving phylogenetic analyses or gene-culture coevolution modelling. On the basis of the above findings, we can speculate that at a population level (i.e. real-life society), information concerning third party social relationships should be more prevalent than non-social ('factual') information (Chapter 5), and information that describes events at a high hierarchical level should be more prevalent than information at a low hierarchical level (Chapter 6). Such phenomena remain to be explored, and more formal tests of these claims will be needed to provide definitive support. An informal example might be the much higher circulation of gossip magazines than factual journals (Table 10.1).

	Publication	**UK circulation per issue**
'Social'	Heat magazine	539,983
	OK! magazine	468,928
	Hello! magazine	323,591
'Non-social'	The Economist	153,184
	New Scientist	91,100
	The Spectator	48,004

Table 10.1 - UK circulation per issue (July-December 2004) of magazines that can informally be described as containing either 'social' or 'non-social' information (Source: www.abc.org.uk)

All of the biases tested here except for the indirect bias of Chapter 7 are what Richerson and Boyd (2005) call 'content-based' biases, in which "the structure of cognition makes some variants easier to learn and remember" (p. 69). The indirect bias, on the other hand, involves the adoption of a trait according to the characteristics of its source rather than its inherent characteristics (Boyd & Richerson, 1985; Richerson & Boyd, 2005). To date, theoretical models of cultural evolution have predominantly focused on indirect bias and the related 'frequency-dependent' bias (e.g. Boyd & Richerson, 1985) over content-based biases. Perhaps empirical studies such as those reported above might redress this imbalance.

Durham (1992) has further argued that content-based biases can either be the result of biological evolution and acquired genetically ('primary values') or the result of other culturally acquired information ('secondary values'). In some of the previous chapters I have explicitly classed the bias under investigation as at least to some degree a biologically evolved primary value (e.g. the social bias of Chapter 5 or the neoteny bias of Chapter 9), while in other cases I have remained agnostic with regards to the origin of the bias. As noted by Richerson and Boyd (2005, p. 72), however, this dichotomous primary-secondary distinction is somewhat simplistic and the true origins of the biases tested here are likely to involve a complex interaction between biologically and culturally acquired information. Generally, it is difficult without further developmental, cross-cultural or comparative evidence, which is beyond the scope of this thesis, to draw specific conclusions regarding the relative influence of these two sources. Even where comparative (e.g. Chapter 5) or developmental (e.g. Chapter 9) evidence does suggest a biological origin, individual or social learning may still play an important role.

A number of general methodological lessons can be learned from the above studies. First, the within-chain transmission chain design, in which all of the types of material to be compared (e.g. both social and non-social) are transmitted along each chain, is more effective than a between-chain design, in which each chain transmits only one type of material (e.g. separate 'social' chains vs. 'non-social' chains) and different chains are compared. This is because random between-chain differences are often large, and the within-chain design eliminates this error. This was specifically demonstrated by comparing Chapter 5 with Mesoudi (2002). While Mesoudi (2002) used a between-chain design and found equivocal evidence for a social bias, Chapter 5 found much stronger evidence for the same hypothesis using a within-chain design. Consequently, the experiments reported here adopted the within-chain design where appropriate. Similarly, where Mesoudi (2002) and previous transmission chain studies (e.g. Bartlett, 1932) used a distractor task between reading and recalling the stimulus, the experiments reported here did not use a distractor, as suggested in Section 4.2.4. Distractor tasks may, therefore, be unnecessary except where specifically theoretically justified. Also as suggested in Section 4.2.4, Kintsch's (1974) propositional analysis was successfully used to divide the recalled texts into constituent units of meaning, allowing quantitative statistical analyses to be performed. Blind second coders showed high agreement on the propositional analyses carried out in Chapters 5 and 6, increasing confidence in its validity.

Chapters 5-9 also generated a number of suggestions for extending or modifying the transmission chain method. One possibility for the failure in Chapter 7 to find an effect of status was that the indirect bias does not extend to second-hand written verbal material. It would be useful in this case and more generally to compare the transmission of written material as in Chapters 5-9 with face-to-face oral transmission. There may be important non-verbal interpersonal cues that affect transmission. Also arising from Chapter 7, it would be useful to study the transmission of behaviour rather than verbal material. Whiten and colleagues are currently running transmission chain studies in which children transmit different methods of opening 'artificial fruits'. Perhaps the behaviours studied by Bandura in his social learning experiments (e.g. Bandura *et al.*, 1963) could also be transmitted along chains of participants to examine their longer-term persistence. Finally, Chapter 9 gave rise to the idea of an 'artificial selection' paradigm in which each successive participant chooses one of a number of variants on the basis of some experimental criteria. The stimuli presented to each new participant would then be shifted in the direction of the previous participant's preference, and the long-term changes in the stimuli tracked. This method was also proposed in Chapter 3, drawing on similar artificial selection experiments in evolutionary biology. As argued in that chapter, there are a number of possibilities for importing methods and theories from biology into the empirical study of cultural transmission. In Part C I will turn to an area which has already heavily borrowed from evolutionary biology with some success: the mathematical modelling of gene-culture coevolution.

Part C - Gene-culture coevolution

In Part C we move from experimental simulations of cultural transmission to mathematical simulations of gene-culture coevolution, in which genes and culture are modelled as separate but interacting inheritance systems. Part C uses two mathematical modelling approaches - the population genetics based methods of Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) and an agent-based technique (Epstein & Axtell, 1996; Kohler & Gumerman, 2000) - to explore the gene-culture coevolution of genetic and cultural influences on mating behaviour, focusing on recent anthropological data concerning ‘partible paternity’ beliefs (where children can have more than one ‘biological’ father). This approach constitutes another branch of Figure 3.1 (equivalent to theoretical population genetics), and another contribution to an overall evolutionary science of culture.

CHAPTER 11 - PARTIBLE PATERNITY AND THE EVOLUTION OF HUMAN MATING BEHAVIOUR

11.1 ABSTRACT

Recent anthropological work has shown that certain Lowland South American societies hold beliefs in 'partible paternity', the idea that children may have more than one 'biological' father. This contrasts with Western beliefs in singular paternity, and biological reality, where children may have only one true father. Here, mathematical models are used to explore the coevolution of paternity beliefs and the genetic variation underlying human mating behaviour. A gene-culture co-evolutionary model (Model 1) found that populations exposed to a range of selection regimes typically converge on one of two simultaneously stable equilibria, one in which the population is monogamous and holds beliefs in singular paternity, and the other in which the population is polygamous and holds beliefs in partible paternity. A second agent-based model (Model 2), with alternative assumptions about the formation of mating consortships, broadly replicated this finding, but only for populations with a strongly female-biased sex ratio. This is consistent with evidence for high adult male mortality in the region. The analyses suggest that beliefs about paternity may have significantly affected the evolution of human mating behaviour, generating divergent selection that helps to explain variation in mating behaviour and paternity beliefs among adjacent South American societies.

11.2 INTRODUCTION

In our society it is frequently taken for granted that every child has one, and only one, true biological father. Indeed, this culturally transmitted belief in what is known as 'singular paternity' coincides with scientific evidence that only one sperm cell can fertilise an ovum, and hence children inherit genes from only one male (and one female) parent. However, this match between our culturally transmitted folk beliefs regarding paternity and the scientific evidence regarding conception may just be a lucky accident. The Western folk belief in singular paternity has a long history: such a belief is evident in the writings of Aristotle, is enshrined in a 451 B.C. Roman law, and is an assumption that runs through the Bible (Beckerman & Valentine, 2002a, pp. 1-2). Scientific evidence for the one-sperm theory of fertilisation, however, was not obtained until the 1870s (Beckerman & Valentine, 2002a, p. 2).

This dissociation between cultural belief on the one hand and scientific reality on the other has recently been highlighted further by anthropological studies of Lowland South American societies. Beckerman and Valentine (2002) have described how members of certain South American societies, such as the Barí of Venezuela (Beckerman *et al.*, 1998; Beckerman *et al.*, 2002), hold beliefs not in singular paternity but in 'partible paternity', the idea that children can have more than one 'biological' father. Conception and foetal growth are seen to result from the accumulation or other combined action of more than one man's semen, and consequently a significant proportion of children in these populations acknowledge 'secondary fathers', i.e. men who slept with their mothers around the time of their conception or during pregnancy. This belief is illustrated by the following quotation concerning one of these South American societies, the Kulina of western Brazil:

> "Conception is a process rather than an event for the Kulina. . in which semen accumulates in a woman's womb until it reaches a large and dense enough bolus to form a fetus. [This process] leaves open the possibility that more than one man may contribute to the seminal growth of a fetus, and thus two or more men will be 'fathers' to the child. Among the Kulina this possibility was commonly a fact." (Pollock, 2002, p. 52)

This belief in partible paternity contrasts with the beliefs of other ecologically similar South American societies (such as the Warao of Venezuela: Heinen & Wilbert, 2002), as well as the majority of the rest of the world, whose inhabitants believe in singular paternity.

Partible paternity is not a trivial, rare or inconsequential belief. It is observed in numerous societies, including the Barì, Kulina, Aché, Yanonami, Canela, Cashinahua, Ese Eja, Mehinaku, Ye'kwana, Mebengokre and Xoclen, which are located across South America, in modern day Brazil, Peru, Venezuela, Paraguay, Bolivia and Colombia (Beckerman & Valentine, 2002b). It also significantly affects these people's lives. The sexual division of labour practised by these societies means that males go out hunting and provide valuable animal proteins and animal fats. If a child has additional fathers as a result of the partible paternity belief, then each one of these fathers provisions the child with extra food. This provisioning occurs directly to the child itself or indirectly to the child's mother when the child is in the womb. Consequently, Bari children with two fathers have a significantly greater chance of survival to age 15 than children with only one father (Beckerman *et al.*, 1998; 2002).

Similarly, Hill and Hurtado (cited in Beckerman & Valentine, 2002a, p. 7) report that 85% of Ache children with two fathers survived to age 10 compared with just 70% of children with one father. It is important to note that there are no known ecological, demographic or linguistic differences between partible societies and neighbouring singular paternity societies, so these survivorship differences are not simply a reflection of one of these factors, rather they seem to be due to the different paternity beliefs.

The existence of partible paternity societies not only highlights the potential dissociation between culturally transmitted folk beliefs and biological reality, but also challenges a number of fundamental assumptions held by the Western scientific establishment. In particular, sociobiology and evolutionary psychology hold that mating behaviour should be driven by essentially genetic interests. Steven Pinker, for example, writes that, "Sexual jealousy is found in all cultures…In most societies, some women readily share a husband, but in no society do men readily share a wife." (Pinker, 1997, p. 488), while E.O. Wilson states that, "men are predicted to stress exclusive sexual access and guarantees of paternity" (Wilson, 1998, p. 170). If it is the case that men who believe in partible paternity do not conform to such predictions, then these assumptions will have to be reconsidered.

The existence of partible paternity societies raises a number of questions accessible to theoretical investigation: (1) How does a belief in partible paternity affect the biological fitness of males and females? (2) What impact do such beliefs have on human mating systems? (3) Can a (partible paternity) belief spread that has fitness benefits for one sex (females) and is disadvantageous to the other (males)? (4) How can two such distinct alternative beliefs about paternity persist when they are likely to have such direct effects on biological fitness? (5) More generally, can a consideration of cultural variation in beliefs about paternity shed light on the evolution of human mating systems?

The present study addressed these issues by mathematically modelling the coevolution of paternity beliefs and the genetic variation underlying human mating behaviour. Two alternative mathematical modelling techniques were used. Model 1 employed the methods of gene-culture coevolution (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Feldman & Cavalli-Sforza, 1976); in Model 1a assuming vertical cultural transmission and in Model 1b assuming oblique cultural transmission, both assuming random mating from an infinite population. Model 2 adopted an agent-based modelling approach (Epstein & Axtell, 1996; Kohler & Gumerman, 2000), which featured more realistic non-random mating rules and demographic factors.

11.3 MODEL 1 - GENE-CULTURE COEVOLUTION MODEL

Gene-culture coevolution (or dual inheritance) models (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Feldman & Cavalli-Sforza, 1976; Laland, Kumm, & Feldman, 1995) represent extensions of population genetics models that incorporate both genetic and cultural inheritance. As well as tracking changes in allele frequencies in the gene pool in successive generations, gene-culture coevolution models also track changes in cultural traits in the cultural pool. Hence each individual is described in terms of their ‘phenogenotype’ (the combined package of their genes and cultural traits), and transmission rules for both genes and culture are specified. Model 1 employed gene-culture coevolution methods to explore the interaction of the genetic bases of mating behaviour and culturally transmitted paternity beliefs, in Model 1a assuming vertical cultural transmission and in Model 1b assuming oblique cultural transmission.

11.3.1 Model 1a - Vertical Cultural Transmission

11.3.1.1 Genetic variation

We assume that genetic variation either now or in the past to some degree underlies variation in human mating behaviour. This genetic variation might act, along with environmental factors, via hormonally controlled emotional states such as ‘jealousy’ or ‘faithfulness’ (although the precise proximate mechanisms are not of primary concern). This is consistent with findings that monogamous behaviours in voles, such as pair-bond formation, are facilitated by transfer of a specific gene into the ventral forebrain (Pitkow *et al.*, 2001). In humans, Cherkas *et al.* (2004) have reported a study of 1600 female twin pairs in which the frequency of infidelity and the number of sexual partners were both found to be under moderate genetic influence (around 40% heritability).

For simplicity, we assume that individuals’ mating behaviour is affected by variation at a single haploid genetic locus (**M**), at which we posit two alleles, *M* and *m*. *M* individuals are more prone towards monogamy and do not actively seek extra mates beyond a monogamous pairing, while *m* individuals are more prone towards polygamy and do seek extra mates. While humans are obviously not haploid, a haploid model has the advantage of greater tractability, and a diploid model has also been analysed which gives equivalent results.

11.3.1.2 Cultural variation

We assume that individuals hold one of two discrete, mutually exclusive beliefs concerning paternity. *Bpp* individuals hold beliefs in partible paternity, while *Bsp* individuals hold beliefs in singular paternity. In Model 1a, vertical transmission was assumed, where these beliefs are assumed to be inherited from parent to offspring. This assumption is consistent with several studies that have found a predominant role for vertical transmission of beliefs in pre-industrial societies similar to the Barí (e.g. Aunger, 2000a; Guglielmino *et al.*, 1995; Hewlett & Cavalli-Sforza, 1986; Hewlett *et al.*, 2002), in some cases specifically for traits regarding mating behaviour. However, the extent of vertical cultural transmission is contentious (Boyd, personal communication; Richerson & Boyd, 2005) so this assumption is relaxed by considering the case of oblique cultural transmission in Model 1b and conformist cultural transmission in Model 2.

11.3.1.3 Phenogenotypes

Two genotypes and two cultural beliefs give the four possible combinations (henceforth ‘phenogenotypes’) shown in Table 11.1. These phenogenotypes are allotted frequencies of *x1-x4* in males and *y1-y4* in females.

PHENOGENOTYPE	**FREQUENCY**	
	Males	**Females**
MBpp	*x1*	*y1*
MBsp	*x2*	*y2*
mBpp	*x3*	*y3*
mBsp	*x4*	*y4*

Table 11.1 - Phenogenotype frequency notation

Mating cluster	**Mating behaviour**
1 male x 1 female	Monogamy
1 male x 2 females	Polygyny
2 males x 1 female	Polyandry
2 males x 2 females	Polygynandry

Table 11.2 – Definitions of patterns of mating behaviour

11.3.1.4 Mating behaviour

Table 11.2 specifies how different combinations of males and females join to form 'mating clusters' of two, three or four individuals. For simplicity, each individual is limited to a maximum of two mates, which is also the common upper limit on mate numbers in the societies studied by the contributors to Beckerman and Valentine (2002b). Note that we assume that mating behaviour across a population can be characterised by the frequencies of individuals behaving monogamously, polygynously, polyandrously and polygynandrously, and distinguish between the mating system as described by this collective activity across the population (which is termed the *demographic mating system*, to which Table 11.2 refers) and the *institutionalised mating system* which specifies the legal or socially sanctioned forms of mating behaviour (e.g. Murdock, 1967). A similar distinction was made by Low (2003), who used the term 'socially monogamous' to describe societies with normative rules limiting a person to a single spouse at a time, and the term ‘genetically monogamous’ to describe populations in which the variance in reproductive success of men and women is approximately equal.

Hence, different combinations of males and females linked by sexual activity are defined as categories of ‘mating behaviour’ according to Table 11.2. One male and one female constitute monogamy; one male and two females constitute polygyny; one female and two males constitute polyandry; and two males and two females constitute polygynandry. Table 11.3 specifies how individuals’ genotypes determine the formation of the mating clusters shown in Table 11.2. In row r1 of Table 11.3, both of the initial mates (Male 1 and Female 1) are *M* and so neither will seek out extra mates. This pair will therefore remain monogamous. In row r2, the male is *m* and so seeks out another female. This second female (Female 2) is here *M*, and so will not in turn seek out an extra male beyond Male 1. This combination thus constitutes polygyny. In row r3 the genotypes of the initial pair are reversed, with the *m* female seeking out a second male (Male 2) who is *M* and does not seek out a second female. This results in polyandry. Rows r4-r11 show all of the cases in which at least one of the initial mating pair are *m* and their second mate is also *m*. This second mate therefore selects a further (fourth) mate, resulting in polygynandry.

	Genotypes of mating individuals				**Mating behaviour**
	Male 1	Female 1	Male 2	Female 2	
r1	*M*	*M*			Monogamy
r2	*m*	*M*		*M*	Polygyny
r3	*M*	*m*	*M*		Polyandry
r4	*M*	*m*	*m*	*M*	Polygynandry
r5	*M*	*m*	*m*	*m*	
r6	*m*	*M*	*M*	*m*	
r7	*m*	*M*	*m*	*m*	
r8	*m*	*m*	*M*	*M*	
r9	*m*	*m*	*M*	*m*	
r10	*m*	*m*	*m*	*M*	
r11	*m*	*m*	*m*	*m*	

Table 11.3 - The formation of mating clusters as determined by genotype in Model 1

11.3.1.5 Fitness

In order to minimise the number of parameters that need to be tracked in the analysis, and hence limit the complexity of the model, the average fitness of the entire mating cluster is specified rather than giving different fitness terms to individual males and females. (Note that Model 2 below specifies individual fitness values.) Accordingly, Table 11.4 gives the fitnesses, w_1-w_4, of each mating cluster. These parameters represent the combined fitness of all females within a cluster, with separate terms for females who hold *Bpp* and *Bsp* beliefs (w_{3pp}, w_{3sp}, w_{4pp} and w_{4sp}). Each female's fitness is expressed as deviations from a baseline fitness of 1. Taking the *Bpp* terms first, the sole fitness parameter is s ($0<s<1$), defined as the fitness benefit associated with the help of one male. Monogamous females, who receive the help of a single male, have a fitness of ($1+s$). Polygynous females must share a male with another female, giving an average fitness of $(1+s/2)$, although as there are two females in polygynous clusters this is doubled to give $2(1+s/2)$. Polyandrous females receive the help of two males so have a fitness of $(1+2s)$. Finally, polygynandrous females receive the help of two males but must share this help with another female, giving an average of one male's help, i.e. $(1+s)$. This is doubled because polygynandrous clusters contain two females, giving $2(1+s)$. This parameterisation is broadly consistent with observed patterns of help and its associated fitness benefits in animal and human societies (Beckerman & Valentine, 2002b; Davies, 1992).

Mating cluster	***Bpp***		***Bsp***	
Monogamy	w_1	$(1 + s)$	w_1	$(1+ s)$
Polygyny	w_2	$2(1+ s/2)$	w_2	$2(1+ s/2)$
Polyandry	w_{3pp}	$(1 + 2s)$	w_{3sp}	$(1+ (1+a)s - r)$
Polygynandry	w_{4pp}	$2(1+ s)$	w_{4sp}	$2(1+ s - r)$

Table 11.4 - Mating cluster fitness terms for Model 1

Females who hold the *Bsp* belief have the same basic fitness terms as *Bpp* females but with two additional parameters. First, r ($0<r<1$) is defined as the fitness cost to polyandrous and polygynandrous *Bsp* females of infanticide and/or injury from male aggression specifically motivated by jealousy or emotional states related to sharing a female. It is assumed that this fitness cost only applies to *Bsp* societies, as *Bpp* males believe that paternity is shared and have no cause for aggression (Beckerman *et al.*, 1998; Beckerman & Valentine, 2002b). In contrast, a significant effect of aggression has been observed in both *Bsp* human societies and non-human species engaged in polyandrous and polygynandrous behaviour (Daly & Wilson, 1988; Davies, 1992).

The second *Bsp* parameter is *a* ($0<a<1$), which parameterises 'paternity confusion'. This parameter determines how cooperative the polyandry is, and hence applies only to polyandrous individuals. When $a=1$, there is maximum paternity confusion; both males believe that the offspring is theirs, and so both help by providing resources to females at a maximum rate. This is a case of fully cooperative polyandry. The female hence receives the full help of both males, i.e. $(1+a)s = 2s$. Conversely, when *a* is at a minimum ($a=0$), there is no paternity confusion, and only the male who is sure of paternity will help. Hence the female will receive only one male's help, i.e. $(1+a)s = s$. Note that this is equivalent to monogamy. The parameter *a* therefore permits a continuum of polyandry from fully cooperative to the equivalent of monogamy. Again, this does not apply to *Bpp* societies, as males will always assume paternity to be fully shared and always help at a maximum rate.

11.3.1.6 Cultural bias

We assume that different phenogenotype matings have different probabilities of producing *Bpp* or *Bsp* offspring. Certain phenogenotypes may suffer some form of 'internal conflict' or 'cognitive dissonance' biasing them towards more compatible beliefs (although again the exact proximate mechanisms are not of primary concern). For instance, individuals genetically predisposed to monogamy might find *Bsp* more attractive than *Bpp*, as the latter belief holds that children are formed through the accumulated action of more than one man's semen, specifically conflicting with monogamous mating.

The specific nature of the bias is summarised in Tables 11.5 and 11.6. We assume that a belief in *Bsp* is more compatible with predispositions towards monogamy than predispositions towards polygamy, so the offspring of *M* x *M* matings are biased towards adopting *Bsp* with a probability *b1*, where $0<b1<0.25$ (Table 11.5). Similarly, we assume the offspring of polygamous *m* x *m* matings are biased towards adopting *Bpp* with a probability *b2*, where $0<b2<0.25$ (Table 11.6). Where the genotypes of the parents differ, we assume that either no bias operates or that parent-specific biases cancel each other out, giving an equal chance of the offspring being either *Bpp* or *Bsp* (if parents differ in their beliefs). Note that the upper limit of 0.25 was required to ensure that total phenogenotype frequencies did not exceed 1. Also note that the mating pair in Table 11.6 will (as specified in Table 11.3) be part of a larger polygynandrous mating cluster.

		Offspring	
Father (*M*)	**Mother (*M*)**	***Bpp***	***Bsp***
Bpp	*Bpp*	1	0
Bsp	*Bpp*	0.5 - *b1*	0.5 + *b1*
Bpp	*Bsp*	0.5 - *b1*	0.5 + *b1*
Bsp	*Bsp*	0	1

Table 11.5 – Cultural bias *b1* ($0<b1<0.25$) favours *Bsp* among the offspring of *M* x *M* parents

		Offspring	
Father (*m*)	**Mother (*m*)**	***Bpp***	***Bsp***
Bpp	*Bpp*	1	0
Bsp	*Bpp*	0.5 + *b2*	0.5 - *b2*
Bpp	*Bsp*	0.5 + *b2*	0.5 - *b2*
Bsp	*Bsp*	0	1

Table 11.6 – Cultural bias *b2* (0<*b2*<0.25) favours *Bpp* among the offspring of *m* x *m* parents

11.3.1.7 Recursions

Appendix D.1 shows the full set of 148 phenogenotype mating combinations (rows r1-r148) based on the basic 11 genotype combinations specified in Table 11.3. Standard haploid rules of inheritance and the biases specified in Tables 11.5 and 11.6 were used to calculate the probabilities that each of these mating clusters will give rise to each phenogenotype in the next generation. The offspring phenogenotype frequencies for each parental mating behaviour are given in columns c1-c14. The frequency of each of the 148 mating clusters occurring is given in column c0, assuming that each mating cluster occurs with a probability equal to the product of each of its constituent members. Hence mating was random apart from the restriction imposed by the mating rules in Table 11.3 (e.g. two *m* individuals cannot be monogamous).

The frequency of each phenogenotype in the next generation can be calculated by summing down the relevant columns of Appendix D.1 (c1-c14) and weighting by the probability that each mating occurs (c0 of Appendix D.1), the fitness associated with that mating system (from Table 11.4) and the sex ratio (*SR* for males and 1-*SR* for females, where *SR* is defined as the proportion of the population that is male).

For example, the frequency of *MBpp* males in the next generation (*x1'*) is given by:

(w_1 Óc0c1 + w_2 Óc0c3 + w_{3pp} Óc0c7 + w_{4pp} Óc0c11) *SR*/W_m.

That is, for each row (r1-r148) we multiply the probability that the mating will give rise to a *MBpp* child (c1, c3, c7 and c11 in Appendix D.1) by the probability that the mating will occur (c0), and weight by the fitness of that mating cluster (monogamy (w_1) for c1, polygyny (w_2) for c3, polyandry (w_{3pp}) for c7 and polygynandry (w_{4pp}) for c11). Finally, we multiply the entire expression by the proportion of males (*SR*) and divide by W_m, the mean fitness of the males (a normalising constant, that ensures that the total frequency of all individuals does not differ from 1; W_f is the equivalent term for females). The full system of recursions is:

x1' = (w_1 Óc0c1 + w_2 Óc0c3 + w_{3pp} Óc0c7 + w_{4pp} Óc0c11) *SR*/ W_m,
x2' = (w_1 Óc0c2 + w_2 Óc0c4 + w_{3sp} Óc0c8 + w_{4sp} Óc0c12) *SR*/ W_m,
x3' = (w_2 Óc0c5 + w_{3pp} Óc0c9 + w_{4pp} Óc0c13) *SR*/ W_m,
x4' = (w_2 Óc0c6 + w_{3sp} Óc0c10 + w_{4sp} Óc0c14) *SR*/ W_m,

y1' = (w_1 Óc0c1 + w_2 Óc0c3 + w_{3pp} Óc0c7 + w_{4pp} Óc0c11) (1-*SR*)/$W_{f,}$
y2' = (w_1 Óc0c2 + w_2 Óc0c4 + w_{3sp} Óc0c8 + w_{4sp} Óc0c12) (1-*SR*)/ W_f,
y3' = (w_2 Óc0c5 + w_{3pp} Óc0c9 + w_{4pp} Óc0c13) (1-*SR*)/ W_f,
y4' = (w_2 Óc0c6 + w_{3sp} Óc0c10 + w_{4sp} Óc0c14) (1-*SR*)/ W_f,

11.3.1.8 Analysis

The system of recursions has been subject to extensive numerical analysis. For each set of parameter values, at least 500,000 generations were run from each of 121 systematically varied starting frequencies of *M*/*m* and *Bsp*/*Bpp* (although equilibria were typically reached in less than 50 generations: see below). The parameter values were in turn systematically varied across a range of biologically plausible values of each (for *s* and *r*: 0, 0.001, 0.01, 0.05, 0.1, 0.2, 0.25; for *a*: 0, 0.5, 0.75, 1.0; for *b1* and *b2*: 0, 0.05, 0.1, 0.15, 0.2, 0.25; and for *SR*: 0.25, 0.4, 0.5, 0.6, 0.75). Each parameter was varied both in isolation (i.e. where all other parameters are not operating) and at each value of every other parameter.

11.3.1.9 Results and Discussion

Figure 11.1 explains the format of the results diagrams presented in subsequent figures. Figure 11.1a shows the phenogenotype space, in which the frequencies of alleles *M* and *m* are plotted on the vertical axis and the frequencies of cultural traits *Bsp* and *Bpp* are plotted on the horizontal axis. Fig 11.1b shows one example simulation from the centre of the phenogenotype space (*M*=*m*=*Bsp*=*Bpp*=0.5). In this case, the population moves from the central starting point to an equilibrium at *MBsp*. Hence a line is drawn from the centre to *MBsp*, which is marked with a circle. Fig 11.1c shows all 121 starting frequencies from which simulations were run. In the subsequent figures, lines are drawn from each of these 121 starting frequencies to equilibrium points (solid lines or circles). The arrows surrounding the graphs indicate the direction of selection. Crosses indicate points of unstable equilibria, while dashed lines represent lines of unstable equilibria.

Figure 11.1 - The format of the outputs. Fig 11.1a shows the phenogenotype space, with *M*/*m* on the vertical axis and *Bsp*/*Bpp* on the horizontal axis. Fig 11.1b shows one example simulation from the centre of the phenogenotype space (*M*=*m*=*Bpp*=*Bsp*=0.5). In this case, the population moves from the centre to an equilibrium at M*Bsp*, which is marked with a circle. Fig 11.1c shows all 121 starting frequencies from which simulations were run.

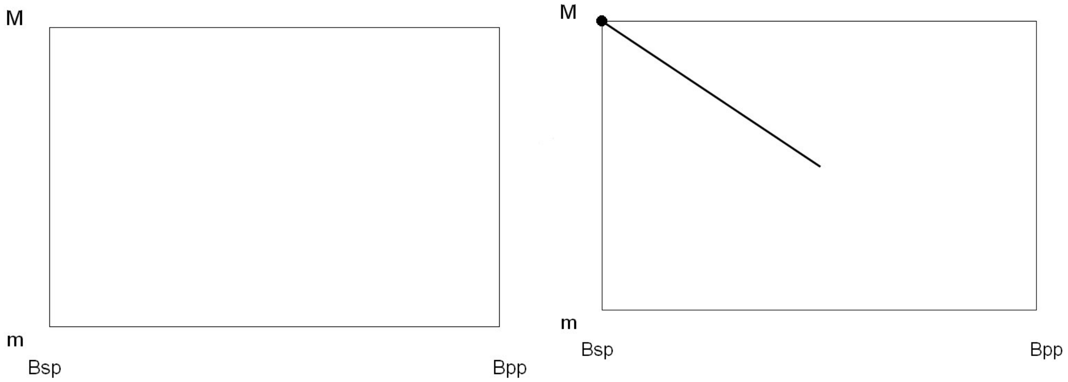

Fig 11.1a - The phenogenotype space

Fig 11.1b - A population moves from the centre to equilibrium at M*Bsp*

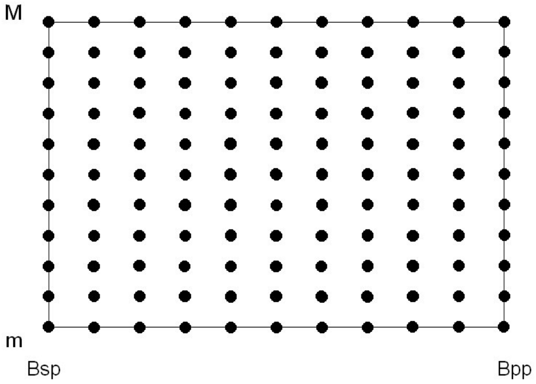

Fig 11.1c - All 121 starting points

Figure 11.2a shows the behaviour of Model 1a when no selection or bias in cultural transmission is acting (*s*=*r*=*b1*=*b2*=0, a=1, *SR*=0.5). Any population starting above the line *M*=0.12 (approx.) undergoes selection for *M* and converges on the line

$M=1$. Any population starting below the line $M=0.12$ undergoes selection for m and converges on the line $m=1$.

Figure 11.2 - Illustrative outputs from Model 1a with no parameters acting (Fig 11.2a) and the individualised effects of s (Fig 11.2b) and r (Fig 11.2c).

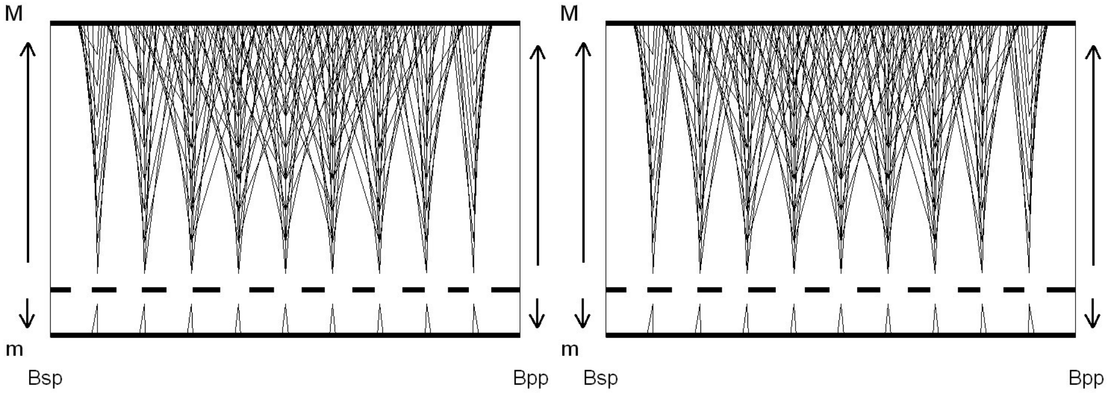

Fig 11.2a - No parameters
($s=r=b1=b2=0$, a=1, $SR=0.5$)

Fig 11.2b - The effect of s
($s=0.1$, $r=b1=b2=0$, a=1, $SR=0.5$)

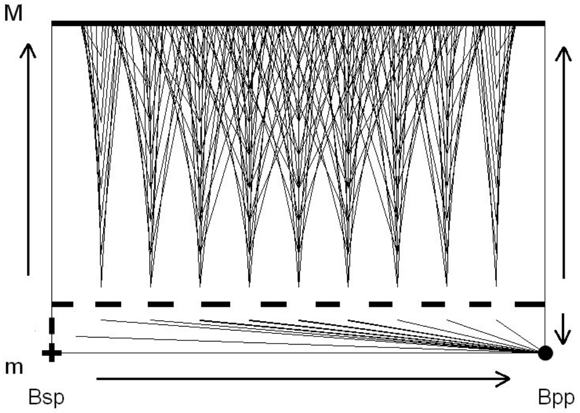

Fig 11.2c - The effect of r
($r=0.01$, $s=b1=b2=0$, a=1, $SR=0.5$)

Selection for M predominates because, under the assumption of random mating, the fewer individuals there are in a cluster the more likely it is to occur. Hence monogamy (2 individuals) is more likely to occur than polygyny (3 individuals), polyandry (3 individuals) and polygynandry (4 individuals). This can be seen in

Appendix D.1, where the frequency of each monogamous cluster (column c0, rows r1-r4) is the product of two terms (e.g. x1y1), each polyandrous/polygynous cluster (c0, r5-r20) is the product of three terms (e.g. x3y1y2) and each polygynandrous cluster (c0, r21-r148) is the product of four terms (e.g. x1y3x3y1). This multiplicative effect outweighs the additive numerical advantage of polygynandry (128 possible mating combinations) and polygyny/polyandry (8 combinations each) over monogamy (4 combinations). This random mating assumption therefore generates selection for monogamy and hence *M* (N.B. in Model 2 the validity of this assumption is addressed).

Where starting populations initially have a large majority of *m* (where *M*<0.12), we see selection for *m*. This is because of the fitness advantage of polygynandry over monogamy, primarily the fact that polygynandrous clusters have twice the females and hence produce twice the offspring of monogamous clusters (Table 11.4: 2(1+*s*) vs. (1+*s*)). When the fitness of polygynandry is not doubled there is no selection for *m*.

Figure 11.2a also shows fluctuation in the *Bsp*/*Bpp* dimension, although there is no systematic selection for either *Bsp* or *Bpp*. This is due to the manner in which beliefs are inherited within clusters, and is discussed further in relation to Model 1b below. Figure 11.2b shows the effect of the fitness benefit to a female of the help of one male (*s*>*0*). This produces an identical result to Figure 11.2a, indicating that *s* does not affect the position of these equilibria. This is because the factors discussed previously causing selection of *M*/*m* (the random mating assumption and the doubling of polygynandrous fitnesses) outweigh any effect of *s* in the *M*/*m* dimension, while the *s* parameter is identical for both *Bsp* and *Bpp* individuals so does not affect the end *Bsp*/*Bpp* frequencies.

Figure 11.2c shows the effect of *r*, the fitness cost of male aggression to *Bsp* believers, which causes selection for *Bpp* in regions where $M<0.12$. Combined with the selection for *m* in this region seen in Figures 11.2a and 11.2b, this results in selection for *mBpp*. This selection for *Bpp* occurs because *r* imposes a cost on *Bsp* individuals, and only occurs in this region because *r* only affects polyandrous and polygynandrous clusters which will be partly or entirely *m*. Monogamous (*M* x *M*) clusters, which dominate above this line, will be unaffected by *r*.

Finally, *a* had no observable effect on the dynamics of the model, and is not shown in the figures or discussed further (in all future figures, $a=1$). This is because the populations shown in Figure 11.2 rapidly become either entirely monogamous or entirely polygynandrous (often in less than 50 generations: see below), and *a* only affects polyandrous matings.

Figure 11.3 shows the effect of the cultural biases *b1* and *b2*. When *b1* is operating ($b1=0.05$: Figure 11.3a) we see selection for *Bsp* from starting conditions where $M>0.12$. This is to be expected given that *b1* promotes *Bsp* in monogamous *M* x *M* matings (Table 11.5). Figure 11.3b shows that *b2* ($b2=0.05$) causes selection for *Bpp* from starting conditions where $M<0.12$. Again, this is to be expected given that *b2* promotes *Bpp* in polygamous *m* x *m* matings (Table 11.6). Note that *b2* has the same effect as *r* shown in Figure 11.2c, although for different reasons.

Figure 11.3 - Individualised effects of *b1* (Fig 11.3a) and *b2* (Fig 11.3b) in Model 1a.

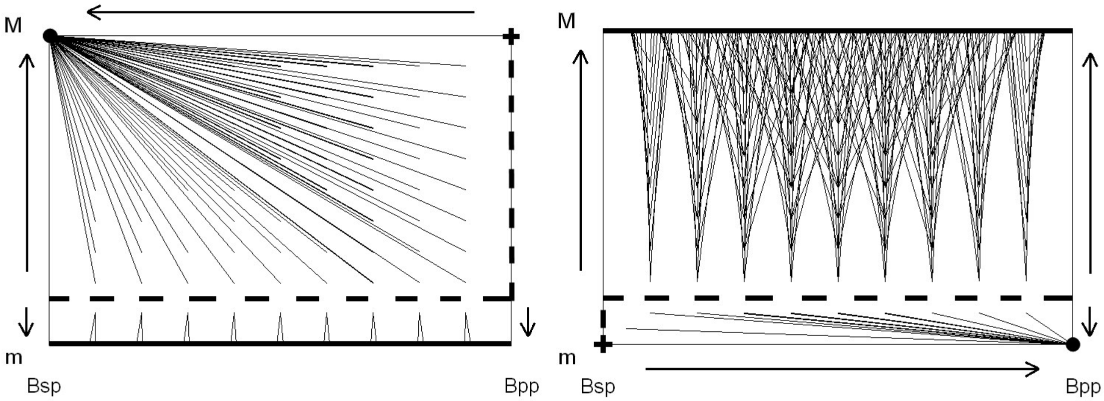

Fig 11.3a - The effect of *b1* (*b1*=0.05, *s*=*r*=*b2*=0, *SR*=0.5)

Fig 11.3b - The effect of *b2* (*b2*=0.05, *r*=*b1*=0, *SR*=0.5)

Figure 11.4a shows all of the previously analysed parameters acting in concert (*s*=0.1, *r*=0.01, *b1*=0.1, *b2*=0.05, *SR*=0.5). Populations in Figure 11.4a converge on one of two equilibria: the *MBsp* equilibrium from starting frequencies with *M*>0.12, and the *mBpp* equilibrium from starting frequencies with *M*<0.12.

These parameter values (*s*=0.1, *r*=0.01, *b1*=0.1, *b2*=0.05) constitute our best approximation of biological reality (N.B. the sex ratio is discussed in more detail below and in Model 2). Estimates of viability deficits caused by jealous aggression in western (Daly & Wilson, 1988) and pre-industrial societies (Hill & Hurtado, 1996; Hill & Kaplan, 1988) suggest that *r* will range between 1 and 3 orders of magnitude smaller than *s*. Additionally, *b1* is assumed to be stronger than *b2* because a belief in

Bpp, in which the formation of a foetus requires the accumulation of semen from more than one man, is specifically incompatible with monogamy. A belief in *Bsp*, on the other hand, does not specifically prohibit polygamy, although may promote it. We would therefore expect *Bsp* to be favoured in monogamous *M* x *M* matings (the effect of *b1*) more strongly than *Bpp* is favoured in polygynandrous *m* x *m* matings (the effect of *b2*).

Figure 11.4 - The combined effect of all parameters in Model 1a (Fig 11.4a) and the effect of skewing the sex ratio (Fig 11.4b)

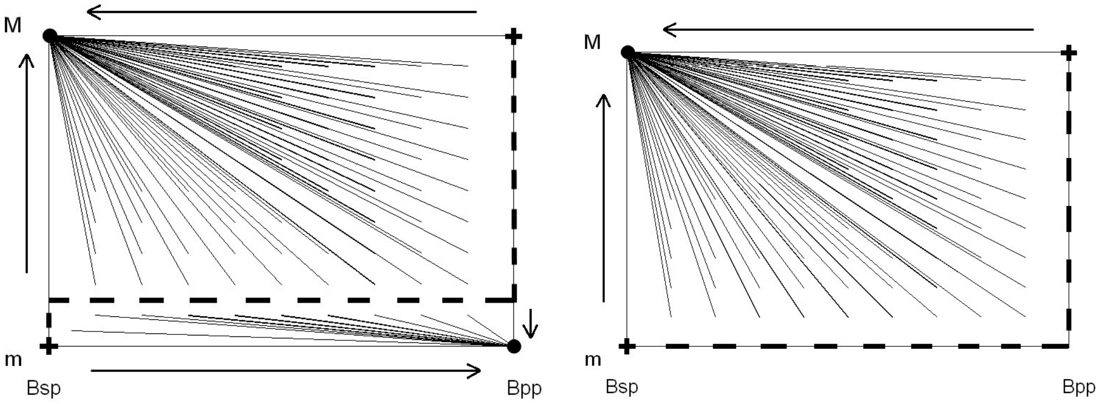

Fig 11.4a - All parameters (s=0.1,r=0.01,$b1$=0.1, $b2$=0.05,SR=0.5)

Fig 11.4b - The effect of *SR* (s=0.1,r=0.01,$b1$=0.1, $b2$=0.05,SR=0.75/0.25)

Figure 11.4b shows the result of extreme skewing of the sex ratio to either *SR*=0.75 (male biased) or *SR*=0.25 (female biased), which both had the identical effect of removing the threshold at *M*=0.12 and causing widespread selection to *MBsp*. Any deviation less than 0.25 from an equal sex ratio (i.e. where $0.25<SR<0.75$) did not have this effect, giving the same result as Figure 11.4a.

Figure 11.5 - Changes in frequencies of mating behaviour at the two stable equilibria shown in Figure 11.4a (where *s*=0.1, *r*=0.01, *b1*=0.1, *b2*=0.05, *SR*=0.5)

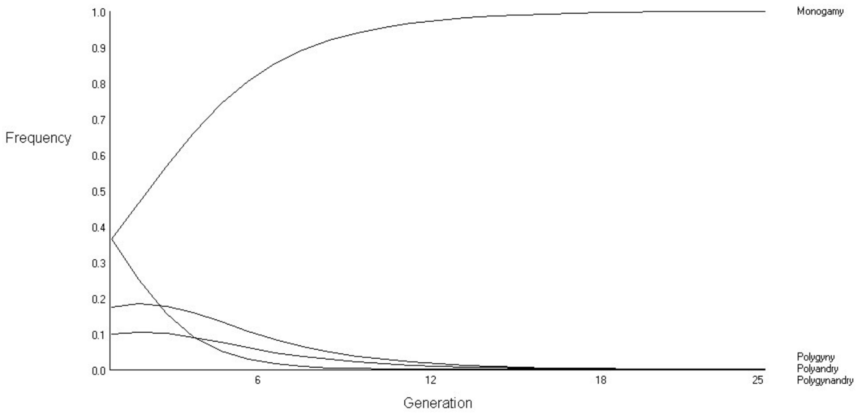

Figure 11.5a: The M*Bsp* equilibrium

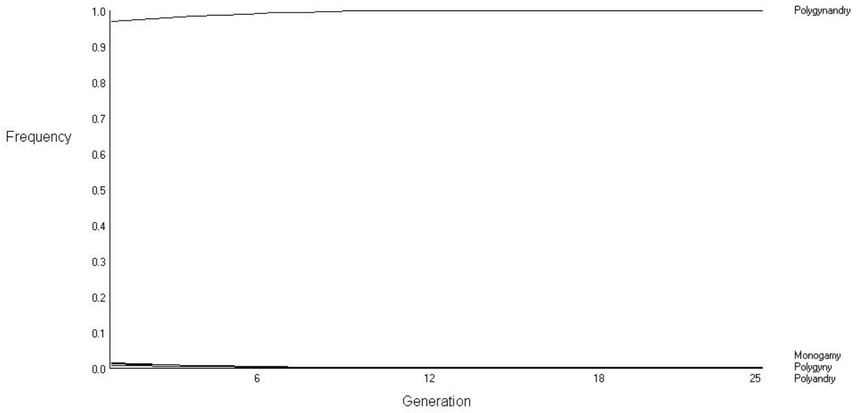

Figure 11.5b: The m*Bpp* equilibrium

Figure 11.5 gives exemplar time-courses depicting the changes in frequencies of the four classes of mating behaviour in the approach to the two equilibria observed in Figure 11.4a. Figure 11.5a shows that the *MBsp* equilibrium is entirely monogamous, while Figure 11.5b shows that the *mBpp* equilibrium is entirely polygynandrous. This is to be expected from the mating rules specified in Table 11.3. Figure 11.5 also shows that populations rapidly converge on these equilibria, the *MBsp* equilibrium after approximately 25 generations and the *mBpp* equilibrium after approximately 15 generations (although polygynandry almost immediately dominates the population).

11.3.2 Model 1b - Oblique Cultural Transmission

In Model 1b the vertical cultural transmission of Model 1a was replaced with oblique cultural transmission, in which cultural beliefs are adopted according to the beliefs not just of the parents but of the entire parental generation (Cavalli-Sforza & Feldman, 1981).

Appendix D.2 shows the probabilities that each phenogenotype will result from each mating under the assumption of oblique transmission. In this case the cultural belief of the parents is not of specific importance, so only their genotypes are given. These are used to calculate the offspring genotypes as before. The cultural beliefs of the offspring are given by the frequencies of beliefs in the previous generation (irrespective of their parents' beliefs or genes). Hence the offspring are *Bpp* with a probability equal to the frequency of *Bpp* in the parental generation (*z*, where z=x1+y1+x3+y3) and *Bsp* with a probability equal to the frequency of *Bsp* in the parental generation (1-*z*). The cultural biases *b1* and *b2* are modified slightly to conform with this new mode of cultural transmission, and are now dependent on the *z* term. (Note that *z* here is equivalent to Cavalli-Sforza and Feldman's 'fu_t'.)

Analysis of the oblique model reveals that each parameter (*s*, *r*, *a*, *b1, b2* and *SR*), individually and combined, generates largely the same results as they did in

Model 1a. Figure 11.6 summarises these effects. Figure 11.6a shows the case where no parameter is acting, and where *s* alone is acting (both are identical, as before). As in Model 1a, there is selection for *M* from starting values where *M*>0.12 and selection for *m* from starting values where *M*<0.12.

One difference is that there is no longer fluctuation in the *Bsp*/*Bpp* dimension. This suggests that the fluctuation observed in Model 1a was caused by the manner in which cultural beliefs are inherited in the clusters. Specifically, in many polygynandrous clusters one female has one mate and the other female has two mates, with the overall frequency of beliefs in the offspring given by the average of these two females' expected frequencies. This imbalance in inheritance, with the single-mate male having a greater influence than either of the males sharing a female, caused the fluctuation seen in Model 1a. Under the assumption of oblique cultural transmission in Model 1b beliefs are no longer inherited via the mating clusters.

Figure 11.6b shows that *r* and *b2* both cause selection for *Bpp* in regions starting from *M*<0.12; Figure 11.6c shows that *b1* causes selection for *Bsp* in regions starting from *M*>0.12; and Figure 11.6d shows the combined effect of all parameters, with two stable equilibria at *MBsp* and *mBpp*. Figure 11.6e shows that skewing the sex ratio causes universal selection to *MBsp*, although this deviation must now be greater than 0.35 (i.e. 0.15>*SR*>0.85).

Figure 11.6 - The dynamics of Model 1b (oblique cultural transmission). Parameter values are the same as for the equivalent outputs in Figures 11.2, 11.3 and 11.4, except Figure 11.6e where *SR*=0.85/0.15

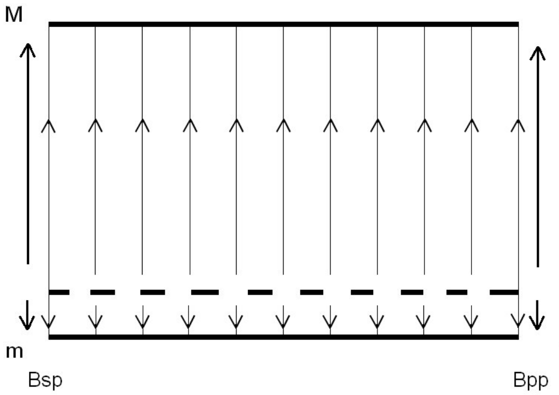

Fig 11.6a - No parameters/the effect of *s*

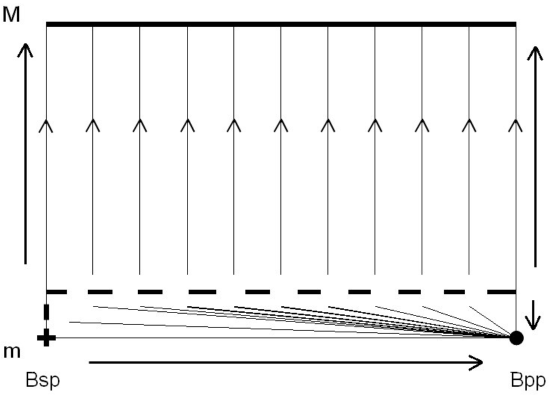

Fig 11.6b - The effect of *r*/*b2*

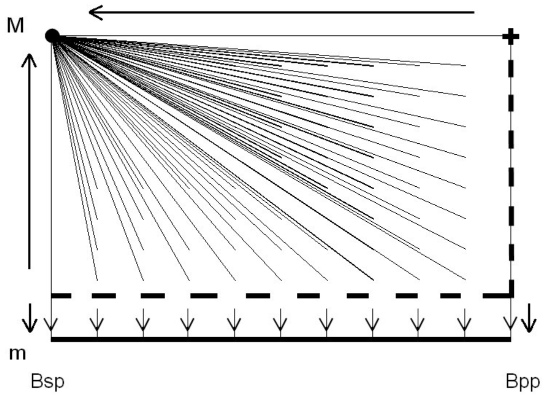

Fig 11.6c - The effect of *b1*

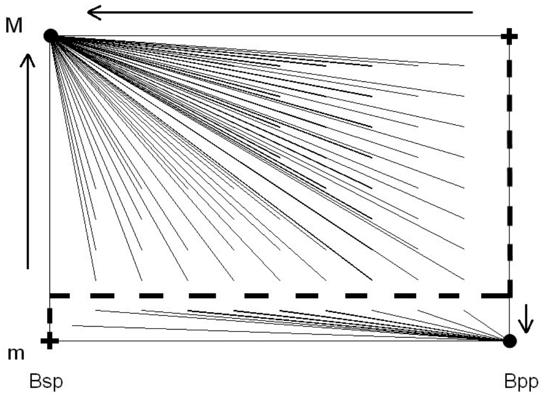

Fig 11.6d - All parameters combined

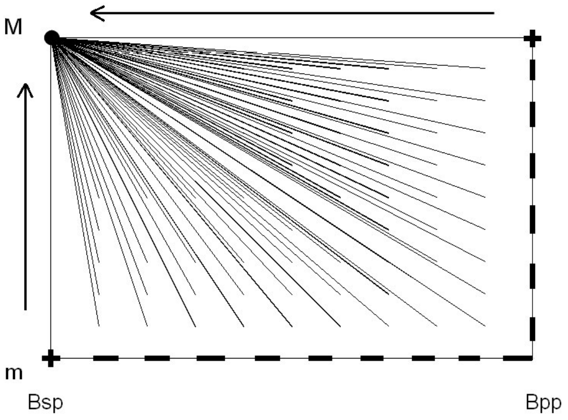

Fig 11.6e - Skewed sex ratio (*SR*=0.85/0.15)

11.3.3 Model 1: Conclusions

The main conclusion to be drawn from the analysis of Model 1 is that the most common outcome, including the outcome derived from the most biologically plausible conditions, is the convergence of populations on two culturally and genetically homogeneous simultaneously stable equilibria, one in which *Bsp* and *M* are fixed, and the other in which *Bpp* and *m* are fixed (e.g. Figure 11.4a). Each parameter was systematically varied across a range of biologically plausible values and, for each set of parameter values, at least 500,000 generations were simulated from each of 121 starting frequencies of *M/m* and *Bsp/Bpp*. For those cases in which all parameters were acting (i.e. $s,r>0$, $a<1$, $b1,b2>0$) and $SR=0.5$, 100% of initially polymorphic simulations resulted in convergence on one of these two equilibria. Where *SR* was also varied ($SR=0.25$, 0.4, 0.5, 0.6, 0.75), the proportion of initially polymorphic simulations converging on one of these two equilibria fell to 91.7%, with the remaining 8.3% comprising the cases where $0.25>SR>0.75$ and only featuring the *MBsp* equilibrium (e.g. Fig 11.4b). These results held under the assumption of both vertical (Model 1a) and oblique (Model 1b) cultural transmission.

The analysis suggests that there are two stable forms of human society: (1) a society in which all members hold the singular paternity belief and are genetically predisposed toward monogamy, and (2) a society in which all members hold the partible paternity belief and are genetically predisposed toward polygamy. These two forms of society correspond well to the partible and singular paternity societies described in Beckerman and Valentine (2002b). The greater incidence of singular paternity societies world-wide, including most if not all post-industrial societies, is also consistent with the model, with the *Bsp* equilibrium reached from a larger number of starting conditions than the *Bpp* equilibrium (e.g. Figure 11.4a).

However, a general limitation of the gene-culture coevolution method is the assumption of random mating from an infinite population. As discussed above, the assumption of random mating generated strong selection for *M* from the majority of the initial starting conditions. It does not seem realistic, however, that monogamy should be orders of magnitude more likely to occur than polygamy simply because it only involves two individuals. Model 1 also assumes that individuals have an infinite number of potential mates available to them, whereas in a realistic finite population the desired mates may not be available. To address these issues, and to verify the results of Model 1, Model 2 used an agent-based modelling approach.

11.4 MODEL 2 - AGENT BASED MODEL

In the agent-based model a number of 'agents' or 'individuals' each with a set of characteristics interact and reproduce according to a set of specified rules. Each non-overlapping generation of *N* agents undergoes first mating, then reproduction. The following sections specify the characteristics of the agents and describe rules of mating and reproduction.

11.4.1 Agent Characteristics

Each agent has four characteristics: *sex* (male or female); *genetic predisposition* (*M* or *m*), where *M* agents do not seek extra mates beyond a single partner (i.e. the *M* allele specifies a genetic predisposition for monogamy), and *m* agents do seek extra mates (i.e. the *m* allele specifies a genetic predisposition for polygamy); *cultural belief* (*Bsp* or *Bpp*), where *Bsp* represents a belief in singular paternity and *Bpp* represents a belief in partible paternity; and finally *mating status* (mated or unmated).

11.4.2 Mating

During the mating phase each unmated agent is selected at random and selects a mate(s) according to their genotype and a set of mating rules. The agent's genotype determines whether the agent will seek or accept one mate or two mates: *M* agents seek or accept only one mate, while *m* agents seek or accept up to two mates (as in Model 1, and the South American societies studied by Beckerman & Valentine (2002b), agents are restricted to a maximum of two mates).

Given these genetically specified constraints, each agent chooses a mate(s) according to a set of preferences. Males strive to maximise reproductive access to females. Hence all males prefer to mate with *M* females to *m* females, as monogamous *M* females will provide exclusive reproductive access while polygamous *m* females may find another mate, forcing the male to share reproductive access. Additionally, *m* males prefer two mates to one mate (as this will result in their receiving twice the reproductive access). Females strive to maximise male help, in the form of provisioning of food or protection from other males. Hence all females prefer to mate with *M* males to *m* males, as monogamous *M* males will provide exclusive help while polygamous *m* males may find another mate (forcing the female to share provisions). Additionally, *m* females prefer two mates to one mate (as they will receive twice the male help). Note that these more realistic mating preferences replace the assumption of random mating in Model 1.

The application of these mating rules results in the formation of clusters of monogamy, polygyny, polyandry or polygynandry, as defined in Table 11.2. Once an agent is designated a mate, their mating status is switched from ‘unmated’ to ‘mated’. Mating continues until there are no unmated agents left in the generation. This contrasts with Model 1, in which the mating population is assumed to be infinitely large.

An additional parameter c determined the control over mating afforded to each sex. With $c = 0.5$, agents were chosen at random by the model to select a mate(s) irrespective of the chooser’s sex. With $c = 1$, only females were chosen to select a mate(s), and with $c = 0$ only males were chosen. This is designed to allow us to explore the claim by Beckerman and Valentine (2002b, pp. 11-12) that South American partible paternity societies are characterised by female control over mating and singular paternity societies are characterised by male control over mating.

11.4.3 Reproduction

Once mating is completed, each mated female is selected at random and reproduces with a probability given in Table 11.7. The parameters used in Table 11.7 are broadly similar to the fitness parameterisation used in Model 1 (Table 11.4). Here, however, each female is given a baseline probability of producing an offspring of 0.5 rather than 1, as the values in Table 11.7 specify probabilities rather than fitnesses and hence cannot exceed 1. We impose the constraints that $s<0.25$ and $r<0.5+s$ to ensure that the probabilities in Table 11.7 remain within the range 0-1. As in Model 1, *s* represents the resources or help received from a single male, *r* represents the cost of polyandrous or polygynandrous *Bsp* males fighting and/or practising infanticide, and *a* represents 'paternity confusion' and determines how cooperative the *Bsp* polyandry is. Note that the probabilities in Table 11.7 are for individual females rather than entire clusters (as in Table 11.4), so polygyny and polygynandry are not doubled.

Mating system	***Bpp female***		***Bsp female***	
Monogamy	w_1	$0.5 + s$	w_1	$0.5 + s$
Polygyny	w_2	$0.5 + s/2$	w_2	$0.5 + s/2$
Polyandry	w_{3pp}	$0.5 + 2s$	w_{3sp}	$0.5 + (1+a)s - r$
Polygynandry	w_{4pp}	$0.5 + s$	w_{4sp}	$0.5 + s - r$

Table 11.7 - The probability of a female producing an offspring in Model 2

Note that with an *s* of around 0.1 or 0.2 these probabilities roughly correspond to survivorship probabilities observed in the Barí by Beckerman *et al.* (1998) of 0.8 for children with two fathers (polyandry: $0.5 + 2s$) and 0.65 for children with one father (monogamy: $0.5 + s$), and similar probabilities in the Aché from Hill (cited in Beckerman & Valentine, 2002b, p. 7) of 0.85 for children with two fathers and 0.7 for children with one father.

If, depending on this probability, a female produces an offspring, then that offspring inherits the genes and beliefs of its parents according to standard haploid inheritance rules. Offspring sex is determined by the sex ratio (*SR*), which represents the probability that an offspring will be male (and hence the proportion of the population that is male). With respect to the South American societies reported in Beckerman and Valentine (2002b), Zaldivar, Lizarralde and Beckerman (1991) report a sex ratio at birth and through childhood in pre- and post-contact Barí close to 1. This model, however, concerns the reproductively active population, and there is evidence of higher male mortality among Barí adults (Beckerman & Lizarralde, 1995) possibly leading to a female-biased adult sex ratio.

The cultural bias again operated to promote *Bsp* in the offspring of monogamous *M* x *M* matings (bias *b1*, where *b1*>0.5) and *Bpp* in the offspring of polygamous *m* x *m* matings (bias *b2*, where *b2*>0.5). Two additional parameters were introduced in Model 2. The assortative cultural mating parameter *d* specified the probability that agents will refuse to mate with an agent with a different belief to themselves. The conformity parameter *k* specified the probability that an offspring adopts the majority belief of the entire parental generation, rather than inheriting beliefs from the parents only.

Females reproduce in this way until all slots of the next generation are filled. The next generation then goes through the same process of mating and reproduction, and this process is repeated for 1000 generations (although equilibria were typically reached long before the 1000th generation). Note that generations are non-overlapping; once a generation has mated and reproduced it is removed and mating continues exclusively within the next generation.

11.4.4 Analysis

To analyse the model, 10 separate 1000-generation simulations were run from each of 164 systematically varied starting values of *M*/*m* and *Bsp*/*Bpp*. This entire analysis was performed for a range of values of each parameter: for *s* and *r*: 0, 0.001, 0.01, 0.1, 0.2, 0.25; for *b1* and *b2*: 0.5, 0.6, 0.75, 0.9; for *d* and *k*: 0, 0.1, 0.5; for *c*: 0, 0.5, 1; and for *SR*: 0.5, 0.25, 0.75. These parameters were varied on their own and in combination with each other.

11.4.5 Results

The majority of the parameter value combinations (83.5%) resulted in the dynamics shown in Figure 11.7a, with selection to $m = 1$. Populations also fixated at either 100% *Bsp* or 100% *Bpp*. A larger proportion of populations (86%) fixated at *mBpp* than at *mBsp* (8.5%) due to the cultural bias *b2* promoting *Bpp* in *m* x *m* matings. Figures 11.7b and 11.7c show the changes in the frequencies of each mating system over the first 150 generations (equilibrium for genotype and belief was typically reached after no more than 50 generations). These largely identical graphs show frequencies of polyandry and polygyny at around 0.4 each, with around 0.2 of polygynandry. These frequencies fluctuate due to the stochastic nature of the agent-based model.

Figure 11.7 - Typical model dynamics of Model 2 (Fig 11.7a). The N values represent the number of starting values ending at each equilibrium. Figures 11.7b and 11.7c show time series of the frequencies of each mating system over the first 150 generations at the *Bsp* equilibrium (Fig 11.7b) and the *Bpp* equilibrium (Fig 11.7c).

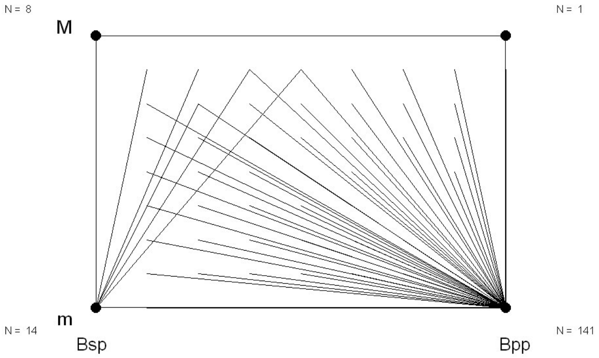

Fig 11.7a: *s*=0.2, *r*=0.25, *d*=0.1, *k*=0.1, *SR*=0.5, c=0.5, *b1*=0.75, *b2*=0.6

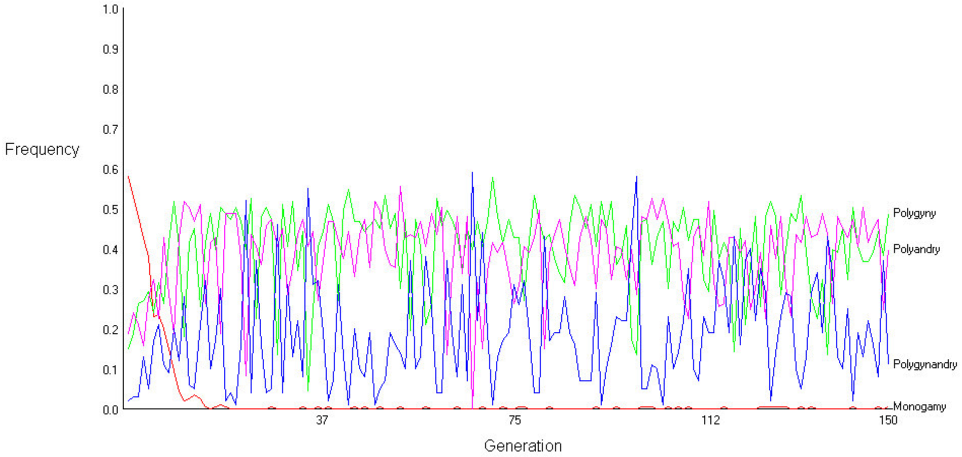

Fig 11.7b: *Bsp*=1

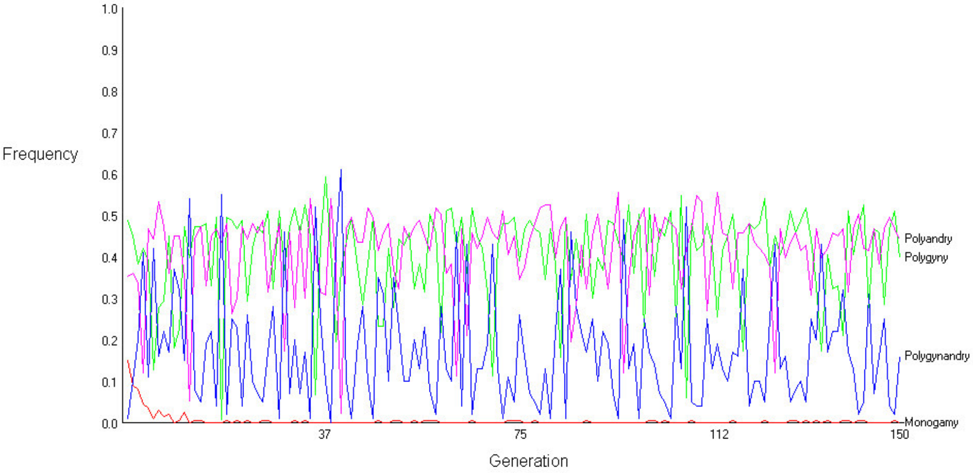

Fig 11.7c: *Bpp*=1

Two factors were responsible for selection for *m* in these cases. First, polygynandrous matings have a numerical advantage over monogamous matings because they have twice as many reproducing females, out-reproducing the mainly *M* monogamous pairs. *m* agents also have an advantage in that they can mate with either one or two mates, whereas *M* agents can mate with only one mate. Hence *m* agents can potentially form any of the four mating types, whereas *M* agents are restricted to monogamy, polygyny and polyandry (the latter two only with at least one *m* agent).

The other 16.5% of parameter combinations that did not result in fixation of *m* featured a skewed sex ratio (*SR*<0.3 or *SR*>0.7). Figure 11.8a shows a female-biased sex ratio (*SR* = 0.3). In this case the majority of populations end at one of three equilibria. There are two equilibria ending at 100% *Bsp*, either fluctuating around *M* = 0.757 (Figure 11.8b) or fixated at *M* = 1 (Figure 11.8c). The third is a 100% *Bpp* equilibrium at which the frequency of *M* fluctuates with a mean of *M* = 0.596 (Figure 11.8d). (Note that the fluctuation in *M*/*m* observed in Figures 11.8b, 11.8c and 11.8d mean that these are not equilibria, but basins of attraction).

This selection for *M* when the sex ratio is skewed occurs because the minority sex are all able to select *M* mates from the majority sex (as *M* mates are preferred over *m* mates), thereby preserving *M* in the population. With an equal sex ratio, on the other hand, *M* agents are quickly used up and agents move on to selecting *m* mates. This results in similar numbers of monogamous *M* clusters and polygynandrous *m* clusters, leading to the polygynandry/*m* advantage discussed above.

Figure 11.8 - A female-biased sex ratio (Fig 11.8a). The N values represent the number of starting values ending at that equilibrium and the *M* values show the proportion of the *M* allele at that equilibrium. Figures 11.8b, 11.8c and 11.8d show time series of mating system frequencies at the polymorphic *Bsp* equilibrium (Fig 11.8b), the monomorphic *Bsp* equilibrium (Fig 11.8c) and the *Bpp* equilibrium (Fig 11.8d).

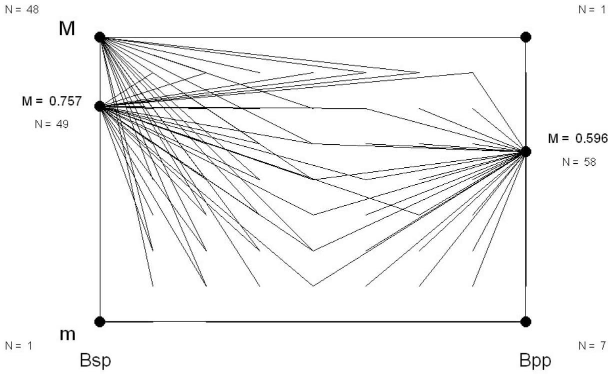

Fig 11.8a: Female-biased sex ratio
(*s*=0.2, *r*=0.25, *d*=0.1, *k*=0.1, *SR*=0.3, c=0.5, *b1*=0.75, *b2*=0.5)

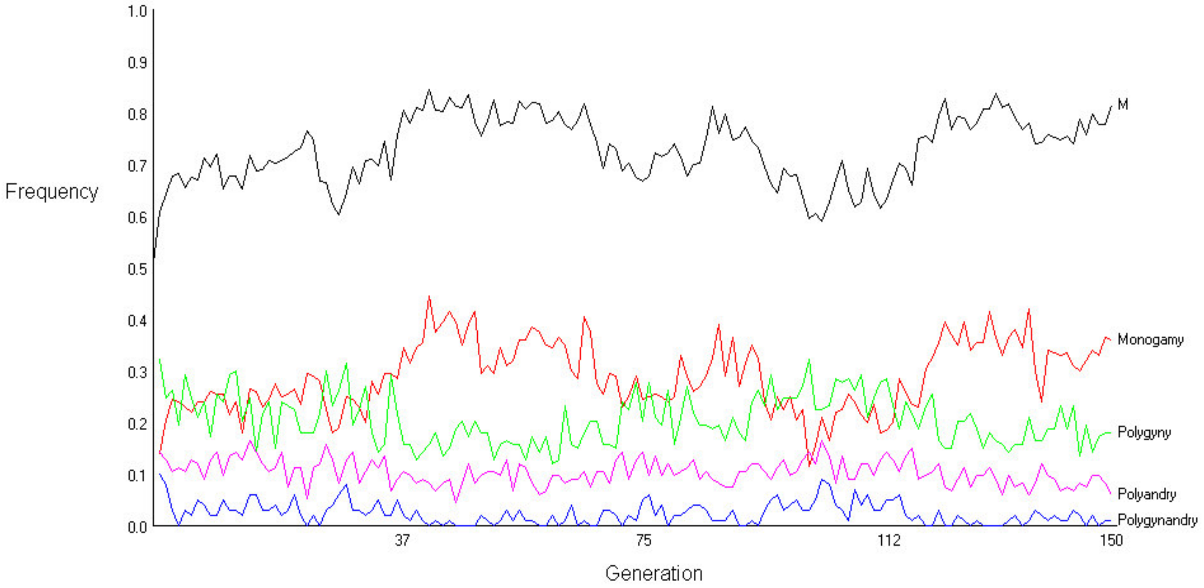

Fig 11.8b: *M*=0.757 *Bsp*=1

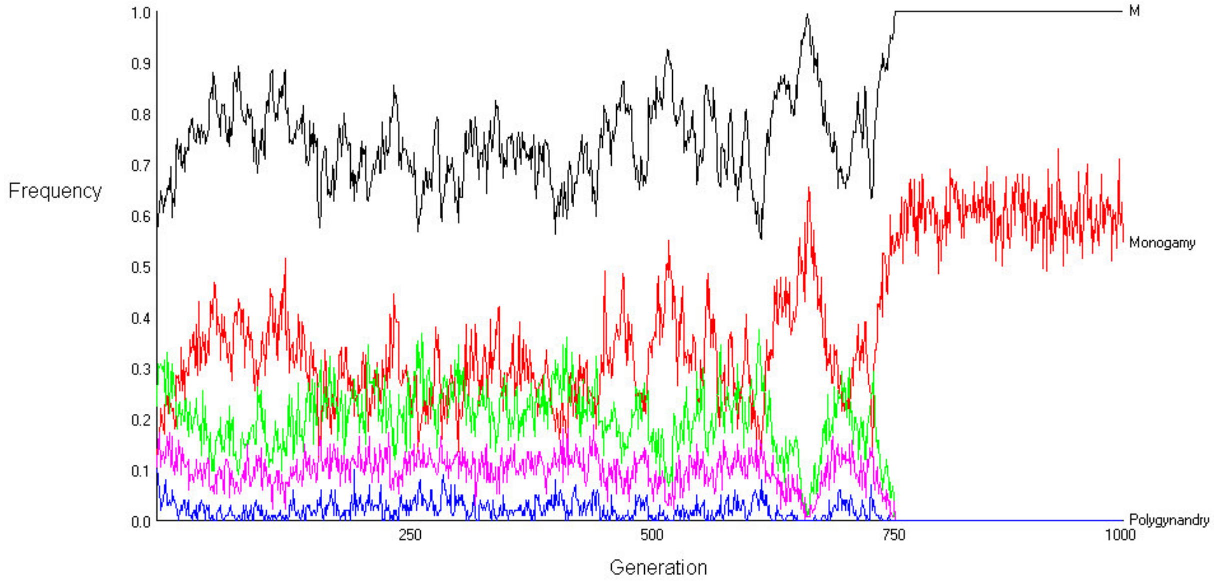

Fig 11.8c: *M*=1, *Bsp*=1

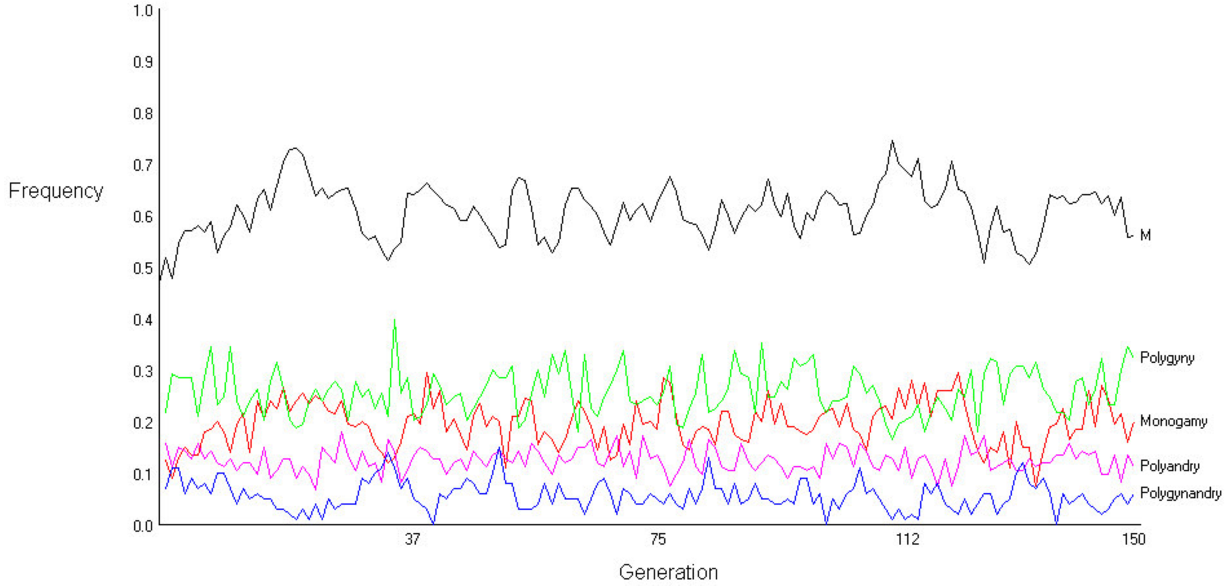

Fig 11.8d: *Bpp*=1

The increased monogamy in *Bsp* populations observed in Figure 11.8a is a result of *r* (male fighting/infanticide), which imposes a fitness cost on polyandrous and polygynandrous *Bsp* agents, thereby increasing the relative fitness of monogamy.

This cost does not apply to *Bpp* agents and creates a more equal mix of *M* and *m* in the *Bpp* population.

Figure 11.9 - The interaction between sex ratio and control over mating

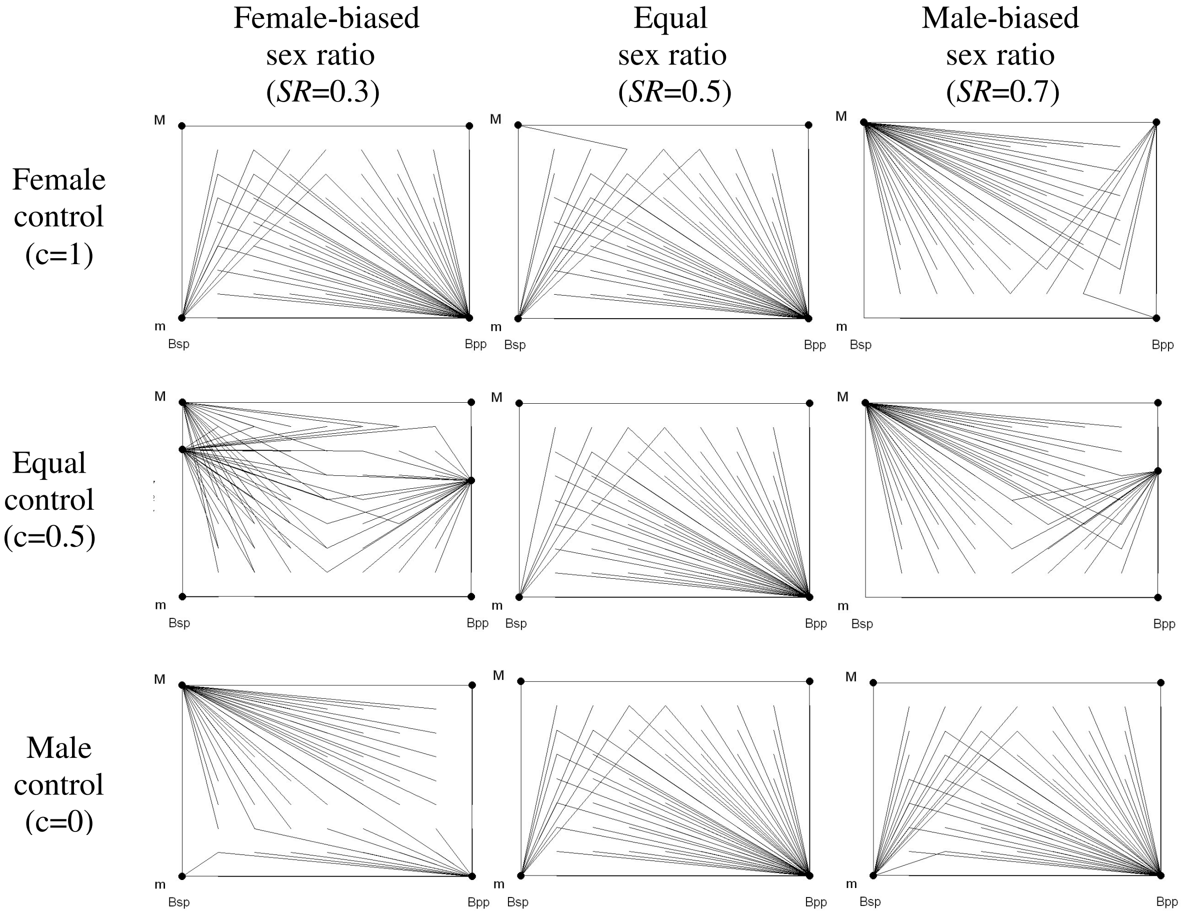

Figure 11.9 illustrates the interaction between the sex ratio (*SR*) and control over mating (*c*). The left-hand column of Figure 11.9 shows that with a female-biased sex ratio, female control over mating causes selection for *mBpp*, while male control over mating causes selection for *MBsp*. This reflects the anthropological evidence in South America (Beckerman & Valentine, 2002b). Note that a male-biased sex ratio

produces the opposite pattern (female control promotes *MBsp* and male control promotes *mBpp*).

Further analyses (not illustrated) suggested that the other parameters had expected effects. *b1* caused selection for *Bsp* in regions where *M* is dominant, and *b2* caused selection for *Bpp* in regions where *m* is dominant. *d* and *k* both increased the likelihood of populations becoming fixated at *Bsp* from *Bsp* dominant regions and at *Bpp* from *Bpp* dominant regions. *s* and *a* had no observable effect on the positions of the equilibria.

11.4.6 Comparison with Model 1

We are now in a position to compare the results of Models 1 and 2. Importantly, all of the parameters (*s*, *r*, *a*, *b1*, *b2* and *SR*) had the same effects in both models (or similarly had no effect in either in the case of *s* and *a*). We have also seen how various additional or alternative cultural transmission rules (oblique cultural transmission in Model 1b, assortative cultural mating and conformist cultural transmission in Model 2) do not significantly alter the dynamics of the basic models. These findings increase our confidence in the validity of the results discussed above.

The only significant difference between the two models lies in the assumptions regarding the formation of mating clusters and the effect of these assumptions on selection in the *M/m* dimension. The random mating assumption of Model 1 generated strong selection for monogamous *M* x *M* mating clusters, as under random mating clusters of two individuals are more likely to occur than clusters of three or four individuals. Model 2 instead featured what might be considered more realistic mating rules, where all individuals express preferences for monopolisable *M* mates, and *m* individuals prefer two mates to one mate. These assumptions led to selection for *m* rather than *M*.

11.4.7 Conclusions

The majority of parameter values in Model 2 resulted in selection for *m*, the genetic predisposition for polygamy. This is because *m* agents are more flexible in mating and the mating clusters they are most associated with are more fecund in reproduction. According to Model 2, therefore, modern societies with equal adult sex ratios (e.g. Western societies) should be genetically polygamous, with individuals willing to mate with more than one person. This is perhaps not an unreasonable assumption, particularly given that this model did not incorporate effects of institutional mating systems. The model also predicts that these polygamous societies should be primarily *Bpp*, which is clearly not observed. If partible paternity beliefs were never present this perhaps explains the absence of *Bpp* in most modern societies, although it does lead to the prediction that if *Bpp had* been present it would have quickly become prevalent.

More interesting were the dynamics of Model 2 when the sex ratio was skewed. With a female-biased sex ratio we saw two patterns which reflect aspects of the anthropological evidence discussed previously. First, two (or three) basins of attraction typically emerged (e.g. Figure 11.8a), one (or two) entirely *Bsp* with a large degree of genetic predispositions for monogamy, and the other one entirely *Bpp* with a more equal mix of genetic predispositions for monogamy and polygamy. These two basins of attraction parallel the relatively monogamous singular paternity and more polygamous partible paternity societies observed by Beckerman and Valentine (2002b), and suggests that the presence of adult sex ratio distortion, perhaps resulting from excess male mortality (Beckerman & Lizarralde, 1995), may be responsible for these differences in mating systems.

The female-biased Model 2 (like Model 1) also predicts possible genetic differences between societies with histories of *Bsp* and *Bpp* beliefs. Specifically, members of *Bpp* societies should show greater tendencies toward and adaptations for polygamy, such as less frequent and less intense jealousy, less faithfulness and less moralistic or jealousy-based aggression. *Bpp* societies should feature less internal male fighting over female infidelity and less male initiated infanticide over paternity issues than otherwise equivalent *Bsp* societies. The aforementioned literature is consistent with these predictions. However, it is also important to recognise there may be no genetic differences between human populations with different mating systems, and that sexual practices may change rapidly due to purely cultural change (that is, cultural beliefs and practices unrelated to singular/partible paternity).

A second parallel between the female-biased model and the anthropological literature lies in the fact that female control over mating causes selection for *mBpp* and male control over mating causes selection for *MBsp*. Beckerman and Valentine (2002b, pp. 11-12) noted a similar association between female control, partible paternity and polygamy on the one hand, and male control, singular paternity and monogamy on the other.

These two parallels suggest a possible evolutionary scenario in which different populations of the ancestors of the present-day inhabitants of Lowland South America, in the presence of a female-biased sex ratio and small differences in belief or genetic predispositions towards monogamy, were subject to divergent selection leading to the present day distribution of singular and partible paternity societies. The higher adult male mortality observed in present-day societies (Beckerman & Lizarralde, 1995) may offer one explanation for this postulated female-biased sex ratio. Beckerman (personal communication) suspects a slightly female-biased sex ratio amongst adult Bari, although not as skewed as the model requires (although an evolutionary bottleneck may have distorted the sex ratio to the level assumed here). Finally, a female-biased sex ratio may also have provided ideal conditions for a belief in partible paternity to evolve. If males are rare then they will be in high demand as resource-providing fathers, perhaps making beliefs in multiple fathers more attractive and more likely to emerge. This evolutionary scenario could be tested by seeking genetic evidence from existing South American populations for a past population bottleneck and a female-biased sex ratio.

The female-biased Model 2 also predicts that, as well as broad differences *between* the two equilibria, there will be significant genetic variation among individuals *within* societies at equilibrium. Even within societies at the largely monogamous *Bsp* equilibrium there is still a significant amount of polygyny, polyandry and polygynandry (see Figure 11.8b). The present analysis is consistent with the view that humans collectively are not well-described as 'naturally' monogamous or 'naturally' polygynous since, if anything, they are 'naturally' variable in their mating behaviour. This does not preclude the possibility, suggested above, that we would expect a large proportion of individuals (the majority) in those societies represented by the *Bsp* equilibrium to be biologically predisposed towards monogamy.

If these analyses are correct it further suggests that anthropological labels describing entire societies as 'monogamous' or 'polygynous' are misleading, and it may be more representative to describe societies in terms of frequencies of individual mating behaviour at equilibrium. There is a mismatch between the *demographic mating system*, as represented by the results of the present model, and the *institutionalised mating system,* as reflected in the patterns observed in Murdock's Ethnographic Atlas (1967). Murdock's (1967) influential anthropological database describes the majority of human societies as 'polygynous' (83.5%) and the rest as 'monogamous' (16%), with a very small minority 'polyandrous' (0.5%). The results presented above suggest that the global percentage of polygynous mating should be smaller than the percentage of societies in which polygyny is the institutionalised mating system. That is, if polygyny is the dominant institutionalised mating system it is not because it is the most frequent human behaviour. It may be that this mismatch is an artefact of the simplicity of the model - for instance, the neglect of sex-linked genes - which prevents the independent evolution of polygyny and polyandry in males and females. However, it is also possible that the mismatch is real, which might suggest that the widespread institutionalisation of polygyny (and corresponding disestablishment of polyandry) is a product of factors such as greater male than female resource-holding power, hierarchically organised societies and/or patrilineal inheritance of wealth (Hrdy, 1981, 1999), conceivably amplified by recent historical trends such as the rise of agriculture (Holden & Mace, 2003).

The genetic variability observed at equilibrium is in part a manifestation of differential and conflicting patterns of selection on the sexes. If, as the model assumes, a significant proportion of such variation is found on autosomes and expressed in both sexes, then the members of each sex will vary in their predispositions toward monogamy and polygamy. Extensions of the present model might incorporate genetic modifiers on sex chromosomes to bias the behaviour of members of each sex (e.g. conceivably selecting for greater polygyny in males than females). This might generate stronger sex differences than observed in the current analysis. However, the presence of autosomal variation will mean that within-sex variation in behavioural strategies is to be expected. This means, for instance, we expect that some monogamous males in institutionally polygynous societies will be monogamous by choice and not because there are insufficient females for them to pursue polygynous mating.

11.5 GENERAL DISCUSSION

We can now begin to address the questions posed at the start of the paper:

How does a belief in partible paternity affect the biological fitness of males and females? A belief in partible paternity, as opposed to a belief in singular paternity or no belief at all, is assumed to affect the biological fitness of individuals in two ways. First, polyandrous and polygynandrous *Bpp* individuals bear no cost of male aggression (the parameter *r*), unlike polyandrous and polygynandrous *Bsp* individuals. Second, *Bpp* polyandry is always fully cooperative (a=1), unlike *Bsp* polyandry which could be potentially no different to monogamy (a<1). In both of these cases, therefore, *Bpp* females receive more help than *Bsp* females. Males, while not given separate fitnesses in the model, will nevertheless be paying greater costs (i.e. resources) and be less certain of paternity (given the lack of jealous aggression) in Bpp societies compared with Bsp societies. Overall, then, *Bpp* can be said to benefit females and impose a cost on males, relative to *Bsp*.

Note that this does not mean that males will *never* benefit from *Bpp*. For example, males would benefit from *Bpp* when the increased survival of offspring due to the help of an extra male offsets the cost to males of sharing paternity. This would most likely occur under harsh ecological conditions, where care is costly and two male providers are much better than one, or where death of husbands is frequent due to starvation or war, so having two husbands increases the chance of one surviving during the period of parental care. The model could be extended by introducing a function which relates offspring fitness to number of carers, with the shape of this function reflecting ecological conditions (Davies, 1992).

What impact do such beliefs have on human mating systems? Partible paternity beliefs have the effect of promoting polygamous mating at the expense of monogamy. In the absence of cultural processes, gene frequencies converge on those observed at the *Bsp* equilibrium. Consequently, the inheritance of cultural beliefs concerning paternity, unique to humans, would appear to have created a new genetic equilibrium (*Bpp*) characterised by different levels of monogamy and polygamy than observed in its absence. In the female-biased Model 2, for example, *Bpp* societies feature a mix of polygyny, polyandry, polygynandry and monogamy, whereas *Bsp* societies are dominated by monogamy. These differences are mainly due to the male aggression parameter *r*, which imposes a cost on all polygamous *Bsp* mating systems, increasing the frequency of *Bsp* monogamy relative to Bpp monogamy, which is unaffected by *r*.

Can a (partible paternity) belief spread that has fitness benefits for one sex (females) and is disadvantageous to the other (males)? Partible paternity societies might be characterised as advantaging females, since females frequently reap the benefits of multiple male help, while incurring additional costs on males. The analysis therefore suggests that human behaviour can evolve that benefits one sex at the expense of the other, without coercion. Model 2 with an unbiased sex ratio predicts that the majority of populations will converge on *Bpp*, due to strong selection for *m*. Model 1 and the female-biased Model 2 predict that fewer populations will converge on *Bpp*, and only from starting points which are already fairly polygamous (i.e. that feature a high initial frequency of *m*).

How can two such distinct alternative beliefs about paternity persist when they are likely to have such direct effects on biological fitness? The biases in cultural transmission (*b1* and *b2*), in combination with the fitness costs of jealous aggression (*r*), are responsible for the persistence of the two cultural beliefs. These biases drive populations to either the 100% *Bsp* or the 100% *Bpp* equilibrium. However, even without the bias (*b2*), jealous aggression can create a *Bpp* equilibrium if believers in singular paternity pay even a weak fitness cost to polyandrous and polygynandrous mating not paid by believers in partible paternity.

Can a consideration of cultural variation in beliefs about paternity shed light on the evolution of human mating systems? Polygamous mating is characteristic of many non-human primates and may conceivably have been a feature of our primate ancestors (Hrdy, 1981, 1997). However, in the absence of cultural transmission, ancestral populations would have approached the genetic equivalent of the *Bsp* equilibrium. When our species evolved the ability to acquire, cognise and transmit belief states about paternity this modified the selection acting on a minority of polygamous populations, allowing them to evolve to the *Bpp* state. This suggests that a phylogenetic analysis of the divergence of these cultural beliefs about paternity, similar to that employed to investigate the geographical distribution and evolution of other cultural traits, including dairy farming (Holden & Mace, 1997), might provide an upper limit on the date of emergence of human belief systems.

Concluding Remarks

CHAPTER 12 - GENERAL DISCUSSION

The three parts of this thesis constituted theoretical, empirical and mathematical approaches to the study of the transmission and evolution of human culture. Part A explored the parallel or analogy between biological and cultural evolution, arguing that there is now as compelling evidence for cultural evolution as Charles Darwin presented in *The Origin of Species* for biological evolution (Chapter 2). Hence human culture was shown to exhibit the key evolutionary properties of variation, selection and inheritance, as well as the accumulation of modifications, adaptation, convergence, and the loss or change of function. It was then argued that if culture does indeed evolve in a manner analogous to that of biological organisms, it follows that the structure of a unified science of cultural evolution should broadly resemble that of the science of biological evolution, i.e. evolutionary biology (Chapter 3). Existing or potential cultural analogues of the different sub-disciplines of evolutionary biology were then examined in detail, and a unified science of cultural evolution was sketched.

Parts B and C presented original empirical and theoretical work contributing to two branches of this science of cultural evolution. Part B comprised a series of experiments testing for a number of hypothesised biases in cultural transmission, updating Bartlett's (1932) under-used transmission chain method according to modern standards of scientific practice. Evidence was found for two of these hypothesised biases: first a 'social bias' that acts to promote information concerning third-party social relationships over non-social information concerning individual behaviour or physical interactions (Chapter 5); and second a ‘hierarchical bias’ that acts to transform knowledge of everyday events from low-level actions into high-level goals and sub-goals (Chapter 6). Three other hypothesised biases concerning status (Chapter 7), anthropomorphism (Chapter 8) and neoteny (Chapter 9) were not supported, although each gave rise to potential future work using this methodology.

Part C presented a theoretical investigation into the coevolution of the genetic bases of human mating behaviour and culturally inherited folk beliefs regarding paternity, using both population-based and agent-based modelling techniques. The models suggested that the inheritance of cultural beliefs regarding paternity, i.e. whether paternity is seen as ‘singular’ (children can have only one true father) or ‘partible’ (children may have more than one ‘true’ father), significantly affects the evolution of human mating behaviour, and can specifically account for the distribution and characteristics of mating systems in Lowland South American societies. Generally, beliefs in partible paternity create a new more polygamous form of society compared with beliefs in singular paternity.

The work presented in Parts B and C covered a wide range of topics, from primate social intelligence to hierarchical script theories to paternity beliefs and mating behaviour. The two methodological approaches of Parts B and C (experimental versus mathematical) were also very different. All of this work, however, is united by the evolutionary framework presented in Part A. Hence the population-based and agent-based models of Part C represent mathematical simulations of cultural evolution (as well as biological evolution), in the same way that purely gene-based population genetics models have long been used to simulate biological evolution. The cultural transmission experiments of Part B, meanwhile, provide data on micro-scale transmission biases that may have important population-level effects, analogous to the breeding experiments of evolutionary biology that are used to explore biological inheritance.

Indeed, Mayr (1982) has argued that one of the most important functions of an evolutionary framework in biology was to integrate the study of micro- and macro-evolution. That is, the micro-scale principles of inheritance discovered by experimental population geneticists, when extrapolated to the population level, can account for the macro-scale historical and geographical patterns observed by palaeontologists and field biologists. It was only after this 'evolutionary synthesis' of the early 20th century that the theory of evolution became truly established within biology. The evolutionary framework presented in Part A offers the potential for the same synthesis of the micro- and macro-scale study of culture. Hence the results of cultural transmission experiments such as those employed in Part B might be extrapolated to the population level to explain certain macro-scale historical or geographical cultural patterns. Although this integration was not formally pursued here, some findings (e.g. the social bias of Chapter 5) are consistent with informal observations of large-scale cultural phenomena (e.g. the prevalence of 'social' over 'non-social' mass media: Chapter 10), and they provide a methodological platform for more explicitly integrative studies in the future (see below).

The mathematical models of gene-culture coevolution presented in Part C also demonstrate how evolutionary principles serve to link micro- and macro-level change. By specifying the precise mating rules and cultural transmission biases that were hypothesised to act upon the inheritance of genes and cultural traits, it was possible to extrapolate up to long-term multiple-generation change at the population level, comparing the resultant dynamics with anthropological evidence of mating system distributions in South America.

As argued in Chapter 3, another benefit of an evolutionary framework is that some of the tools, methods and approaches used by evolutionary biologists to study biological evolution can be borrowed and adapted to study cultural evolution. One general tactic commonly used by biologists is the use of highly simplified experimental or mathematical simulations of complex real-life biological phenomena. Similarly, Parts B and C both constituted simplified simulations of complex real-life *cultural* phenomena, in Part B experimentally and in Part C mathematically. As noted in Section 3.4.1, such simulations are frequently criticised by social scientists for failing to capture the complexity of human culture. The response to this criticism given in Section 3.4.1 is worth repeating: the fact that simulations are highly simplified is the very reason for their usefulness. They allow, for example, researchers to isolate and manipulate single variables, and force them to exactly and explicitly specify their theoretical assumptions. Simplified experimental and mathematical models of reality have allowed biologists to make great strides in understanding biological phenomena, which are in many respects at least as complex as cultural phenomena. Hopefully more social scientists will adopt these experimental and mathematical means of studying culture (for further discussion of the use of simulations in the social sciences see Epstein & Axtell, 1996; Kohler & Gumerman, 2000; Richerson & Boyd, 1987).

An evolutionary approach to culture also highlights the relationship between cultural and biological evolution, where they may be seen as separate but interacting evolutionary processes within a larger hierarchical framework (e.g. Odling Smee, Laland, & Feldman, 2003; Plotkin & Odling Smee, 1981). As argued by Plotkin (2002) and Richerson and Boyd (2005), the complexity of the human capacity for cumulative cultural evolution suggests that it is a biologically evolved adaptation, made possible by a number of biologically evolved psychological mechanisms such as imitation, language or theory of mind (Plotkin, 2002; Richerson & Boyd, 2005). Theoretical analyses (e.g. Aoki *et al.*, 2005; Boyd & Richerson, 1985; Boyd & Richerson, 1988), however, indicate that the adaptive value of culture is to respond to environmental change that is too rapid or unpredictable to be encoded genetically (although not so rapid as to make culturally transmitted information quickly out-of-date). Culture must therefore be to some degree de-coupled from biological evolution, making possible the spread of genetically maladaptive cultural traits. As Richerson and Boyd (2005) argue, horizontal transmission from non-kin and imperfect transmission biases may also lead to the spread of genetically maladaptive traits. This general view of cultural and biological evolution as intimately inter-related yet causally independent typifies the broad ‘gene-culture coevolution’ perspective (Boyd & Richerson, 1985; Durham, 1992; Richerson & Boyd, 2005).

The interaction between biological and cultural evolution was explored in this thesis in two ways. First, some of the experiments of Part B tested for biases in cultural transmission that were argued to have been at least partly the result of biological evolution. For example, the social bias of Chapter 5 was argued to have been due in part to biologically evolved features of human cognition that have been shaped by social selection pressures. Second, the mathematical models employed in Chapter 11 concluded that the capacity to transmit cultural beliefs regarding paternity may have significantly altered the biological evolution of human mating behaviour. The plurality of this approach, in which biologically evolved features of cognition may bias cultural transmission and cultural inheritance may affect the selection of genes, is recommended in contrast to the more exclusionary and narrow views of certain evolutionary psychologists (e.g. Barkow *et al.*, 1992; Pinker, 1997), who tend to downplay the role of transmitted culture in human behaviour, and certain social scientists (e.g. Rose, Lewontin, & Kamin, 1984; Rose & Rose, 2000), who remain hostile to any biological or genetic interpretation of human behaviour.

An evolutionary approach to culture also highlights a number of potentially fruitful directions for future study, some of which follow from the work presented in Parts B and C. More work is needed regarding the experimental study of cultural transmission, to add to the findings of Part B. Chapter 10 outlined a number of extensions and modifications to the basic Bartlett (1932) methodology, such as the study of face-to-face transmission and the transmission of behaviour. Chapter 3 raised a number of possibilities for adapting the methods of experimental population genetics to study cultural processes, such as artificial selection or natural selection paradigms, and measures of the rate or strength of selection such as the darwin or the haldane. There is a real need to provide formal empirical demonstrations of cultural evolution 'in action'.

Future work might more explicitly explore the relationship between cultural micro- and macro-evolution. For example, the experimental methods used in Part B to study micro-scale cultural transmission might be used to simulate in the laboratory the macro-scale historical patterns found by archaeologists, in order to better understand the transmission processes originally responsible for generating those patterns. For example, it is often claimed (e.g. Dunnell, 1978; O' Brien & Lyman, 2003b) that certain archaeological traits are either 'functional' (the result of selection) or 'stylistic' (the result of random drift). Such hypothesised selection histories might be tested by experimentally transmitting lineages of a tradition under conditions of either selection or a lack of selection, comparing the resulting data with the equivalent archaeological patterns. Other archaeological patterns have been hypothesised to have arisen through processes of conformity (e.g. Kohler, VanBuskirk, & Ruscavage-Barz, 2004) or indirect bias (e.g. Bettinger & Eerkens, 1999), which could be simulated in the laboratory by manipulating the type of information available to participants (e.g. which trait was most popular in the previous generation, or which trait was associated with the most successful participants). Experimental methods afford a number of advantages not available to archaeologists and historians, such as the ability to isolate and manipulate single variables, the generation of complete data sets, and the ability to 're-run' history several times to study contingency.

As noted at the end of Part A, biological evolution should not be used as too strict a model for cultural evolution, and there may be significant evolutionary phenomena that are unique to culture. Plotkin (2002), for example, has argued that intangible ‘social constructions’ such as justice or money that only exist because of shared agreement may require a fundamentally different evolutionary explanation to anything seen in biology. This highlights the need for a complete taxonomy of cultural traits (e.g. social constructions, semantic knowledge, technological artifacts, procedural skills) and the associated and probably different evolutionary forces acting on each. This will also require a detailed understanding of the social learning mechanisms that are responsible for their persistence. For example, semantic knowledge is continuously acquired and updated throughout one’s lifetime via spoken and written language, whereas behavioural skills such as learning to use a knife and fork (or chopsticks) are acquired only once in a lifetime, via imitation or affordance learning (Whiten *et al.*, 2004). A combination of experimental and field studies will be necessary to explore these issues.

To sum up, the theoretical integrations of Part A, the experimental simulations of Part B, and the mathematical models of Part C have all aimed to contribute to our understanding of the transmission and evolution of human culture. As yet, this understanding is relatively poor, especially when compared with that achieved by biologists for the immense complexity and diversity of biological forms. In many respects human culture is at least as complex and diverse. The capacity to accumulate successful cultural variants across multiple generations has transformed the human species, allowing us to eradicate diseases, walk on the moon, and begin to unravel the intricate workings of the universe. At the end of *The Origin of Species*, Charles Darwin famously remarked of his theory of evolution that ‘there is grandeur in this view of life” (Darwin, 1859, p. 459). Hopefully our view of culture will one day become just as grand.

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Appendices

APPENDIX A - MATERIAL FOR CHAPTER 5

Appendix A.1 - MATERIAL FOR EXPERIMENT 5A

The first participant of each chain in Experiment 5a read the following three paragraphs. The bracketed labels, indicating the type of material and the numbers of words, sentences and propositions, were not presented to the participants.

[Individual]

Nancy is a 22 year old college student studying history at the University of Denver. Her father works as an accountant and her mother is a teacher. At weekends, she works part-time in a book store. When she finishes her studies, Nancy plans to travel abroad before pursuing a career as either a novelist or a journalist. [58 words, 4 sentences, 14 propositions]

[Gossip]

Nancy is having an affair with her married college professor. She has been lying to her friends about seeing him. Nancy recently became pregnant with the professor's child. The professor promised Nancy that he would leave his wife, but since she told him she was pregnant, the professor has refused to see her. Nancy is threatening to tell his wife about the affair. [63 words, 5 sentences, 14 propositions]

[Physical]

Denver is the state capital of Colorado, located in the western United States near the Rocky Mountains. An early stopping place for Indians, Denver was settled permanently after the gold rush of 1859. Its main industry is agriculture. Denver is a major centre for winter sports, and also contains a branch of the US mint, which produces most of America's coinage. [61 words, 4 sentences, 14 propositions]

Appendix A.2 - MATERIAL FOR EXPERIMENT 5B

The first participant of each chain in Experiment 5b read the following four paragraphs. The bracketed labels, indicating the type of material and the numbers of words, sentences and propositions, were not presented to the participants.

[Gossip]

Nancy is having an affair with her married college professor. Nancy recently became pregnant with the professor's child. The professor promised Nancy that he would leave his wife, but since Nancy told him she was pregnant, the professor refused to see her. So Nancy told the professor's wife about the affair. The professor's wife was so upset that she left the professor. [62 words, 5 sentences, 14 propositions]

[Social]

Nancy enjoys swimming. Nancy was going to the swimming pool but got lost, so she asked an old man waiting at a bus stop for directions. The old man could not give her directions. A bus arrived at the bus stop and the old man asked the driver for directions. The driver gave Nancy directions to the swimming pool, so Nancy was able to go swimming. [66 words, 5 sentences, 14 propositions]

[Individual]

One morning Nancy's alarm clock broke and she overslept. When she woke up she realised that she was late for an important lecture. She got dressed as quickly as she could, left the house and ran to the lecture theatre. When she got there the lecture theatre was empty. Nancy had missed the lecture. [54 words, 5 sentences, 14 propositions]

[Physical]

The weather in Colorado gets hot and dry in the summer. This removes moisture from the soil and dries out the plants that grow there. The dry vegetation catches fire easily, leading to frequent forest fires. These fires release smoke containing carbon monoxide into the atmosphere. This smoke contributes to global warming, increasing temperatures further. [55 words, 5 sentences, 14 propositions]

APPENDIX B - MATERIAL FOR CHAPTER 7

Appendix B.1 - MATERIAL FOR EXPERIMENT 7A

B.1.1 Argument for fluoridation, as presented to the first participants in each chain.

‘Fluoride makes teeth more resistant to decay. This is especially important given modern diets high in sugar, which form the acids that attack tooth enamel. For example, in Birmingham, where tap water has been fluoridated for almost 40 years, childrens’ teeth are three times healthier than in Manchester, where there is no fluoridation. This is a cheap way of helping poorer families, who can’t afford healthy diets and expensive dental services. And there is no strong evidence that adding fluoride creates any adverse effects, such as cancer or an increased risk of bone fractures. There really is no reason why we should not be adding fluoride to our water, given the obvious health benefits.”

B.1.2 Argument against fluoridation, as presented to the first participant in each chain.

“Although there are small health benefits to fluoridation, there are also considerable risks. There is a strong link between taking extra fluoride and a disease called dental fluorosis, which causes permanently mottled and discoloured teeth. Adding fluoride to peoples’ diets has also been linked to an increased risk of cancer, Downs Syndrome and bone disease, and may interfere with the functioning of the thyroid gland. With more and more use of high-fluoride toothpaste, mouthwash and chewing gum, extra fluoride in the water may be pushing overall fluoride levels over healthy limits. And ultimately, I think that people should be left to decide for themselves whether or not they want to take fluoride, not have the substance force-fed to them in tap water without being consulted."

Appendix B.2 - FORMULA FOR CALCULATING POWER

Potvin and Schutz's (2000) formula for calculating the noncentrality parameter λ_A for the effect of Factor A (here 'status') in a two-factor repeated measures ANOVA is:

$$\lambda_A = \frac{nq\Sigma(\mu_i - \mu)^2}{\sigma^2(1 - \rho_A) + \sigma^2(q - 1)(\rho_B - \rho_{AB})}$$

where n is the sample size, q is the number of levels of Factor B (here 'generation'), μ_i is the marginal mean for Factor A (where i is each level of Factor A), μ is the grand mean, σ^2 is the within-cell variance, and ρ_A, ρ_B and ρ_{AB} are the averages of the off-diagonal correlation coefficients of the A, B and AxB matrices respectively. Note that where the correlations came out negative then on the advice of R.W. Schutz (personal communication, 12 February 2005) the averages were calculated using these negative correlations (rather than taking their absolute values). The noncentrality parameter was then used to calculate power using the table provided by Howell (1997).

Appendix B.3 - MATERIAL FOR EXPERIMENT 7B

B.3.1 Argument for the euro, as presented to the first participants in each chain.

"I think the UK should join the euro. The UK does half of its trade with other European countries, and adopting the euro will make this trade easier and encourage economic growth. Increased political ties with Europe will mean less chance of disagreements and conflicts. A single European currency is more convenient for travellers, who won't have to change their money when visiting Europe. People will be quick to adapt to the new currency, just as they were when the pound was decimalised and shillings were replaced."

B.3.2 Argument against the euro, as presented to the first participants in each chain.

"I'm against the euro. Adopting the euro means that the UK will lose control over its economy, for example by being able to set independent interest rates. The UK will also lose political independence, and decisions will be made by unelected officials in Brussels. It will cost UK businesses to convert cash tills, vending machines and accounting systems to a new currency. The pound is a symbol of British national identity, and people will be reluctant to change the currency they grew up with."

APPENDIX C - MATERIAL FOR CHAPTER 8

Appendix C.1 – MATERIAL FOR EXPERIMENT 8A

C.1.1 Emotional concealment (adapted from Mitchell & Hamm, 1997)

‘Male Child A is sitting with female Child B. Another male, Child C, approaches, and Child A moves away from Child B. Child C sits down close to Child B. Child A turns away and looks intently at his hand.”

‘Male Chimp A is sitting with female Chimp B. Another male, Chimp C, approaches, and Chimp A moves away from Chimp B. Chimp C sits down close to Chimp B. Chimp A turns away and looks intently at his hand.”

‘Male Dog A is sitting with female Dog B. Another male, Dog C, approaches, and Dog A moves away from Dog B. Dog C sits down close to Dog B. Dog A turns away and looks intently at his paw.”

‘Male Newt A is swimming with female Newt B. Another male, Newt C, approaches, and Newt A swims away from Newt B. Newt C swims close to Newt B. Newt A turns away and looks intently at his foot.”

C.1.2 Jealousy (adapted from Mitchell & Hamm, 1997)

‘Male Child A is sitting with female Child B. Child A touches Child B on the arm. Another male, Child C, rushes over and moves between them, facing and staring at Child A.”

‘Male Chimp A is sitting with female Chimp B. Chimp A touches Chimp B on the arm. Another male, Chimp C, rushes over and moves between them, facing and staring at Chimp A.”

‘Male Dog A is sitting with female Dog B. Dog A touches Dog B on the arm. Another male, Dog C, rushes over and moves between them, facing and staring at Dog A.”

‘Male Newt A is swimming with female Newt B. Newt A touches Newt B on the fin. Another male, Newt C, swims over and moves between them, facing and staring at Newt A.”

C.1.3 Deception (after Whiten & Byrne, 1988)

‘Child A is playing in the kitchen and finds some sweets hidden in a cupboard. Child B enters the kitchen and Child A quietly closes the cupboard and looks away. When Child B leaves, Child A opens the cupboard and eats the sweets.”

“Chimp A is playing in an enclosure and finds some food hidden under a box. Chimp B enters the enclosure and Chimp A quietly places the box back over the food and looks away. When Chimp B leaves, Chimp A lifts the box and eats the food.”

“Dog A is digging in the garden and unearths an old bone. Dog B enters the garden and Dog A sits in front of the bone and faces the other way. When Dog B leaves, Dog A turns around and starts to chew on the bone.”

“Newt A is swimming in a pond and finds some food behind a rock. Newt B swims over and Newt A swims away from the rock and faces the other way. When Newt B swims off again, Newt A swims back to the rock and eats the food.”

C.1.4 Reconciliation (after de Waal & van Roosmalen, 1979)

“While playing a game, Child A backs into Child B and knocks Child B over. Child B gets up and hits Child A in the arm, then walks away. Later that day, Child A offers Child B some chocolate. Child B takes the chocolate and sits down next to Child A.”

“While climbing in their enclosure, Chimp A backs into Chimp B and knocks Chimp B over. Chimp B gets up and bites Chimp A on the arm, then walks away. Later that day, Chimp A offers Chimp B some food. Chimp B takes the food and sits down next to Chimp A.”

‘While running in the park, Dog A backs into Dog B and knocks Dog B over. Dog B gets up and bites Dog A on the leg, then runs off. Later that day, Dog A offers Dog B a bone. Dog B takes the bone and sits down next to Dog A.”

‘While swimming, Newt A knocks into Newt B. Newt B swims over and bites Newt A, then swims off. Later that day, Newt A offers Newt B some food. Newt B eats the food and swims along beside Newt A.”

C.1.5 Problem-solving (after Kohler, 1925)

‘Child A sees some biscuits on a high shelf in the kitchen. Child A moves a chair over from the table so that it is beneath the shelf, climbs up onto the chair and reaches the biscuits. Child A eats the biscuits.”

‘Chimp A sees some food on a high ledge in the enclosure. Chimp A moves a large box over from one side of the enclosure so that it is beneath the ledge, climbs up onto the box and reaches the food. Chimp A eats the food.”

‘Dog A sees some food on a high shelf. Dog A moves a chair over from the table so that it is beneath the shelf, climbs up onto the chair and reaches the food. Dog A eats the food.”

‘Newt A sees an insect resting on a high blade of grass. Newt A moves a pebble so that it is beside the blade of grass, climbs up onto the pebble and reaches the insect. Newt A eats the insect.”

Appendix C.2 – MATERIAL FOR EXPERIMENT 8B

C.2.1 Emotional concealment (adapted from Mitchell & Hamm, 1997)

“A male child is sitting with a female child. Another male child approaches, and the first male moves away from the female child. The second male child sits down close to the female. The other male turns away and looks closely at his hand.”

“A male chimp is sitting with a female chimp. Another male chimp approaches, and the first male moves away from the female chimp. The second male chimp sits down close to the female. The other male turns away and looks closely at his hand.”

“A male dog is sitting with a female dog. Another male dog approaches, and the first male moves away from the female dog. The second male dog sits down close to the female. The other male turns away and looks closely at his paw.”

“A male newt is swimming with a female newt. Another male newt approaches, and the first male swims away from the female newt. The second male newt swims close to the female. The other male turns away and looks closely at his foot.”

C.2.2 Jealousy (adapted from Mitchell & Hamm, 1997)

“A male child is sitting with a female child. The male child touches the female child on the arm. Another male child rushes over and moves between them, facing and staring at the first male child.”

“A male chimp is sitting with a female chimp. The male chimp touches the female chimp on the arm. Another male chimp rushes over and moves between them, facing and staring at the first male chimp.”

“A male dog is sitting with a female dog. The male dog touches the female dog on the leg. Another male dog rushes over and moves between them, facing and staring at the first male dog.”

“A male newt is swimming with a female newt. The male newt touches the female newt on the arm. Another male newt swims over and moves between them, facing and staring at the first male newt.”

C.2.3 Deception (after Whiten & Byrne, 1988)

“A child is playing in the kitchen and finds some sweets hidden in a cupboard. A second child enters the kitchen and the first child quietly closes the cupboard and looks away. When the second child leaves, the first child opens the cupboard and eats the sweets.”

“A chimp is playing in an enclosure and finds some food hidden under a box. A second chimp enters the enclosure and the first chimp quietly places the box back over the food and looks away. When the second chimp leaves, the first chimp lifts the box and eats the food.”

"A dog is digging in the garden and unearths an old bone. A second dog enters the garden and the first dog sits in front of the bone and looks away. When the second dog leaves, the first dog turns around and starts to chew on the bone."

"A newt is swimming in a pond and finds some food behind a rock. A second newt swims over. The first newt swims away from the rock and faces the other way. When the second newt swims off again, the first newt swims back to the rock and eats the food."

C.2.4 Reconciliation (after de Waal & van Roosmalen, 1979)

"While playing a game, one child backs into a second child and knocks him over. The second child gets up and hits the first child in the arm, then walks away. Later that day, the first child offers the second some chocolate. He takes the chocolate and sits down next to the first child."

"While climbing in their enclosure, one chimp backs into a second chimp and knocks him over. The second chimp gets up and bites the first chimp on the arm, then walks away. Later that day, the first chimp offers the second some food. He takes the food and sits down next to the first chimp."

"While running in the park, one dog backs into a second dog and knocks him over. The second dog gets up and bites the first dog on the leg, then runs off. Later that day, the first dog offers the second dog a bone. He takes the bone and sits down next to the first dog."

"While swimming, one newt knocks into a second newt. The second newt swims over and bites the first newt on the arm, then swims away. Later that day, the first newt offers the second some food. The first newt eats the food and swims alongside the first newt."

C.2.5 Problem-solving (after Kohler, 1925)

"A child is in the kitchen. Some biscuits are on a high shelf. The child moves a chair over from the table so that it is beneath the shelf, climbs up onto the chair and reaches the biscuits. The child eats the biscuits."

"A chimp is in an enclosure. Some food is on a high ledge. The chimp moves a large box over from one side of the enclosure so that it is beneath the ledge, climbs up onto the box and reaches the food. The chimp eats the food."

"A dog is in the kitchen. Some food is on a high shelf. The dog moves a chair over from the table so that it is beneath the shelf, climbs up onto the chair and reaches the food. The dog eats the food."

"A newt is swimming in a pond. An insect is resting on a high blade of grass near the pond. The newt moves a pebble so that it is beside the blade of grass, climbs up onto the pebble and reaches the insect. The newt eats the insect."

APPENDIX D - TABLES FOR CHAPTER 11

Appendix D.1 – MATING PROBABILITIES FOR MODEL 1A

The probabilities that each of the 148 possible matings will give rise to each phenogenotype in Model 1a.

	MATING				FREQ	OFFSPRING									
						Monogamy		Polygyny				Polyandry			
					c0	c1	c2	c3	c4	c5	c6	c7	c8	c9	c10
	Male1	Female1	Male2	Female2		*MBpp*	*MBsp*	*MBpp*	*MBsp*	*mBpp*	*mBsp*	*MBpp*	*MBsp*	*mBpp*	*mBsp*
r1	*MBpp*	*MBpp*			x1y1	1									
r2	*MBpp*	*MBsp*			x1y2	1/2-*b1*	1/2+*b1*								
r3	*MBsp*	*MBpp*			x2y1	1/2-*b1*	1/2+*b1*								
r4	*MBsp*	*MBsp*			x2y2		1								
r5	*mBpp*	*MBpp*		*MBpp*	x3y1y1			1/2		1/2					
r6	*mBpp*	*MBpp*		*MBsp*	x3y1y2			3/8	1/8	3/8	1/8				
r7	*mBpp*	*MBsp*		*MBpp*	x3y2y1			3/8	1/8	3/8	1/8				
r8	*mBpp*	*MBsp*		*MBsp*	x3y2y2			1/4	1/4	1/4	1/4				
r9	*mBsp*	*MBpp*		*MBpp*	x4y1y1			1/4	1/4	1/4	1/4				
r10	*mBsp*	*MBpp*		*MBsp*	x4y1y2			1/8	3/8	1/8	3/8				
r11	*mBsp*	*MBsp*		*MBpp*	x4y2y1			1/8	3/8	1/8	3/8				
r12	*mBsp*	*MBsp*		*MBsp*	x4y2y2				1/2		1/2				
r13	*MBpp*	*mBpp*	*MBpp*		y3x1x1							1/2		1/2	
r14	*MBpp*	*mBpp*	*MBsp*		y3x1x2							3/8	1/8	3/8	1/8
r15	*MBsp*	*mBpp*	*MBpp*		y3x2x1							3/8	1/8	3/8	1/8
r16	*MBsp*	*mBpp*	*MBsp*		y3x2x2							1/4	1/4	1/4	1/4
r17	*MBpp*	*mBsp*	*MBpp*		y4x1x1							1/4	1/4	1/4	1/4
r18	*MBpp*	*mBsp*	*MBsp*		y4x1x2							1/8	3/8	1/8	3/8
r19	*MBsp*	*mBsp*	*MBpp*		y4x2x1							1/8	3/8	1/8	3/8
r20	*MBsp*	*mBsp*	*MBsp*		y4x2x2								1/2		1/2

Appendix D.1 (cont.)

	MATING				FREQ	OFFSPRING			
						Polygynandry			
					c0	c11	c12	c13	c14
	Male1	Female1	Male2	Female2		*MBpp*	*MBsp*	*mBpp*	*mBsp*
r21	*MBpp*	*mBpp*	*mBpp*	*MBpp*	x1y3x3y1	3/8		5/8	
r22	*MBpp*	*mBpp*	*mBpp*	*MBsp*	x1y3x3y2	2/8	1/8	4/8	1/8
r23	*MBpp*	*mBpp*	*mBpp*	*mBpp*	x1y3x3y3	1/8		7/8	
r24	*MBpp*	*mBpp*	*mBpp*	*mBsp*	x1y3x3y4	1/8		5/8	2/8
r25	*MBsp*	*mBpp*	*mBpp*	*MBpp*	x2y3x3y1	5/16	1/16	9/16	1/16
r26	*MBsp*	*mBpp*	*mBpp*	*MBsp*	x2y3x3y2	3/16	3/16	7/16	3/16

r27	*MBsp*	*mBpp*	*mBpp*	*mBpp*	x2y3x3y3	1/16	1/16	13/16	1/16
r28	*MBsp*	*mBpp*	*mBpp*	*mBsp*	x2y3x3y4	1/16	1/16	9/16	5/16
r29	*MBpp*	*mBsp*	*mBpp*	*MBpp*	x1y4x3y1	5/16	1/16	7/16	3/16
r30	*MBpp*	*mBsp*	*mBpp*	*MBsp*	x1y4x3y2	3/16	3/16	5/16	5/16
r31	*MBpp*	*mBsp*	*mBpp*	*mBpp*	x1y4x3y3	1/16	1/16	11/16	3/16
r32	*MBpp*	*mBsp*	*mBpp*	*mBsp*	x1y4x3y4	1/16	1/16	7/16	7/16
r33	*MBpp*	*mBpp*	*mBsp*	*MBpp*	x1y3x4y1	2/8	1/8	3/8	2/8
r34	*MBpp*	*mBpp*	*mBsp*	*MBsp*	x1y3x4y2	1/8	2/8	2/8	3/8
r35	*MBpp*	*mBpp*	*mBsp*	*mBpp*	x1y3x4y3	1/8		4/8	3/8
r36	*MBpp*	*mBpp*	*mBsp*	*mBsp*	x1y3x4y4	1/8		2/8	5/8
r37	*MBsp*	*mBsp*	*mBpp*	*MBpp*	x2y4x3y1	2/8	1/8	3/8	2/8
r38	*MBsp*	*mBsp*	*mBpp*	*MBsp*	x2y4x3y2	1/8	2/8	2/8	3/8
r39	*MBsp*	*mBsp*	*mBpp*	*mBpp*	x2y4x3y3		1/8	5/8	2/8
r40	*MBsp*	*mBsp*	*mBpp*	*mBsp*	x2y4x3y4		1/8	3/8	4/8
r41	*MBsp*	*mBpp*	*mBsp*	*MBpp*	x2y3x4y1	3/16	3/16	5/16	5/16
r42	*MBsp*	*mBpp*	*mBsp*	*MBsp*	x2y3x4y2	1/16	5/16	3/16	7/16
r43	*MBsp*	*mBpp*	*mBsp*	*mBpp*	x2y3x4y3	1/16	1/16	7/16	7/16
r44	*MBsp*	*mBpp*	*mBsp*	*mBsp*	x2y3x4y4	1/16	1/16	3/16	11/16
r45	*MBpp*	*mBsp*	*mBsp*	*MBpp*	x1y4x4y1	3/16	3/16	3/16	7/16
r46	*MBpp*	*mBsp*	*mBsp*	*MBsp*	x1y4x4y2	1/16	5/16	1/16	9/16
r47	*MBpp*	*mBsp*	*mBsp*	*mBpp*	x1y4x4y3	1/16	1/16	5/16	9/16
r48	*MBpp*	*mBsp*	*mBsp*	*mBsp*	x1y4x4y4	1/16	1/16	1/16	13/16
r49	*MBsp*	*mBsp*	*mBsp*	*MBpp*	x2y4x4y1	1/8	2/8	1/8	4/8
r50	*MBsp*	*mBsp*	*mBsp*	*MBsp*	x2y4x4y2		3/8		5/8
r51	*MBsp*	*mBsp*	*mBsp*	*mBpp*	x2y4x4y3		1/8	2/8	5/8
r52	*MBsp*	*mBsp*	*mBsp*	*mBsp*	x2y4x4y4		1/8		7/8
r53	*mBpp*	*MBpp*	*MBpp*	*mBpp*	x3y1x1y3	3/8		5/8	
r54	*mBpp*	*MBpp*	*MBsp*	*mBpp*	x3y1x2y3	5/16	1/16	9/16	1/16
r55	*mBpp*	*MBpp*	*mBpp*	*mBpp*	x3y1x3y3	4/16		12/16	
r56	*mBpp*	*MBpp*	*mBsp*	*mBpp*	x3y1x4y3	2/8		5/8	1/8
r57	*mBpp*	*MBsp*	*MBpp*	*mBpp*	x3y2x1y3	2/8	1/8	4/8	1/8
r58	*mBpp*	*MBsp*	*MBsp*	*mBpp*	x3y2x2y3	3/16	3/16	7/16	3/16
r59	*mBpp*	*MBsp*	*mBpp*	*mBpp*	x3y2x3y3	2/16	2/16	10/16	2/16
r60	*mBpp*	*MBsp*	*mBsp*	*mBpp*	x3y2x4y3	2/16	2/16	8/16	4/16
r61	*mBsp*	*MBpp*	*MBpp*	*mBpp*	x4y1x1y3	2/8	1/8	3/8	2/8
r62	*mBsp*	*MBpp*	*MBsp*	*mBpp*	x4y1x2y3	3/16	3/16	5/16	5/16
r63	*mBsp*	*MBpp*	*mBpp*	*mBpp*	x4y1x3y3	2/16	2/16	8/16	4/16
r64	*mBsp*	*MBpp*	*mBsp*	*mBpp*	x4y1x4y3	2/16	2/16	6/16	6/16
r65	*mBpp*	*MBpp*	*MBpp*	*mBsp*	x3y1x1y4	5/16	1/16	7/16	3/16
r66	*mBpp*	*MBpp*	*MBsp*	*mBsp*	x3y1x2y4	2/8	1/8	3/8	2/8
r67	*mBpp*	*MBpp*	*mBpp*	*mBsp*	x3y1x3y4	4/16		8/16	4/16
r68	*mBpp*	*MBpp*	*mBsp*	*mBsp*	x3y1x4y4	2/8		3/8	3/8
r69	*mBsp*	*MBsp*	*MBpp*	*mBpp*	x4y2x1y3	1/8	2/8	2/8	3/8
r70	*mBsp*	*MBsp*	*MBsp*	*mBpp*	x4y2x2y3	1/16	5/16	3/16	7/16
r71	*mBsp*	*MBsp*	*mBpp*	*mBpp*	x4y2x3y3		2/8	3/8	3/8
r72	*mBsp*	*MBsp*	*mBsp*	*mBpp*	x4y2x4y3		1/4	1/4	1/2
r73	*mBpp*	*MBsp*	*MBpp*	*mBsp*	x3y2x1y4	3/16	3/16	5/16	5/16

r74	*mBpp*	*MBsp*	*MBsp*	*mBsp*	x3y2x2y4	1/8	2/8	2/8	3/8
r75	*mBpp*	*MBsp*	*mBpp*	*mBsp*	x3y2x3y4	1/8	1/8	3/8	3/8
r76	*mBpp*	*MBsp*	*mBsp*	*mBsp*	x3y2x4y4	1/8	1/8	2/8	4/8
r77	*mBsp*	*MBpp*	*MBpp*	*mBsp*	x4y1x1y4	3/16	3/16	3/16	7/16
r78	*mBsp*	*MBpp*	*MBsp*	*mBsp*	x4y1x2y4	1/8	2/8	1/8	4/8
r79	*mBsp*	*MBpp*	*mBpp*	*mBsp*	x4y1x3y4	1/8	1/8	2/8	4/8
r80	*mBsp*	*MBpp*	*mBsp*	*mBsp*	x4y1x4y4	1/8	1/8	1/8	5/8
r81	*mBsp*	*MBsp*	*MBpp*	*mBsp*	x4y2x1y4	1/16	5/16	1/16	9/16
r82	*mBsp*	*MBsp*	*MBsp*	*mBsp*	x4y2x2y4		3/8		5/8
r83	*mBsp*	*MBsp*	*mBpp*	*mBsp*	x4y2x3y4		2/8	1/8	5/8
r84	*mBsp*	*MBsp*	*mBsp*	*mBsp*	x4y2x4y4		1/4		3/4
r85	*mBpp*	*mBpp*	*MBpp*	*MBpp*	x3y3x1y1	3/8		5/8	
r86	*mBpp*	*mBpp*	*MBpp*	*MBsp*	x3y3x1y2	2/8	1/8	4/8	1/8
r87	*mBpp*	*mBpp*	*MBpp*	*mBpp*	x3y3x1y3	1/8		7/8	
r88	*mBpp*	*mBpp*	*MBpp*	*mBsp*	x3y3x1y4	1/8		5/8	2/8
r89	*mBpp*	*mBpp*	*MBsp*	*MBpp*	x3y3x2y1	5/16	1/16	9/16	1/16
r90	*mBpp*	*mBpp*	*MBsp*	*MBsp*	x3y3x2y2	3/16	3/16	7/16	3/16
r91	*mBpp*	*mBpp*	*MBsp*	*mBpp*	x3y3x2y3	1/16	1/16	13/16	1/16
r92	*mBpp*	*mBpp*	*MBsp*	*mBsp*	x3y3x2y4	1/16	1/16	9/16	5/16
r93	*mBpp*	*mBpp*	*mBpp*	*MBpp*	x3y3x3y1	1/4		3/4	
r94	*mBpp*	*mBpp*	*mBpp*	*MBsp*	x3y3x3y2	1/8	1/8	5/8	1/8
r95	*mBpp*	*mBpp*	*mBpp*	*mBpp*	x3y3x3y3			1	
r96	*mBpp*	*mBpp*	*mBpp*	*mBsp*	x3y3x3y4			3/4+*b2*	1/4-*b2*
r97	*mBpp*	*mBpp*	*mBsp*	*MBpp*	x3y3x4y1	2/8		5/8	1/8
r98	*mBpp*	*mBpp*	*mBsp*	*MBsp*	x3y3x4y2	1/8	1/8	4/8	2/8
r99	*mBpp*	*mBpp*	*mBsp*	*mBpp*	x3y3x4y3			7/8	1/8
r100	*mBpp*	*mBpp*	*mBsp*	*mBsp*	x3y3x4y4			5/8	3/8
r101	*mBpp*	*mBsp*	*MBpp*	*MBpp*	x3y4x1y1	5/16	1/16	7/16	3/16
r102	*mBpp*	*mBsp*	*MBpp*	*MBsp*	x3y4x1y2	3/16	3/16	5/16	5/16
r103	*mBpp*	*mBsp*	*MBpp*	*mBpp*	x3y4x1y3	1/16	1/16	11/16	3/16
r104	*mBpp*	*mBsp*	*MBpp*	*mBsp*	x3y4x1y4	1/16	1/16	7/16	7/16
r105	*mBpp*	*mBsp*	*MBsp*	*MBpp*	x3y4x2y1	2/8	1/8	3/8	2/8
r106	*mBpp*	*mBsp*	*MBsp*	*MBsp*	x3y4x2y2	1/8	2/8	2/8	3/8
r107	*mBpp*	*mBsp*	*MBsp*	*mBpp*	x3y4x2y3		1/8	5/8	2/8
r108	*mBpp*	*mBsp*	*MBsp*	*mBsp*	x3y4x2y4		1/8	3/8	4/8
r109	*mBpp*	*mBsp*	*mBpp*	*MBpp*	x3y4x3y1	1/4		1/2	1/4
r110	*mBpp*	*mBsp*	*mBpp*	*MBsp*	x3y4x3y2	1/8	1/8	3/8	3/8
r111	*mBpp*	*mBsp*	*mBpp*	*mBpp*	x3y4x3y3			3/4+*b2*	1/4-*b2*
r112	*mBpp*	*mBsp*	*mBpp*	*mBsp*	x3y4x3y4			1/2+*b2*	1/2-*b2*
r113	*mBpp*	*mBsp*	*mBsp*	*MBpp*	x3y4x4y1	2/8		3/8	3/8
r114	*mBpp*	*mBsp*	*mBsp*	*MBsp*	x3y4x4y2	1/8	1/8	2/8	4/8
r115	*mBpp*	*mBsp*	*mBsp*	*mBpp*	x3y4x4y3			5/8+*b2*	3/8-*b2*
r116	*mBpp*	*mBsp*	*mBsp*	*mBsp*	x3y4x4y4			3/8+*b2*	5/8-*b2*
r117	*mBsp*	*mBpp*	*MBpp*	*MBpp*	x4y3x1y1	2/8	1/8	3/8	2/8
r118	*mBsp*	*mBpp*	*MBpp*	*MBsp*	x4y3x1y2	1/8	2/8	2/8	3/8
r119	*mBsp*	*mBpp*	*MBpp*	*mBpp*	x4y3x1y3	1/8		4/8	3/8
r120	*mBsp*	*mBpp*	*MBpp*	*mBsp*	x4y3x1y4	1/8		2/8	5/8

r121	*mBsp*	*mBpp*	*MBsp*	*MBpp*	x4y3x2y1	3/16	3/16	5/16	5/16
r122	*mBsp*	*mBpp*	*MBsp*	*MBsp*	x4y3x2y2	1/16	5/16	3/16	7/16
r123	*mBsp*	*mBpp*	*MBsp*	*mBpp*	x4y3x2y3	1/16	1/16	7/16	7/16
r124	*mBsp*	*mBpp*	*MBsp*	*mBsp*	x4y3x2y4	1/16	1/16	3/16	11/16
r125	*mBsp*	*mBpp*	*mBpp*	*MBpp*	x4y3x3y1	1/8	1/8	4/8	2/8
r126	*mBsp*	*mBpp*	*mBpp*	*MBsp*	x4y3x3y2		2/8	3/8	3/8
r127	*mBsp*	*mBpp*	*mBpp*	*mBpp*	x4y3x3y3			5/8+*b2*	3/8-*b2*
r128	*mBsp*	*mBpp*	*mBpp*	*mBsp*	x4y3x3y4			3/8+*b2*	5/8-*b2*
r129	*mBsp*	*mBpp*	*mBsp*	*MBpp*	x4y3x4y1	1/8	1/8	3/8	3/8
r130	*mBsp*	*mBpp*	*mBsp*	*MBsp*	x4y3x4y2		2/8	2/8	4/8
r131	*mBsp*	*mBpp*	*mBsp*	*mBpp*	x4y3x4y3			4/8+*b2*	4/8-*b2*
r132	*mBsp*	*mBpp*	*mBsp*	*mBsp*	x4y3x4y4			2/8+*b2*	6/8-*b2*
r133	*mBsp*	*mBsp*	*MBpp*	*MBpp*	x4y4x1y1	3/16	3/16	3/16	7/16
r134	*mBsp*	*mBsp*	*MBpp*	*MBsp*	x4y4x1y2	1/16	5/16	1/16	9/16
r135	*mBsp*	*mBsp*	*MBpp*	*mBpp*	x4y4x1y3	1/16	1/16	5/16	9/16
r136	*mBsp*	*mBsp*	*MBpp*	*mBsp*	x4y4x1y4	1/16	1/16	1/16	13/16
r137	*mBsp*	*mBsp*	*MBsp*	*MBpp*	x4y4x2y1	1/8	2/8	1/8	4/8
r138	*mBsp*	*mBsp*	*MBsp*	*MBsp*	x4y4x2y2		3/8		5/8
r139	*mBsp*	*mBsp*	*MBsp*	*mBpp*	x4y4x2y3		1/8	2/8	5/8
r140	*mBsp*	*mBsp*	*MBsp*	*mBsp*	x4y4x2y4		1/8		7/8
r141	*mBsp*	*mBsp*	*mBpp*	*MBpp*	x4y4x3y1	1/8	1/8	2/8	4/8
r142	*mBsp*	*mBsp*	*mBpp*	*MBsp*	x4y4x3y2		2/8	1/8	5/8
r143	*mBsp*	*mBsp*	*mBpp*	*mBpp*	x4y4x3y3			3/8+*b2*	5/8-*b2*
r144	*mBsp*	*mBsp*	*mBpp*	*mBsp*	x4y4x3y4			1/8	7/8
r145	*mBsp*	*mBsp*	*mBsp*	*MBpp*	x4y4x4y1	1/8	1/8	1/8	5/8
r146	*mBsp*	*mBsp*	*mBsp*	*MBsp*	x4y4x4y2		2/8		6/8
r147	*mBsp*	*mBsp*	*mBsp*	*mBpp*	x4y4x4y3			2/8+*b2*	6/8-*b2*
r148	*mBsp*	*mBsp*	*mBsp*	*mBsp*	x4y4x4y4				1

Appendix D.2 – MATING PROBABILITIES FOR MODEL 1B

The probabilities that each of the 11 possible matings will give rise to each phenogenotype in Model 1b (oblique cultural transmission). z is the frequency of *Bpp* in the parental generation.

	MATING				FREQ	OFFSPRING					
						Monogamy		Polygyny			
					c0	c1	c2	c3	c4	c5	c6
	Male1	Female1	Male2	Female2		*MBpp*	*MBsp*	*MBpp*	*MBsp*	*mBpp*	*mBsp*
r1	*M*	*M*			(x1+x2)(y1+y2)	$z - b1\ z$	$1-z+b1\ z$				
r2	*m*	*M*		*M*	(x3+x4)(y1+y2)(y1+y2)			$0.5\ z$	$0.5(1-z)$	$0.5\ z$	$0.5(1-z)$
r3	*M*	*m*	*M*		(x1+x2)(y3+y4)(x1+x2)						
r4	*M*	*m*	*m*	*M*	(x1+x2)(y3+y4)(x3+x4)(y1+y2)						
r5	*M*	*m*	*m*	*m*	(x1+x2)(y3+y4)(x3+x4)(y3+y4)						
r6	*m*	*M*	*M*	*m*	(x3+x4)(y1+y2)(x1+x2)(y3+y4)						
r7	*m*	*M*	*m*	*m*	(x3+x4)(y1+y2)(x3+x4)(y3+y4)						
r8	*m*	*m*	*M*	*M*	(x3+x4)(y3+y4)(x1+x2)(y1+y2)						
r9	*m*	*m*	*M*	*m*	(x3+x4)(y3+y4)(x1+x2)(y3+y4)						
r10	*m*	*m*	*m*	*M*	(x3+x4)(y3+y4)(x3+x4)(y1+y2)						
r11	*m*	*m*	*m*	*m*	(x3+x4)(y3+y4)(x3+x4)(y3+y4)						

Appendix D.2 (cont.)

	MATING				FREQ	OFFSPRING							
						Polyandry				Polygynandry			
					c0	c7	c8	c9	c10	c11	c12	c13	c14
	Male1	Female1	Male2	Female2		*MBpp*	*MBsp*	*mBpp*	*mBsp*	*MBpp*	*MBsp*	*mBpp*	*mBsp*
r1	*M*	*M*			(x1+x2)(y1+y2)								
r2	*m*	*M*		*M*	(x3+x4)(y1+y2)(y1+y2)								
r3	*M*	*m*	*M*		(x1+x2)(y3+y4)(x1+x2)	0.5 *z*	0.5(1-*z*)	0.5 *z*	0.5(1-*z*)				
r4	*M*	*m*	*m*	*M*	(x1+x2)(y3+y4)(x3+x4)(y1+y2)					3/8 *z*	3/8(1-*z*)	5/8 *z*	5/8(1-*z*)
r5	*M*	*m*	*m*	*m*	(x1+x2)(y3+y4)(x3+x4)(y3+y4)					1/8 *z*	1/8(1-*z*)	7/8 *z*	7/8(1-*z*)
r6	*m*	*M*	*M*	*m*	(x3+x4)(y1+y2)(x1+x2)(y3+y4)					3/8 *z*	3/8(1-*z*)	5/8 *z*	5/8(1-*z*)
r7	*m*	*M*	*m*	*m*	(x3+x4)(y1+y2)(x3+x4)(y3+y4)					1/8 *z*	1/8(1-*z*)	7/8 *z*	7/8(1-*z*)
r8	*m*	*m*	*M*	*M*	(x3+x4)(y3+y4)(x1+x2)(y1+y2)					0.5 *z*	0.5(1-*z*)	0.5 *z*	0.5(1-*z*)
r9	*m*	*m*	*M*	*m*	(x3+x4)(y3+y4)(x1+x2)(y3+y4)					1/8 *z*	1/8(1-*z*)	7/8 *z*	7/8(1-*z*)
r10	*m*	*m*	*m*	*M*	(x3+x4)(y3+y4)(x3+x4)(y1+y2)					1/4 *z*	1/4(1-*z*)	3/4 *z*	¾(1-*z*)
r11	*m*	*m*	*m*	*m*	(x3+x4)(y3+y4)(x3+x4)(y3+y4)							*z*+*b2*(1-*z*)	1-*z*-*b2*(1-*z*)