Evolution and Human Behavior 35 (2014) 285–290

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.ehbonline.org

Original Article

An experimental demonstration of the effect of group size on cultural accumulation☆

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ARTICLE INFO

Article history:
Initial receipt 3 May 2013
Final revision received 27 February 2014

Keywords:
Cumulative culture
Group size
Human evolution

ABSTRACT

Cumulative culture is thought to have played a major role in hominin evolution, and so an understanding of the factors that affect cultural accumulation is important for understanding human evolution. Population size may be one such factor, with larger populations thought to be able to support more complex cultural traits. This hypothesis has been suggested by mathematical models and empirical studies of small-scale societies. However, to date there have been few experimental demonstrations of an effect of population size on cultural accumulation. Here we provide such a demonstration using a novel task, solving jigsaw puzzles. 80 participants divided into ten transmission chains solved puzzles in one of two conditions: one in which participants had access to one semi-completed puzzle from the previous generation, and the other in which participants simultaneously saw three semi-completed puzzles from the previous generation. As predicted, the mean number of pieces solved increased over time in the three-puzzle-per-generation condition, but not in the one-puzzle-per-generation condition. Thus, our experiment provides support for a hypothesized relationship between population size and cultural accumulation. In particular, our results suggest that the ability to simultaneously learn from multiple cultural models, and combine the knowledge of those multiple models, is most likely to allow larger groups to support more complex culture.

1. Introduction

Cultural evolution is likely to have played a crucial role in hominin evolution. Examples of this include the spread of cooking and tool-use in earlier hominin species (Carmody & Wrangham, 2009; Foley & Lahr, 2003), and agriculture and writing in our own (Goody & Watt, 1963; O'Brien & Laland, 2012). Moreover, while social learning and cultural differences between populations are common in several non-human species (Galef & Laland, 2005), cumulative culture, defined as cultural traits that are dependent on other cultural traits (Boyd & Richerson, 1996; Enquist, Ghirlanda, & Eriksson, 2011), may be unique to hominins (e.g. Dean, Kendal, Schapiro, Lambeth, Thierry, & Laland, 2012). Cumulative culture is often characterised by the presence of traits that are too complex to have been invented by a single individual, instead having accumulated over multiple generations (Boyd & Richerson, 1996; Tomasello, Kruger, & Ratner, 1993). Such traits are ubiquitous in human domains such as technology, science, and mathematics (Basalla, 1988; Hodgkin, 2005; Longair, 2003), and clearly played a crucial role in our current ecological success. Thus, an understanding of the factors that help or hinder the emergence of cumulative culture is important for understanding hominin evolution.

One factor that has been proposed to be related to the emergence and maintenance of cumulative culture is population size. In an influential paper, Henrich (2004) constructed a mathematical model providing a potential mechanism by which population size partly determines the cultural complexity attainable by that population. In Henrich's model, a population of a given size reproduces in discrete generations, and in each generation every adult member of the population acquires a cultural trait which can be more or less functional, the functionality being measured quantitatively. For example, the trait could be a bow-and-arrow, and its functional measurement how far it shoots, or the trait could be a stone handaxe and its functional measurement how sharp it is. Each individual acquires the trait by copying the single individual in the previous generation with the most functional (i.e. 'best') version of the trait. However, they copy this individual imperfectly, so that most individuals make copying errors and acquire a version of the trait that is worse than that of their model, and a few individuals innovate successfully and acquire a version of the trait that is better than that of their model. This imperfect copying process is assumed to be random, so that each individual acquires a trait of different quality compared to other individuals.

Henrich (2004) showed that, given these assumptions, a population of a given size can maintain the transmission of a trait only up to a given functional level, or 'complexity'. Versions of the trait with greater complexity than the stable level will tend through transmission to get worse, and versions with lesser complexity than the stable

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☆ This research was funded by the Leverhulme Trust.

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http://dx.doi.org/10.1016/j.evolhumbehav.2014.02.009
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level to improve, until the stable level is reached. This stable level increases with the size of the population, because the more individuals there are, the greater is the chance that large gains in functionality will occur through innovation and be copied by the next generation. In essence, more innovation takes place in larger populations. The stable level is of course determined by other factors in addition to the size of the population, most importantly its inherent complexity and difficulty to learn. Henrich's model has been extended by Powell, Shennan, and Thomas (2009; see also Shennan, 2001) to look at population density and migration between sub-populations; by Mesoudi (2011a) to include the cost of acquiring more complex knowledge; and by Kobayashi and Aoki (2012) to the case of overlapping rather than discrete generations.

Empirical support for the link between population size and cultural accumulation is generally supportive. Henrich (2004) himself used his model to explain the loss of various technologies (e.g. complex bone tools, spears, boomerangs, fire-making) in Tasmania after rising seas cut it off from Australia approximately 11,000 years ago, thereby creating a smaller sub-population. Powell et al. (2009) used their extended model to explain the emergence of ‘modern human behavior’ (e.g. symbolic artefacts, complex tools, musical instruments) during the Pleistocene, noting that human population density in Africa, Europe and the Middle East was, according to estimates made using population genetic data and theory, similar at the times when these behaviours emerged. Four studies have investigated the relationship between population sizes of hunter-gathering and food-producing societies on the size and complexity of their toolkits. Collard, Kemery, and Banks (2005) did not find a relationship in a sample of 20 hunter–gatherer populations mainly from North America; Kline and Boyd (2010) did find a relationship with both toolkit size and complexity among 10 Oceanic island populations; Collard, Buchanan, Ruttle, and O'Brien (2011) also did find a relationship with both toolkit size and complexity among 45 food-producing societies from around the world, but not among a similar sample of 34 hunter–gatherer societies; and finally, Collard, Ruttle, Buchanan, and O'Brien (2013) similarly found a relationship with both toolkit size and complexity among 40 food-producing societies from around the world. At greater time depths, Lycett and von Cramon-Taubadel (2008) showed that Acheulean handaxe diversity fitted the predictions of a serial founder effect model, i.e. diversity decreased with predicted decreasing population size as early hominins migrated from an African origin (see also Lycett & Norton, 2010). Thus, there is clearly some empirical support for a link between population size and cultural accumulation.

However, Henrich's (2004) model provides not only a population-level prediction – that cultural complexity should be dependent on population size – but also an individual-level mechanism underpinning that prediction. Regarding the latter, a crucial aspect of Henrich's model is that new, unknowledgeable individuals acquire their cultural knowledge from a single individual of the previous generation, and that this individual has the highest cultural complexity of their generation (i.e. individuals employ success-biased oblique cultural transmission). Under this mechanism, the population-size effect therefore works because larger populations are more likely, by chance, to contain highly successful individuals who are copied by the subsequent generation. While the assumption of success-biased cultural transmission is a reasonable one (see, for example, McElreath, Bell, Efferson, Lubell, Richerson, & Waring, 2008; Mesoudi, 2008, 2011b), learning from just a single individual may be less plausible. Indeed, Enquist, Strimling, Eriksson, Laland, and Sjöstrand (2010) found analytically that cultural transmission from multiple individuals is more likely to maintain knowledge in a population than learning from a single individual, albeit in a non-cumulative cultural system. One might expect that learning from multiple skilled individuals, and combining their knowledge in each generation, would be at least as effective a mechanism for maintaining and accumulating complex cultural knowledge than relying on just the most-skilled individual, particularly when such knowledge can be easily combined. Under this alternative mechanism, then, the population-size effect outlined by Henrich (2004) would still occur, but would occur instead because in larger populations, there are more models available from whom knowledge can be additively combined.

While archaeological and paleoanthropological studies of the kind described above can address the general prediction of cultural–demographic models (a positive relationship between population size and cultural complexity), they cannot test the validity of the underlying mechanism responsible for this effect, given that we cannot directly observe cultural transmission dynamics in long-dead populations (e.g. whether people typically copied one or more individuals, or whether they copied successful individuals). As such, even though there is general support for the link between population size and cultural complexity, this may not necessarily be through the mechanism assumed in existing models. To probe such mechanisms, laboratory experiments are needed, in which cultural transmission dynamics can be directly observed and factors can be isolated and their effects precisely measured (Mesoudi & Whiten, 2008).

To date, three studies have experimentally tested the link between population size and cultural accumulation. Caldwell and Millen (2010) asked participants to build paper airplanes that would fly as far as possible, with participants observing either one, two, or three previous participants building their paper airplanes as well as those participants' completed airplanes. They did not find that the distance the airplanes flew increased more rapidly or to a higher level as the number of models increased. Derex, Beugin, Godelle, and Raymond (2013) had groups of 2, 4, 8 or 16 participants design computer-generated arrowheads (a simple trait) and fishing nets (a complex trait), allowing participants to copy the design of one other participant given information about other participants' success. Derex et al. found that only in the two larger groups (8 and 16) were the simple designs improved, and the complex designs maintained, over successive generations. Finally, Muthukrishna, Shulman, Vasilescu, and Henrich (2014) had chains of participants – either one per generation or five per generation – draw a symbol using a complex graphics software package, or tie a complicated knot. Written instructions, final products and/or videotaped behaviour were transmitted between generations. As predicted, the symbols drawn by chains of five participants increased in complexity due to increasingly effective instructions compared to the chains of single participants, and the knots tied by chains of five participants were more likely to be maintained than the knots tied by the chains of single participants.

Derex et al. (2013) and Muthukrishna et al. (2014) therefore provide support for the overall prediction that cultural complexity is more likely to be maintained and accumulated in larger groups, although Caldwell and Millen (2010) found no effect. Regarding the mechanism, both Derex et al. (2013) and Muthukrishna et al. (2014) found that Henrich's (2004) assumption of success-biased transmission from a single model is a plausible means by which the population-size effect works. However, none of these studies provided a proper test of the alternative mechanism outlined above, where information is integrated from multiple sources. Derex et al. (2013) only allowed participants to learn from a single person at a time, given information about other participants' relative success. Muthukrishna et al. (2014) allowed the five-per-generation participants to view the solutions of all five previous participants simultaneously, potentially allowing the integration of multiple participants' knowledge, but in practice participants predominantly copied the single most successful participant of those five. Caldwell and Millen's (2010) participants could also view two or three models simultaneously, but the task used, building paper airplanes, was not conducive to integrating information across models because different airplane designs may be incompatible. That is, combining elements of

Fig. 1. The painting on the jigsaw puzzle. Image by John Francis; used with the kind permission of the copyright holder, Gibsons Games.

two different designs may sometimes lead to a better design, but often to an even worse design. The tasks used by Derex et al. and Muthukrishna et al. – making fishing nets and tying knots – similarly have solutions that are difficult to combine. Interestingly, a recent study by Eriksson and Coultas (2012), looking at the cultural transmission of written texts, found that more information was preserved during transmission when each generation had access to two previous participants' recall, compared to one previous participant's recall. While not designed as a test of cultural accumulation or the cultural–demographic models reviewed above, Eriksson & Coultas' study provides some support for the notion that having access to multiple cultural models can at least maintain information in a population better than having access to just a single model.

Our aim in this study is to explicitly test the population size hypothesis for cultural accumulation along the lines of previous experimental studies, but with a task – completing jigsaw puzzles – in which observations from multiple models can be easily combined into one solution. We compare transmission chains composed of a single individual per generation with chains composed of three individuals per generation, with the latter able to see the partially-completed puzzles of all three members of the previous generation simultaneously. If our prediction is upheld – that the three-participants-per-generation chains are more likely to accumulate knowledge (in the form of proportion of the puzzle completed) than the one-participant-per-generation chains – then this would suggest an additional mechanism by which population size influences cultural complexity to the one-parent success-biased cultural transmission currently assumed by population-demographic models and tested in previous experiments.

2. Methods

2.1. Participants

80 unpaid participants, undergraduate students at the Universities of Durham and Exeter, completed the study as part of their undergraduate courses. Ethical permission for the experiment was given by the Research Ethics and Data Protection Committee, Department of Anthropology, Durham University, and all participants read and signed informed consent forms.

2.2. Task and design

The experimental task was to complete a jigsaw puzzle. The puzzle had 100 pieces and measured 33.5 cm by 45 cm; the puzzle picture can be seen in Fig. 1. Participants were divided into 10 transmission chains, 5 in each of two conditions: *individuals* and *groups* of three (Fig. 2). Each transmission chain had four non-overlapping generations. Each participant was asked to complete as much of the puzzle as possible in 12 min, starting from scratch. (The written instructions were: 'You have 12 minutes to complete a jigsaw puzzle. Complete as much as you can.') Participants were not given a photo of the completed puzzle to help them; however, in generations after the first, participants were able to see the partially-completed puzzles created by the participants in the generation before them. In the individual condition this was one partially-completed puzzle, and in the group condition this was three partially-completed puzzles. In the latter condition, each of the three participants in one generation sat next to each other, but were divided by screens that obscured each others' puzzles, and they did not interact in any way; however they could each see all three of the previous generation's partially-completed puzzles. Before being presented to successive generations,

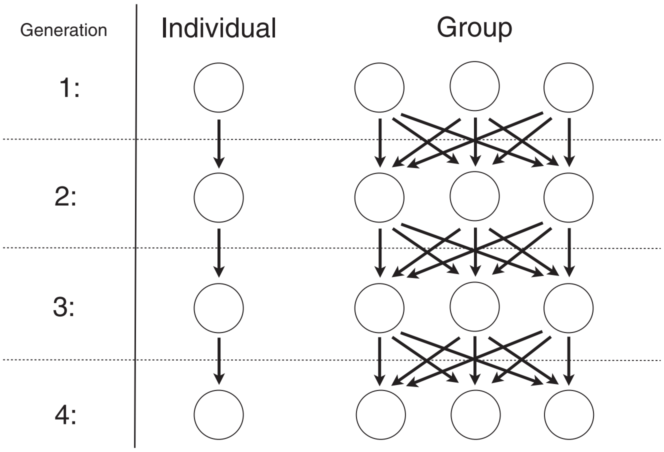

Fig. 2. An illustration of the experimental design. There were 5 replicate chains in each condition, giving 10 chains in all.

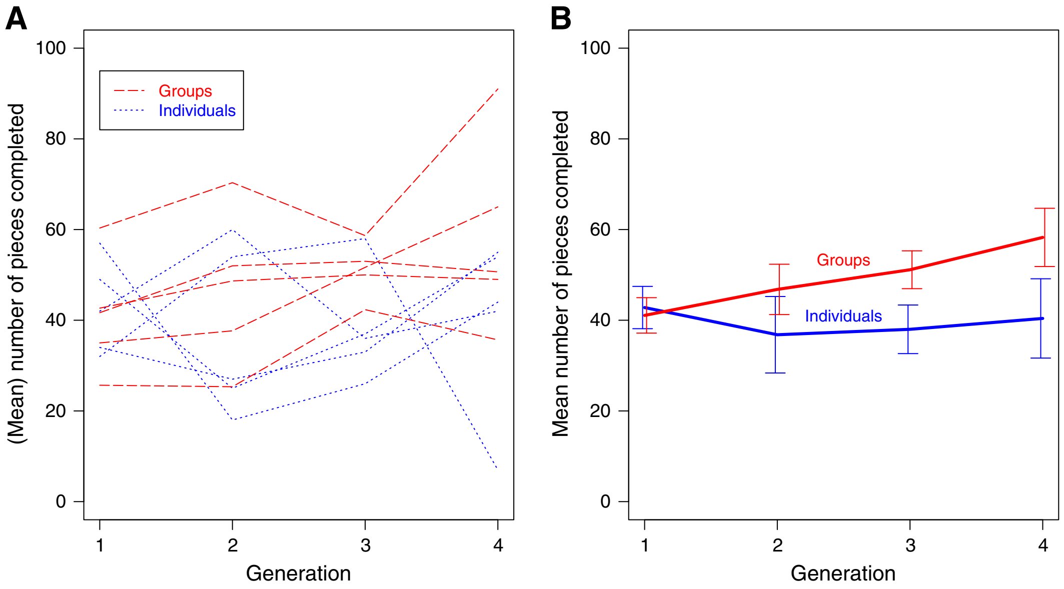

Fig. 3. The results of the experiment. (A) The number of pieces completed in each individual chain in both conditions. Each datapoint for the group condition shows the mean number of completed pieces across the three participants in that group. The full dataset is available in the electronic supplementary material. (B) Mean number of pieces completed in each condition. The error bars show standard errors.

all loose single pieces were removed from partially-completed puzzles, but the physical layout of completed pieces was not altered or standardised.

The outcome measure for each participant was the number of puzzle pieces that they correctly connected to at least one other puzzle piece. Sets of completed puzzle pieces did not need to form one large set to be counted; multiple small sets of completed pieces contributed in the same way to the outcome measure. In the group condition, we also measured the number of distinct puzzle pieces correctly connected to at least one other puzzle piece across all three puzzles completed by the participants in each generation. This gives a measure of the amount of information about the puzzle that the following generation was able to observe, accounting for the duplication of completed pieces across different observed puzzles.

3. Results

The results of the experiment are shown in Fig. 3. It is visually evident that the mean number of pieces completed trends upward in the group condition but not in the individual condition. To test this hypothesis statistically, we used Page's (1963) trend test, which tests for a hypothesised ordered monotonic trend (in this case, an increasing trend) in the means of a number of different treatments (in this case, generations). The test was non-significant for the individual condition ($L_{5,4} = 123$, $p > 0.05$, $n = 20$), and significant for the group condition ($L_{5,4} = 141$, $p = 0.01$, $n = 20$). We also compared the means of the first and last generations in each condition using Welch's two-sample t-test: for the individual condition there was no significant difference in the number of puzzle pieces

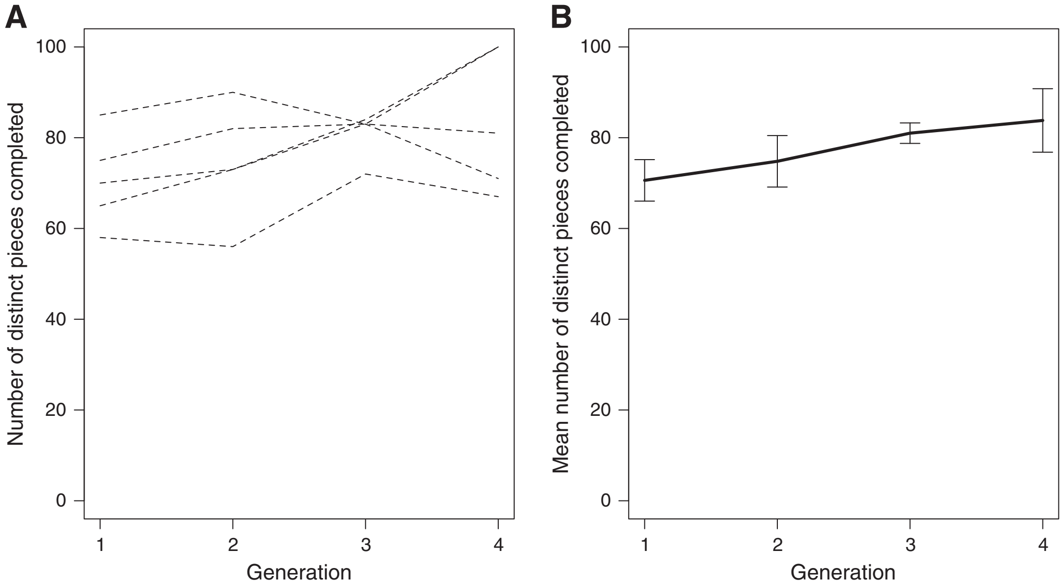

Fig. 4. The number of distinct pieces completed in the group condition. (A) Number of distinct pieces completed in each chain. The full dataset is available in the electronic supplementary material. (B) Mean number of pieces completed. Error bars show standard errors.

connected ($t_{6.1} = 0.2422$, $p = 0.5917$, one-sided, $n = 10$), while for the group condition there was ($t_{23.2} = -2.2882$, $p = 0.0158$, one-sided, $n = 30$), with more pieces connected by the final than first generation.

The number of distinct pieces completed in the three puzzles of each group is shown in Fig. 4. As with the mean number of pieces completed, this trends upwards, with Page's trend test showing a significant increasing trend ($L_{5,4} = 139$, $p < 0.05$, $n = 20$).

4. Discussion

Our experiment showed no increasing trend in the mean number of jigsaw pieces completed in the individual condition, when each generation of the transmission chains was a single individual, but a significant increasing trend in the group condition, when each generation consisted of three individuals. The larger number of individuals is clearly able to maintain the transmission of a greater amount of information about the puzzle. Thus, the results of the experiment support the proposed link between population size and cultural accumulation put forward by Shennan (2001), Henrich (2004), Powell et al. (2009) and others.

The upward trend in the number of distinct pieces completed across a group shown in Fig. 4 suggests that participants were integrating information from multiple models, as predicted. This therefore provides an alternative mechanism by which the population-size effect operates, in addition to the success-biased cultural transmission from a single demonstrator assumed in previous models (e.g. Henrich, 2004) and tested in previous experiments (e.g. Derex et al., 2013). Our finding supports recent modelling (Enquist et al., 2010) and experimental (Eriksson & Coultas, 2012) work showing the benefits of multiple cultural parents on cultural transmission, although extended here to a cumulative cultural context.

It is instructive to compare our results with those of Caldwell and Millen (2010), who found no effect of group size despite similar group sizes and generations. As discussed in the Introduction, different tasks will be more or less conducive to cultural accumulation. In our jigsaw puzzle task it is easy to combine information from multiple different puzzles completed by members of a previous generation into one's own puzzle. By contrast, information about multiple different paper airplane designs may conflict, and combining multiple designs may lead to a worse design than any of the models. While copying the single airplane design of the most successful individual may be effective in larger groups or over more generations than were employed by Caldwell & Millen, the fact that we observed accumulation with similar group sizes and generations suggests that combining knowledge from multiple cultural sources can be an equally potent mechanism for cultural accumulation compared to copying a single successful individual, given the appropriate task.

Our experiment shows that the characteristics of the task are important in determining the extent to which population size will affect its cultural accumulation, and future modeling work on the relationship between population size and cumulative culture should take into account not only factors extrinsic to the task but also factors intrinsic to it. One way of conceptualizing task differences is by considering uni-modal vs. multi-modal utility, or ‘fitness’, landscapes (see Mesoudi, 2008; Mesoudi & O'Brien, 2008a, 2008b). The task of finishing a jigsaw puzzle constitutes a unimodal, single-peaked fitness landscape, because the more pieces a participant has completed, the closer to completion they are; in our experiment, it did not matter which particular combination of, say, 40 pieces was completed, so long as the number was 40. However, the task of building paper airplanes may create a multimodal, multi-peaked fitness landscape, in which there are multiple locally optimal designs that can solve the task relatively well (though there may be a single globally optimal design). These multiple designs may be rather distinct from each other, and designs which mix features of two or more ‘good’ designs may fall into a fitness valley and be relatively inefficient at solving the task.

It may be that there is a continuum along which real-world technologies can be placed, from simple fitness landscapes with one peak to complex fitness landscapes with very many distinct peaks of quite unequal height. An engineering correlate of this continuum may be the extent to which the technology consists of independent vs. interdependent parts. Moreover, these differences may occur at different levels of granularity. For example, complex post-Industrial Revolution technologies such as cars and computers incorporate large numbers of different parts, which must work together in order for the technology to function. However, if a certain part is required for a specific task, it may not matter exactly how it achieves that task, and so the overall functioning of the technology (e.g. car) may be relatively independent of the exact mechanism in which the constituent part fulfills its function (see Arthur, 2009). Another example of such hierarchical structure is found in modern computer software, which is often written using ‘object-oriented’ and ‘functional’ techniques in which the external behavior of various system sub-parts is highly constrained but the internal implementation of these sub-parts is relatively unconstrained (Mitchell, 2002).

Future experiments and empirical work may provide more evidence on what tasks are particularly conducive to the build-up of cumulative culture, the way in which independence and interdependence of technological sub-components affect technological accumulation, and allow us to ‘measure’ the fitness landscape of a given task. A promising path may be to use experimental tasks with direct ecological validity to a specific domain, such as mathematics, tool-use, or construction, unlike the tasks used here and in other recent experiments, which require little specialist knowledge. Such experiments may help to show whether certain domains are more amenable to cultural accumulation than others. Experimental work such as this can then be used to inform historical, anthropological and archaeological data, to make specific predictions regarding which kinds of cultural traits are most likely to have been impacted by demography, and thus provide substantial insight into human biological and cultural evolution.

Supplementary Materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2014.02.009.

Acknowledgments

We thank Shakti Lamba and Rachel Kendal for providing access to participants, and Rachel Kendal for useful comments on an earlier draft. We are also grateful to Gibsons Games for permission to use the image in Fig. 1.

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