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Comment

Untenable propositions and alternative avenues. Comment to "Blind alleys and fruitful pathways in the comparative study of cultural cognition" by Andrew Whiten.

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Whiten [1] highlights three core propositions of Tomasello et al.'s influential paper [2] that became "conventional wisdoms" and spawned the "Zone of Latent Solutions" (ZLS) approach. We agree with Whiten that, 30 years on, none of these propositions remain tenable, and suggest alternative avenues for research.

(a) Untenable propositions

The first proposition is that cumulative cultural evolution (CCE) is uniquely human. However, if we define CCE as the sequential improvement of innovations over successive rounds of social learning [3], then there is compelling evidence for CCE in other species (reviewed in [1], [3]), and no doubt the list will grow.

The second proposition is that CCE depends on uniquely human modes of high-fidelity information transmission. However, not only do we see evidence for CCE in other species, but transmission chain experiments with humans show cumulative improvements in the efficacy of tools and technologies through supposedly "low-fidelity" processes [4–6].

The third proposition is that motor imitation is necessary for CCE. Yet regardless of one's stance on the evidence for imitation in animals (reviewed by Whiten [1]), there is no evidence that motor imitation is necessary for human CCE. Motor imitation is clearly necessary for the transmission of gestures and dance (which are not, strictly speaking, forms of CCE [3]), but we know of no evidence that copying the precise form of bodily actions is involved in the production or use of cumulatively evolving tools and technologies, be they Acheulean hand-axes, canoes or smartphones.

We therefore concur with Whiten [1] that it is time to leave these conventional wisdoms behind, but where does this leave us? We propose three alternative avenues that must be explored if we are to further our understanding of CCE.

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(b) Alternative avenues

(1) Limits on innovation

Research under the ZLS framework often presents captive apes with artificial versions of problems they solve in the wild. Whiten points out a central problem with this approach: if captive animals succeed in "inventing" a solution to a problem, this does not mean that the loosely-analogous but more complex problem in the wild was equally trivial to solve. The reverse is also true: if no captive animal solves the problem this does not mean that no wild animal could have solved it. Thus, the idea is fundamentally untestable.

Rather than trying to establish whether a given behaviour is within a species' putative ZLS, we think a more productive approach is to unravel the limits on innovation. Correlations between brain size and innovation rates in the wild [7] suggest a key role for cognitive abilities. Accordingly, much of the work on apes has sought to identify cognitive constraints on innovation, such as conformity. However, the wider animal literature indicates that the main determinants of innovation may be motivational, rather than cognitive: innovators are typically low-ranking individuals forced to try new things out of necessity and willing to persevere to obtain rewards [8], [9]. This implies that when individuals do not innovate it is not because they lack the cognitive abilities but because the incentives are insufficient. Thus, we must consider the benefits of innovating in the context of socio-ecological conditions. This includes developmental conditions. Just as enculturation by humans is conducive to the development of motor imitation in apes [1], we must examine the conditions conducive to the development of innovativeness across species (including humans). Finally, we must not forget that innovation is constrained by morphology: a beak or a fin cannot do what a hand can do, and an ape's precision grip cannot match a human's. A better understanding of the limits of innovation therefore requires multi-faceted examination of cognitive, motivational, developmental and morphological factors.

(2) Effects of network structure: on what does selection act?

Growing evidence suggests that network structure can constrain or facilitate the spread of information, the recombination of cultural traits and the accumulation of knowledge [10], [11]. The sparsely interconnected, hierarchical network structure characteristic of human populations, for example, seem optimally "designed" to enable cumulative cultural evolution [10]. This raises two important points. First, we must be cautious in interpreting any failure of innovations to arise, spread or improve in groups with artificially impoverished network structures (e.g. in captive animals and many human laboratory experiments). Second, and more fundamentally, to understand the basis of cumulative cultural evolution we must examine how selection acts on networks and establish the appropriate level of selection. Network structure could arise purely as an emergent product of selection on decision-making processes governing individuals' social interactions. Individual social network positions have been shown to be heritable [12], suggesting there may be genetic selection for sociability. However, evidence that social decisions, such as when to cooperate, can be socially learned both in humans and other animals [13], raises the possibility that cultural evolution acting on individual behaviour may also shape network structure. It is also conceivable that selection (be it genetic or cultural) could act directly on network structure itself, e.g. through multi-level selection acting on the differential success of groups of differing structure.

(3) Co-evolutionary dynamics

A central flaw of the ZLS approach is that it confuses end-points with explanations and thereby limits the scope to ask evolutionary questions. The fact that we wrote this commentary on a word processor that we could not have invented on our own is not an explanation for, but an end-point of cumulative cultural evolution. The ZLS suggests that the explanation lies in the "magic ingredient" of motor imitation, but we did not learn to type by copying anybody's finger movements and the computer manufacturers' operating procedures use written manuals not "do-as-I-do" forms of copying. More importantly, the ZLS perspective cannot explain where the magic ingredient came from. If imitation is only useful because it allows us to copy causally opaque products of CCE (beyond our ZLS), then why did imitation evolve in the first place?

We argue that to resolve this problem we must leave behind the ZLS and focus instead on the co-evolution of culture and cognition. Evidence from both humans and non-human animals shows that phylogenetically widespread, evolutionarily ancient learning mechanisms can enable cumulative improvements to culturally transmitted cultural information (i.e. the "core criteria" for CCE [3]). If individuals become increasingly reliant on increasingly complex cultural products, this may then select for higher-fidelity learning mechanisms, which in turn facilitate further cultural elaboration, promoting increasingly open-ended cumulative cultural evolution [6]. Such feedback loops may help to explain the origins of human teaching and language: verbal teaching provides no advantage over other forms of social transmission in experiments involving simple tools, but becomes advantageous as tools become more causally opaque [6], [14]. There may also be culture-culture coevolution, with the products of CCE themselves enhancing cultural innovation (e.g. microscopes, telescopes) and cultural transmission fidelity (e.g. books, the internet) [15], [16]. Further work must now move beyond experimentally tractable but simplistic transmission chain designs to examine the co-evolutionary dynamics between cognition, culture and social structure.

Declaration of competing interest

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