

## Comment

# What animal cultures may beget: Comment on “Blind alleys and fruitful pathways in the comparative study of cultural cognition” by Andrew Whiten

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Animal cultures are increasingly documented and purported to have significant relevance for our understanding of animal behavior and the evolutionary origins of human culture [1–4] – but what is meant when we mention “animal culture”? Andrew Whiten provides a comprehensive and thoughtful review of past and contemporary findings that shed light on this question [5]. Specifically, Whiten [5] takes issue with the suite of studies that are conducted to show that nonhuman animals (henceforth ‘animals’), especially apes, cannot copy the behavioral forms they observe in others [6]. Under the banner of the ‘Zone of Latent Solutions’ (ZLS) hypothesis, these studies claim that all hitherto documented ape cultures (e.g., [7,8]) can be explained by all apes re-inventing the wheel, with possibly a little help from group members in getting them started, but devoid of the highest-fidelity social learning variant referred to as *form copying* which is supposedly pivotal to human culture.

In line with Whiten [5], we question *i*) whether the evolutionary precedent for human form copying is lacking, and *ii*) the extent to which this matters for understanding culture. Furthermore, we wish to expand on Whiten’s account by highlighting how culture, and especially cumulative cultural evolution (CCE), in animals has largely been studied at micro-levels, devoid of the rich macro-levels known to affect human culture. In this expansion, we will provide a plausible, non-exhaustive set of determinants that may (similarly) be relevant in explaining the possible cultural differences between humans and other animals.

Corroborating Whiten’s account of the absence of evidence regarding the lack of imitative capacities in animals, we wish to draw particular attention to form copying of presumably non-functional behavior in chimpanzees. Whereas directly functional behavior like nut cracking could be envisioned as possessing sufficient incentive to trigger individual re-innovation (cf. [9]), the arbitrary forms that chimpanzees have been observed to copy are less plausibly reframed in these ZLS terms. When chimpanzees adopt the unconventional postures and gaits of others in the group [10,11], or put grass in their ears after one of their group members’ favorite pastime [12], how likely can this be ex-

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plained as an emergent property of a series of individual re-innovations? Here, we place considerably more value on natural observations (in which the apes showcase intrinsic motivation to copy) than on artificial experiments in which case motivation and especially relevance are difficult to establish (cf., [13,14]). Moreover, there is ample evidence of accurate vocal matching in animals in which the song structures and repertoires are faithfully transmitted within groups and clans of birds and cetaceans [4,15]. These examples suggest both phylogenetic conservatism and independent, “individual re-innovation” (i.e., convergent evolution) of the extended social learning faculty,<sup>1</sup> which deems the respective ZLS proposition unlikely.

Zooming out, while the endeavor to pinpoint social learning mechanisms is an interesting project for the study of comparative cognition in its own right, we question its relevance to understanding the intricacies of (animal) culture. Despite purported correlations between the existence of form copying and CCE, in line with [5], we fail to see how the former is necessary for the latter (also see [16–18]). Granted, form copying enables an efficient means to adopt (detailed) information from others, but when slightly less faithful mechanisms can yield the within-group homogeneity and between-group heterogeneity characteristic of the cultural phenomenon, why could they not form the impetus for CCE? We do see how form copying may be instrumental for adopting complex techniques and rituals that exist by virtue of the details, but here we refer back to the earlier conclusion that it seems incorrect to pose that only humans are capable of form copying (also see [5]) and thus, in conjunction, arrive back at the outstanding question of why human culture seemingly differs so substantially from animal cultures.

Where Whiten [5] answers this question by stating that apes may (have evolved to) be more conservative than humans in adopting new inventions, we wish to expand this answer by highlighting how CCE in animals has typically been studied at micro-levels, excluding the rich macro-levels known to affect human culture. Humans are socially organized in vastly different ways than the great apes, or arguably any other species. For starters, for every single chimpanzee on earth, there are currently at least 30000 human beings, which already equates to a large difference in the sheer amount of available (social) information to be copied. Furthermore, humans live in complex multilevel social structures which facilitates their CCE [19], presumably even when population sizes were relatively low. Such social structures do not only expedite information diffusion [20,21], but may also function as a collective storage space of generated (within groups) and harvested (outside groups) units of cultural knowledge, be it in the form of artifacts, stories, or rituals. Over time, this function has been tremendously expanded with the inventions of external information condensations (e.g., books, manuals, instruction videos), which are seemingly uniquely human and unparalleled by any capacity or process in animals. Importantly, where we envision these factors to be conducive to CCE and by extension to explaining the cultural divide between humans and other animals, they may simultaneously represent a hitherto overlooked source of variation explaining cultural proliferations within animal species, in particular different social network structures [22].

The primary lesson from Whiten [5] is that the current quest for finding form copying in animals should be decoupled from the endeavor to chart and construe animal culture. Both projects are faced with scientific challenges not unbeknownst to the field of comparative psychology. Yet, where empirical demand exists in connecting the two, they would both benefit from independent assessments of their merit for the field at large. Overall, we think that a macro-level analysis of cultural determinants in humans could serve as further inspiration for ultimately unraveling what culture may beget in animals.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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<sup>1</sup> Here, it is worth noting that social learning is ubiquitous across the animal kingdom, ranging from insects to primates to even include solitary living animals.

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