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Comment

Chimpanzee culture in context
Comment on "Blind alleys and fruitful pathways in the comparative study of cultural cognition" by Andrew Whiten

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1. Introduction

We welcome Whiten's timely article [1] evaluating the zone of latent solutions (ZLS) hypothesis, which has developed into a hot topic with new findings both from captive [2–4] and natural settings [5,6]. As such, a review of its usefulness is timely and helpful. Here, we will focus on the ZLS part of Whiten's paper - section 3 therein - providing views based on our collective decades of field experience studying wild chimpanzee behaviour across Africa. As scientists engaging in long-term field studies, we value experimental work on culture in captivity and see it as complementary to our own field observations and field experiments. In order to develop a complete understanding of chimpanzee behaviour and cognition we need an integrated approach: observations and experiments in captivity and in the wild [7]. However, we share some of the main concerns raised by Whiten about the concept of a ZLS, especially in terms of the lack of ecological validity of ZLS tests in captivity and the binary hyper-simplistic approach to cultural abilities. Below, we outline our thoughts on some of the issues raised by Whiten [1], address additional concerns, and present future directions.

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2. Shared concerns about the ZLS

2.1. Cultural variation is more nuanced than depicted under the ZLS

For any culturally transmitted behaviour, e.g., nut-cracking, events of invention and innovation must have happened in the past. Importantly, however, to fully understand cultural processes we need to go beyond such *Eureka* or *aha!* moments of behavioural innovation and focus on more subtle behavioural modifications, both across time [8] and between communities [9]. In humans, most aspects of culture do not pertain to whether a behaviour is present/absent but rather to variation in its form, function, complexity, and usage [10,11]. In this sense, 'cultural variation' is more nuanced than its depiction under the ZLS hypothesis. Shifting focus from presence/absence to incorporate more refined dimensions of variation better reflects the complexity of cultural processes. For example, the mere action of pounding or fishing could well be part of the repertoire of all chimpanzees, but the choice of which actions to deploy, the combination of those actions into a meaningful sequence, and the integration of those actions within a complex understanding of the environment differs substantially across social groups. By providing a limited set of materials and pre-defining the goal in captive experiments, the task no longer captures the complexity of natural behaviours. Hence, finding that a "naive" chimpanzee can pound one object on another is not at all surprising - this action occurs in a variety of contexts (e.g., play, feeding without tools, display) and is likely to be found in most primates including humans. The cultural foundation of how these actions are used in specific environmental contexts to produce naturally varying behaviours incorporates a complex web of knowledge.

2.2. ZLS experiments fail to represent cultural behaviours

A further fundamental problem is that ZLS experiments in captivity are inadequate in representing behaviours in the wild. Particularly for complex behaviours like nut cracking and termite fishing, the 'captive versions' of the behaviours do not represent the key aspects of their natural complexity. The physical action of a task, e.g., crack nut, is not impressive cultural knowledge *per se*. However, in the case of nut cracking, as well as in algae fishing [12] or pestle pounding [13], the actual food source is hidden and the cultural knowledge is a long chain of complex transmission of information. Knowing when and where to find the food source, knowing it is edible, and how to efficiently access it is all part of the cultural knowledge that has to be acquired. For some tool tasks, further steps are required to source raw materials from among many alternatives and make modifications that align with a specific final design (e.g., brush-tipped probe to gather termites [14]), and may show variation in aspects of task performance not shaped by task constraints [6]. However, the focus of ZLS studies, and associated work, in captivity is limited to the very last step of the cultural process, i.e., the physical action to reach the end goal. Naturally transmitted knowledge is much more than this final step, and it cannot be meaningfully disentangled from all the other types of knowledge an individual needs to acquire to successfully achieve the task. Further, ZLS experiments do not approximate the constructed niches and the broader set of ecological and social opportunities [5] that support the emergence of these behaviours.

3. Additional considerations about the ZLS

3.1. Captive individuals are never 'unenculturated'

All apes living in captivity are exposed to humans and human artefacts on a daily basis [4]. Moreover, captive apes are frequently - for good reasons related to welfare - presented with a host of diverse puzzles and problems to solve. Thus, these apes often have substantial exposure to experimental contexts even if they have never seen a specific test before. Hence, such captive ZLS experiments (e.g., orangutans stone tool-making experiments [3]) are not meaningful in terms of generalising to species-wide abilities.

3.2. Not all behaviours are alike, not all chimpanzees are alike

Behaviours differ in complexity and thus in their ease of innovation and subsequent transmission. Several long-term chimpanzee study sites have provided evidence for numerous innovations, of which only a small number

are transmitted to others [15–17]. We see so-called fads and fashions that emerge in chimpanzee groups [18–20]. Such innovations or variations do not catch on for long or get rapidly extinguished. Moreover, learning is a heterogeneous phenomenon. There are many potential dimensions to this heterogeneity, including across tasks (e.g., complexity, salience), individuals (e.g., sex, age), or populations (e.g., size, cohesiveness). This heterogeneity precludes the utility of seeking one rule that can explain all chimpanzee cultural behaviour, either in the wild or in captivity.

3.3. Future directions

Given these hurdles, what are some next meaningful steps to study cultural cognition and reconcile work done in captivity and in the wild? First, involving field researchers in the development of protocols for captive experiments is critical. Second, inviting researchers working in captivity to spend time in the wild would help close the gap between captive and wild approaches. Similarly, experimental psychologists are welcome collaborators on studies of chimpanzee cultures in the wild. Third, applying new methods (e.g., deep learning), to process longitudinal data sets can unveil the nuances, contexts, and affordances that may underlie cultural behaviours. Lastly, quantifying the forms, techniques, and subtleties of behavioural expressions holistically is critical. These nuances in behaviour and the range of dimensions in which variation is expressed are at the heart of understanding cultural processes and chimpanzee culture in context.

Declaration of competing interest

The author declares 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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