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Appropriate Knowledge of Wild Chimpanzee Behavior ('Know-What') and Field Experimental Protocols ('Know-How') are Essential Prerequisites for Testing the Origins and Spread of Technological Behavior:

Response to "Unmotivated subjects Cannot Provide Interpretable Data and Tasks with Sensitive Learning Periods Require Appropriately Aged Subjects" by C. Tennie and J. Call

Kathelijne Koops[1*], Dora Biro[2,3], Tetsuro Matsuzawa[4,5,6], William C. McGrew[7] and Susana Carvalho[8,9,10]

[1]Ape Behaviour & Ecology Group, Department of Evolutionary Anthropology, University of Zurich, Zurich, Switzerland
[2]Brain and Cognitive Sciences, University of Rochester, Rochester, NY, USA
[3]Department of Biology, Oxford University, Oxford, UK
[4]Division of the Humanities and Social Sciences, California Institute of Technology, Pasadena, CA, USA
[5]Department of Pedagogy, Chubu Gakuin University, Gifu, Japan
[6]College of Life Sciences, Northwest University, Xi'an, China
[7]School of Psychology and Neuroscience, University of St Andrews, St Andrews, UK
[8]Primate Models for Behavioural Evolution Lab, University of Oxford, Oxford, UK
[9]Interdisciplinary Centre for Archaeology and Evolution of Human Behaviour (ICArEHB), Universidade do Algarve, Faro, Portugal
[10]Gorongosa National Park, Sofala, Mozambique

*Corresponding author (Email: kathelijne.koops@uzh.ch)

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Abstract – We respond to the commentary by Tennie and Call (2023) on the article by Koops et al. (2022) in *Nature Human Behaviour* titled 'Field experiments find no evidence that chimpanzee nut cracking can be independently innovated.' Koops et al. (2022) showed that chimpanzee nut cracking is not a so-called 'latent solution.' Chimpanzees (*Pan troglodytes verus*) in the Nimba Mountains (Guinea) did not crack nuts when presented with nuts and stones in ecologically valid field experiments. In their Commentary, Tennie and Call (2023) argued that the experiments were inconclusive for two reasons: 1) the chimpanzees were not motivated to treat the nuts as food, and 2) the chimpanzees were not within the appropriate 'sensitive learning period.' In our response, we argue that Tennie and Call (2023) incorrectly use the term 'motivation' to mean 'willingness to eat the nut', which requires existing knowledge of the edibility of the nuts. We also point out that it is unnatural and uninformative to inject nuts with honey to motivate the chimpanzees to eat them, as suggested by Tennie and Call (2023). Finally, we highlight that Koops et al. (2022) tested appropriately aged subjects (N=32 immatures). Moreover, we argue that there is no evidence to suggest that there is a strictly sensitive learning period restricted to juvenility. Finally, we emphasize the need for researchers doing experiments in captivity to visit their study species in the wild, and for field researchers to be involved in efforts to design ecologically valid experiments in captivity.

Keywords – Chimpanzee, Culture, Nut cracking, Sensitive learning period, Social learning

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Recently, Tennie and Call (2023) wrote a commentary in *Animal Behavior and Cognition* on the article by Koops et al. (2022) published in *Nature Human Behaviour* titled 'Field experiments find no evidence that chimpanzee nut cracking can be independently innovated.' In this paper, Koops et al. (2022) tested whether chimpanzee nut cracking can be considered a 'latent solution.' The zone of latent solutions hypothesis states that only humans have cultural forms that require copying and that non-human ape cultural behaviors are latent solutions, which can be independently innovated (e.g., Tennie et al., 2009, 2020). Koops et al. (2022) showed that wild western chimpanzees in the Nimba Mountains (Guinea) did not crack nuts when presented with nuts and stones in ecologically valid field experiments. Hence, they concluded that these findings are consistent with chimpanzee nut cracking falling outside what Tennie and colleagues (2009, 2020) called the zone of latent solutions (or ZLS) of chimpanzees - in other words, that this behavior is not spontaneously innovated by naïve chimpanzees. The commentary by Tennie and Call (2023) focuses on two main criticisms, which we address below. Our reply ends with some additional comments on the piece by Tennie and Call (2023).

Criticism 1: "Unmotivated subjects cannot provide interpretable data''

Tennie and Call (2023) suggest that the chimpanzees (*Pan troglodytes*) in the experiments by Koops et al. (2022) were unmotivated to treat the nuts as food, which they assert is a prerequisite for testing if nut cracking is outside the chimpanzee ZLS. In their conclusion, they suggest that a better way to proceed would be to build on Koops et al. (2022)'s experiment: "...one could first provide naïve subjects with open nuts mixed with food that is known to be valued locally, and perhaps even with shelled nuts injected with such food (e.g., honey)" (p. 93). Tennie and Call (2023) define latent solutions as "behavioral and/or artefact forms whose underlying know-how can be *spontaneously innovated* [italics added] by ecologically relevant individuals (i.e., not trained or enculturated by another species) in the absence of cultural access" (p. 89) - *not*, in the case of nut cracking, as "behavioral and/or artefact forms whose underlying know-how can be achieved by ecologically relevant individuals in the absence of cultural access," *so long as humans coax them towards this by mixing open nuts with honey etc* [italics added]. Instead, Koops et al. (2022) directly tested whether the "underlying know-how" of nut cracking "can be spontaneously innovated by ecologically relevant individuals …. in the absence of cultural access" (as per Tennie and Call's (2023) definition above). It was not. This negative result contrasts with what happens in chimpanzee communities that habitually crack nuts, in which juveniles almost universally acquire the skill. Presumably, at some time in the past, an ancestral ape cracked nuts, so it had to have been innovated "in the absence of cultural access" (and in the absence of humans injecting nuts with honey). For the vast majority of contemporary wild chimpanzees, including those tested by Koops et al. (2022), the acquisition of nut cracking is *culturally dependent*.

We agree that, in theory, there is a distinction between 'know-what' (i.e., desirable food in these items) and 'know-how' (i.e., to crack open nuts). But, in practice, one cannot meaningfully separate know-what from know-how for an embedded resource in an ecologically valid setting. In nature, a chimpanzee only discovers the edibility of nuts once the action of nut cracking is done. The ZLS scenario is that chimpanzees in nut-cracking cultures have access to this information because nuts are cracked and they initially scrounge kernels, but that somehow the action of cracking the nuts is within the capacity of chimpanzees to acquire without actually copying it from others. It is logically impossible to test this hypothesis because, in any natural community where young chimpanzees can learn about the edibility of nuts, they will also witness the cracking actions for their extraction. So, for all embedded resources (e.g., nut cracking, Matsuzawa, 1994; termite fishing, Goodall, 1964; pestle pounding, Yamakoshi & Sugiyama, 1995) a young chimpanzee is simultaneously exposed to the know-what (that nuts/termites/palm-heart are edible) and the associated know-how (technique to crack nuts, how to termite fish, how to pestle pound, etc.). In fact, this is exactly what makes the knowledge transmission of these tool-use behaviors so challenging, yet robust: archaeological excavations have shown that chimpanzees at Taï (Ivory Coast) have been nut-cracking for over 4,300 years (Mercader et al., 2007). To acquire the skill to crack nuts, young chimpanzees must learn not only how to access nuts, but also when to find nuts, where to find nuts, and most importantly, that you can eat the kernel inside the nuts (Koops et al., 2023).

In light of this, we note that Tennie and Call (2023) conflate the meaning of motivation and knowledge. Used in a biological sense, the term 'motivation' refers to an intrinsic drive to satisfy a current need, such as hunger. Tennie and Call (2023) instead use the term to mean 'willingness to eat the nut' which seems to require existing knowledge of the edibility of the nuts. Oil palm nuts are extremely high in energy, and chimpanzees at Bossou can consume as many as 1,200-2,400 kcal (i.e., 90-180 nuts) over the course of 30-60 min of nut cracking (Matsuzawa, 2003). It is highly unlikely that the chimpanzees in Nimba would never be motivated to eat such a high-energy resource (McGrew, 1992). In fact, one adult female was observed to eat oil-palm fruit (the nuts' soft outer layer before they dry out) in the experiments by Koops et al. (2022) and was thus motivated to eat the food provided. Moreover, Koops et al. (2022) conducted their experiments at times of both high and low fruit availability, thus accounting for the possibility that chimpanzees may have been satiated at times when ready-to-eat foods were abundant. Exploration of the experimental items was in fact higher at times of high *versus* low fruit availability. Also, the nearby chimpanzees in Yealé (6 km away) and Bossou (6 km away) eat oil palm nuts (Koops et al. 2022), suggesting that Nimba chimpanzees in Seringbara would be motivated to eat these nuts, if they knew these nuts were edible. Moreover, Nimba chimpanzees use percussive technology (*Treculia* fracturing, Koops et al., 2010) and they use other tools in extractive foraging (ant dipping, Koops et al., 2015). Hence, they are clearly cognitively and physically prepared to learn to nut-crack (cf. McGrew et al., 1997), but in these experiments lacked a model to learn from, unlike their nut-cracking neighbors in Yealé and Bossou. Importantly, wild chimpanzees do not have the luxury of humans pointing out to them what is edible and what is not. In the case of nut cracking this presents a double challenge. First, one has to discover that nuts are edible, which is extremely unlikely without one first being cracked. Second, one has to learn a highly complex tool use technique. This combined difficulty may well be what places nut cracking outside the chimpanzee ZLS.

Criticism 2: "Tasks with sensitive learning periods require appropriately aged subjects"

The second principal criticism by Tennie and Call (2023) is that only one individual tested by Koops et al. (2022) was of an appropriate age. This is simply untrue. In fact, chimpanzees of all ages visited the experimental sites and thus took part in the experiments, including a total of 32 immatures (i.e., 4-11 years old; van Leeuwen et al., 2020). A subset of the chimpanzees who visited (N=19) also closely investigated (i.e., touched, sniffed) the experimental set-up. However, even chimpanzees who visited without investigating the items still came within close visual range of the experimental set up and thus were considered 'tested' individuals. Differences in exploratory tendencies would predict different responses across individuals (Massen et al., 2013), and this is thus not surprising. In Koops et al.'s (2022) experiments, the number of immatures visiting the experiments (N=32) far exceeds sample sizes in most captive studies. Of these 32 youngsters, five (i.e., one juvenile, four adolescents) closely investigated the experimental items. Tennie and Call (2023) focus on the age range from 3 to 5 years as the 'sensitive age range' or 'learning window' for social learning of nut-cracking, based on findings at Bossou (Biro et al., 2003). Hence, they claim that only the one juvenile was a valid test subject. However, the adult skill level in nut cracking is not reached until 9-10 years of age (Berdugo et al., 2022; Matsuzawa, 1994). So, including both juveniles and adolescents is not only reasonable, but necessary. It would actually be surprising that, if any chimpanzee were to spontaneously invent nut cracking, it would be younger than 5 (or even 7) years old.

More importantly, the term "sensitive period" in a strict sense may, in fact, be misleading. We do not know if it gets increasingly difficult or even impossible for individuals to learn the skill with age. As such, we do not use the term in the cognitive sense, but instead consider it to be a learning window bounded by other variables. For example, age-related changes occur in the level of tolerance that other community members display towards young chimpanzees' close observation of their tool use. Such tolerance wanes as individuals get older, with close observation no longer being tolerated. Hence, opportunities for social learning greatly diminish over time (see "Education by Master-Apprenticeship" Model, Matsuzawa et al., 2001). Thus, the learning window can be seen as a result of channels of social transmission closing, rather than a consequence of a lack of ability to learn (were these channels still open) later in life. Crucially, captive studies have shown that non-nutcrackers *may* learn to crack nuts after being given the opportunity to watch a model, even if they are well beyond the so-called sensitive learning period (Hannah & McGrew, 1987; Hayashi et al., 2004; Hirata et al., 2009). Captive experiments have also shown that adult chimpanzees are able to *socially* learn alternative forms of tool use (e.g., alternative "panpipe tool-use techniques", Whiten et al., 2005). Wild *adult* chimpanzee females at Taï are able to learn a new nut-cracking technique after migrating to a new community, having already acquired the nut-cracking technique of their natal community before emigration (Luncz et al., 2012).

A strictly sensitive learning period restricted to juvenility is also lacking when one considers the age of acquisition of other complex types of tool use like using a perforating tool before beginning to termite fish (Sanz et al., 2004). This complex and physically demanding two-stage tool set is acquired only from the age of 10.5 years (Musgrave et al., 2016). In a similar vein, nut-cracking efficiency may also continue to improve up to about 10 years (Berdugo et al., 2022). Furthermore, from a purely evolutionary perspective, a strict learning window would be particularly costly for emigrating adolescent females, as this would decrease their chances of integration into other communities, which requires learning new individuals, foods, foraging techniques, etc. Hence, there is little current support for a strict chimpanzee learning period, if used in the sense of individuals losing the ability to learn new skills later in life. The criticism by Tennie and Call (2023) regarding the lack of appropriately aged subjects tested by Koops et al. (2022) is thus not only unfair (i.e., >1 individual was tested), but also unwarranted (learning is not restricted to individuals <5-years-old).

Further comments on the response by Tennie and Call (2023)

We highlight some issues with the ever-evolving theory and language surrounding the 'zone of latent solutions' concept. Since the ZLS was first proposed (Tennie et al., 2009), the goal posts have kept moving in seeking latent solutions in wild apes. Initially, it was deemed sufficient to do an 'island test' (or 'latent solution test') to show if a behavioral pattern (e.g., nut cracking) could appear in an individual when exposed to the materials without cultural access (e.g., Tennie et al., 2009, 2016). Now, Tennie and Call (2023) suggest that this 'latent solution test' is only valid if the individual tested is first taught about the presence and edibility of the embedded food source. Rather than an 'island test', it now resembles a workshop on nut cracking.

Moreover, the proliferation of new terms (often undefined and hence obfuscating) in the discussions regarding the ZLS hypothesis is not helpful. For example, in the piece commenting on Koops et al.'s (2022) paper, the term 'supra-individual' know-how is introduced but not defined. Perhaps this just means 'cultural know-how'? But if so, why introduce a new term? Or, consider the description of a latent solution itself. Initially, it was argued that latent solutions were *individually* invented (i.e., asocial learning, Tennie et al., 2009). In later versions of the ZLS hypothesis, this changed, and latent solutions could be 'socially-mediated' individually learned innovations (e.g., Tennie et al., 2020). In sum, the ZLS playing field is ever-changing, making it hard to test its claims.

It is evident from the experimental design "improvements" proposed by Tennie and Call (2023) that neither author has studied wild apes, and thus is sufficiently familiar with the challenges and constraints of studying chimpanzees in their natural habitat. For example, consider their suggestion to provide chimpanzees with nuts mixed with honey in order to 'teach' them about the edibility of palm nuts. It is both ethically questionable and artificial to provide honey mixed with nuts to wild chimpanzees. In nature, chimpanzees only sporadically access honey (and never on the forest floor). Hence, providing this extremely high calorie resource on a regular basis is problematic. Consider too their suggestion of a minimum number of 16 (motivated) individuals needed to test for latent solutions of complex tool (re)innovations (see Bandini & Tennie, 2018). In nature, this is impractical, as very few communities (especially in West Africa) contain 16 juveniles at any one time. The nut-cracking chimpanzees of Bossou have not had that many juveniles since records began decades ago, yet they crack nuts (Matsuzawa et al., 2011). Moreover, latent solution tests in captivity have not had this minimum number of chimpanzee subjects (e.g., Bandini et al., 2021; Neadle et al., 2020), which worryingly seems like double standards are being applied.

We suggest that a productive way forward would be to design ecologically valid nut-cracking field experiments at more study sites, whilst making sure the protocols are ethically sound. Also, it would be fruitful for researchers doing experiments with captive apes to visit their study species in the wild and observe the apes' day-to-day lives in natural settings. Moreover, it would be beneficial if field researchers were involved in efforts to design more ecologically valid experiments in captivity (Whiten, 2022).

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