

## What kind of culture did early hominin toolmakers have?

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The lives of living modern humans are entrenched in and enabled by cumulative culture of know-how – indeed, cultural transmission of know-how defines the human experience (Boyd, 2018; Boyd & Richerson, 1996; Henrich, 2016; Stout & Hecht, 2017; Tennie et al., 2020a; Tomasello, 1999). Cumulative culture of know-how is driven by so-called copying social learning mechanisms, whereby the copying of behavioral and artifact forms enables the cultural transmission of know-how (Boyd & Richerson, 1996; Tennie et al., 2009, 2020a; Tomasello, 2003). For example, the know-how of the tango needs to be culturally transmitted in order for it to be danced, and whatever material or device you are reading this text from also required cultural transmission of know-how for its production. Copying social learning leads to the development of novel know-how, e.g., via processes of drift from copying error (Eerkens & Lipo, 2005; Schillinger, 2014) and – in conjunction with the ability to keep ‘better’ versions – results in successive ratcheting of know-how innovations/modifications until the culturally transmitted know-how exceeds individual capacities for re-innovation (Tennie et al., 2009, 2020a; see also Boyd & Richerson, 1996). Various other processes could potentially moderate these changes (cf. Lycett et al., 2015; Sterelny & Hiscock, in press) – but this does not change the need for cultural transmission of know-how. For example, we may envision that these other processes play larger roles only if there is weak cultural transmission of know-how or know-how transmission is totally absent. In the case of human culture, there is a sheer diversity of copying-dependent know-how – that is, know-how that cannot be individually re-innovated (Motes-Rodrigo & Tennie, 2021; Reindl et al., 2016; Tennie et al., 2020a; Tomasello, 1999).<sup>1</sup> This phenomenon of cultural transmission and cumulative culture of know-how is often said to be exclusive – at least as far as living ape taxa are concerned – to *Homo sapiens* (Dean et al., 2012; Schuppli & van Schaik, 2019; Tomasello, 1999; see also Heyes, 2021).

Although cumulative culture of know-how seemingly distinguishes living modern humans from our

closest relatives, it is not the only type of culture that exists, with other taxa also possessing culture of some types (e.g., Dean et al., 2013; Whiten et al., 1999). Indeed, many animal species seem capable of using social learning – the minimum requirement for culture (cf. Boyd & Richerson, 1988; Dean et al., 2013; Heyes, 2020, 2021; Neadle et al., 2017) – but there are many different mechanisms of social learning and these lead to distinct cultural transmission pathways. Here, it is meaningful to distinguish between cultural transmission of *know-how* (see above) and cultural transmission of other information types. Whereas copying social learning mechanisms can lead to the cultural transmission of know-how, other, “non-copying”, social learning mechanisms do not transmit know-how and instead lead to the cultural transmission of information like know-where, know-what, and know-when (compare with Arbilly & Laland, 2014; Bandini et al., 2020; Heyes, 1994; Tennie et al., 2020a; Zuberbühler et al., 1996). Non-copying social learning mechanisms – indirectly via cultural transmission of know-where, know-what, and know-when – can also lead to socially-mediated individual development of know-how without the know-how itself between transmitted from one individual to another (i.e., without copying; Bandini & Tennie, 2017; Buskell & Tennie, in press; Tennie et al., 2010). Know-how can also be released more directly. A very basic example of this is social contagions, such as yawning or laughing, which involve the triggering (cf. Sperber, 2000) of know-how via social influences without the know-how for yawning or laughing being copied (Tennie et al., 2020b). These non-copying mechanisms can create cultural patterns (Acerbi et al., in press; Barrett, 2019) that can be labelled as minimal cultures (Neadle et al., 2017; Snyder et al., 2022; Tennie et al., 2020a – compare with Galef, 1992).

This general outline for minimal culture is currently the best explanation for cultures in non-human apes (see Bandini et al., 2020; Tennie et al., 2020a, 2020b – see also Sterelny & Hiscock, in press). First, there is a lack of unequivocal evidence for copying social learning abilities in untrained, unenculturated apes,<sup>2</sup>

<sup>1</sup> Alternatively, this can be defined as *supraindividual* know-how (see Tennie & Call, in press).

<sup>2</sup> There is some evidence for copying social learning abilities in captive, *enculturated*/trained apes. However, the processes of

enculturation – the undue influence of human training and/or rearing – can lead to structural changes in ape brains that consequently grant them cognitive abilities that are not representative of their wild counterparts (see Pope et al., 2018;

with numerous studies demonstrating that they are unable to copy copying-dependent know-how (e.g., Clay & Tennie, 2018; Neadle et al., 2021; Tennie et al., 2012). Second, wild tool use behaviors have largely been shown to be re-innovatable by naïve, unenculturated individuals (cf. Bandini & Tennie, 2017, 2019; Bandini et al., 2020, 2021; Tennie et al., 2020a). Similar patterns are found even across wild ape populations (Motes-Rodrigo & Tennie, 2021). Finally, population-scale behavior distributions like those observed in wild apes can be produced without the presence of copying social learning abilities (Acerbi et al., 2022).

Human children from different cultural backgrounds are also capable of re-innovating a variety of wild primate tool use behaviors (Neldner et al., 2020; Reindl et al., 2016). As such, it can be said that minimal cultural pathways also exist in humans, but these are more difficult to see in current contexts due to the predominance of cumulative culture of know-how and its stark influences on human behavior and lifeways (cf. Bandini et al., 2020; Boyd, 2018; Boyd & Richerson, 1996; Henrich, 2016; Henrich et al., 2010; Motes-Rodrigo & Tennie, 2021; Tennie et al., 2020a; Tomasello, 1999).

If cumulative culture of know-how – beyond the individual reach – is indeed unique among the apes to living modern humans, the search for the origins of cumulative culture of know-how should be directed towards the hominin lineage post-divergence from the chimpanzee and bonobo lineage (i.e., the least common ancestor, LCA, of humans and *Pan* would not have possessed abilities for cultural transmission of know-how; see Snyder et al., 2022; Sterelny & Hiscock, in press; Stout et al., 2019; Tennie et al., 2016, 2017; compare with Toth & Schick, 2018; Wynn & McGrew, 1989; Wynn et al., 2011). This investigation is, however, limited by the available preserved physical evidence for hominin cognition and behavior.

Other than some (potential) bone excavating tools from the early Pleistocene of South Africa (Backwell & d'Errico, 2008; d'Errico & Blackwell, 2003), there is little to no preserved evidence of organic tools from the pre-Oldowan and Oldowan periods. Generally, the organic tool repertoire of early hominins is predicted to have been similar to that of living primate species (Ambrose, 2001; Bandini et al., 2022; Haslam et al., 2009; Hovers, 2012; Rolian & Carvalho, 2017; Toth

& Schick, 2009). Living primates have been shown capable of spontaneously re-innovating organic tool use know-how – including excavating (Motes-Rodrigo et al., 2019, 2022a) – so if early hominins inherited similar technological capacities in this domain, then it can be most parsimoniously assumed to have been part of minimal cultures in those extinct taxa (Bandini & Tennie, 2017, 2019; Bandini et al., 2020, 2021; Reindl et al., 2016; Sterelny & Hiscock, in press; Tennie et al., 2020; Westergaard & Suomi, 1993, 1995a).

Stone tools provide an inherently much better option for studying cognitive and cultural evolution, because of the ubiquity of stone tools and stone-tool-related behavioral traces throughout the hominin record (Foley & Lahr, 2003; Schick & Toth, 1993; Stout & Chaminade, 2009; Tennie et al., 2016, 2017; Toth & Schick, 1994, 2018). Some researchers have previously regarded Oldowan (and later Eurasian Mode 1) artifacts as being based on or requiring ape-like capacities for learning and cognition (Pradhan et al., 2012; Putt et al., 2017; Whiten et al., 2003; Wynn & McGrew, 1989; Wynn et al., 2011), but here it depends of course on what abilities are assumed to exist in these apes. It is important to note that many of these publications have (we believe, erroneously) attributed abilities for cultural transmission of know-how via copying to non-human primates (e.g., Whiten et al., 2003; Wynn et al., 2011). There have been many claims made for similar cultural transmission of know-how for the acquisition of stone toolmaking skills<sup>3</sup> (e.g., Cataldo et al., 2018; Eren et al., 2020; Lombao et al., 2017; Morgan et al., 2015; Schick & Toth, 1993; Shipton, 2020; Stout & Chaminade, 2007; Stout & Semaw, 2006; Stout et al., 2010, 2019; Toth et al., 1993; Whiten, 2015). In fact, there have even been outright claims for the origins of cumulative culture of know-how in the earliest Oldowan at the nearly 2.6-million-year-old site of Gona in Ethiopia (Stout et al., 2019). On the other hand, stone tools have alternatively been interpreted as not having required cultural transmission of know-how beyond the individual reach (cf. Acerbi & Tennie, 2016; Cueva-Temprana et al., 2022; Davidson & McGrew, 2005; Mithen, 1996; Tennie et al., 2016, 2017; van Schaik et al., 2019).

During the Oldowan, there is a considerable and lengthy stasis in both artifacts and technical know-how (Cueva-Temprana et al., 2022; Foley & Lahr, 2003;

Tennie, 2019). Captive, unenculturated/untrained apes do not demonstrate these abilities (Clay & Tennie, 2018; Neadle et al., 2021; Tennie et al., 2012). Wild apes are likewise not enculturated or trained by humans and yet, they, to show a repetition of know-how across culturally unconnected populations (Motes-Rodrigo & Tennie, 2021).

<sup>3</sup> There have been more general claims for the presence of cultural transmission of know-how in the Oldowan, as well as claims where specific copying social learning mechanisms are identified, including variants of emulation, imitation, (proto-) language, and teaching.

Isaac, 1972, 1984; Jelinek, 1977; Semaw et al., 2003; Tennie et al., 2016, 2017). This – and similar stases in the record – has been suggested to have resulted from high fidelity copying and conformity bias (Lycett & Gowlett, 2008; Lycett et al., 2015; Morgan et al., 2015; Schillinger et al., 2014), but these mechanisms are not appropriate explanations for the stasis, as copying should hypothetically lead to a radiation of forms just from copying error alone (Eerkens & Lipo, 2005) and they would also require levels of copying fidelity and conformity beyond what is exhibited by humans today (see Foley & Lahr, 2003). Even further, non-human apes are unable to copy copying dependent know-how even under conformity conditions (Needle et al., 2021), so neither capacity can be assumed for early toolmaking hominins. Instead, the limited within-Oldowan variability, can best be explained by raw material differences, species-typical cognition, and other non-know-how-transmitting factors (Cueva-Temprana et al., 2022; Tennie et al., 2016, 2017; but compare with Stout et al., 2019). Indeed, the overall pattern of stasis is to be expected, and thus makes sense, under a minimal culture model wherein know-how development never truly kicks off to go beyond individual re-innovation capacities (see below). Minimal cultures can change but only very slowly over extensive, biologically meaningful time units (Snyder et al., 2022). While minimal cultures surely interact with such slow, biological change (Tennie et al., 2020b), the lack of sufficient levels of copying social learning and cultural transmission of know-how would prevent fast changes and simultaneously would keep the range of know-how bounded, thereby resulting in stasis. Stases therefore are a natural and expected outcome for the minimal culture model.

The specific forms of Oldowan stone artifacts have generally not been the basis of arguments for cultural determinism. These forms can clearly appear without the cultural transmission of know-how being involved, and independent experimental frameworks have indeed validated the notion that Oldowan artifacts are the unintentional (and non-cultural) byproducts of least-effort flaking behaviors (e.g., Toth, 1985). In one case, Oldowan artifact forms appeared in stochastic knapping sequences during spandrels experiments (Moore & Perston, 2016), while in another, naïve novices who had never been exposed to Oldowan artifact

forms reproduced all those core types that were possible from the provided knapping blank form (Snyder et al., 2022).

The cultural status of Oldowan toolmaking know-how is much more contentious than that of the artifact forms. As common practice, participants in knapping experiments are provided with opportunities for cultural transmission of know-how, with emulation (via end-state copying) typically regarded as the minimum condition (Morgan et al., 2015). These experimental conditions led to the acquisition of basic toolmaking abilities by their participants, but with different efficiencies and efficacies based on the particular learning mechanisms that were allowed in the respective testing methods applied (Cataldo et al., 2018; Lombao et al., 2017; Morgan et al., 2015). From these experimental outcomes, archaeologists have claimed that (at least some) early knapping techniques *require* some kind of cultural transmission of know-how (see Cataldo et al., 2018; Lombao et al., 2017; Morgan et al., 2015; Ship-ton, 2020; Sterelny & Hiscock, in press). That is, the claim is that the Oldowan contained some copying-dependent know-how.

A claim for copying-dependency can be tested by removing know-how related copying possibilities (Tennie et al., 2017). The question here is therefore: can all Oldowan stone toolmaking know-how appear in the absence of possibilities for cultural transmission of said know-how? If the empirical answer is yes, then it would mean that the cultural transmission of know-how is not necessary for the development of knapping know-how, and thus, artifacts made in the procedure of this know-how cannot be used as undeniable evidence that cultural transmission of know-how occurred (i.e., because it can principally exist without said cultural transmission). The underlying techniques would be proven to be copying-*independent*. And indeed, the answer to this question is yes – the know-how can be re-innovated. Human test participants produced all four early knapping techniques (passive hammer, bipolar, freehand, and projectile) when tested without any demonstrations, teaching, or other exposure to stone tools – in short, in the absence of know-how models to copy (Snyder et al., 2022). Moreover, both the toolmaking techniques and the artifactual outcomes produced by naïve human novices were valid representatives of Oldowan technology(-ies).<sup>4</sup> This is

<sup>4</sup> With enough opportunities for behavioral expressions, we predict that knapping skill levels of naïve novices in copying-free conditions would further improve (see Snyder et al., 2022). At some point, we predict their skill to match what is shown by humans in studies that use know-how models, and to match hominin skills at early Oldowan sites (Stout & Semaw, 2006).

Another possibility is that eventually humans exceed these skills – and the open question is whether this then would depend on know-how models given to them. We are not sure that know-how models are necessary to make, e.g., handaxes – but we acknowledge that this is an open question that can be pursued empirically.

proof-of-principle – from one living species (humans) – that the evidence of Oldowan stone artifacts in the archaeological record cannot be used to infer cultural transmission of know-how beyond the individual range. As such, the existing evidence is not suited to point beyond minimal culture.

Nonetheless, there still may be objections to this logic. One suggestion is that ‘indirect’ transmission of know-how (i. e., before participants entered the test) influenced the behavioral outcomes in the study of Snyder et al. (2022). First, in our view, this is an unlikely possibility as the participants were evaluated on their past experiences directly related to stone tools, and other types of experiential information (e. g., that sharp things can be used to cut) would not inform them on the desired behavioral outcome – e. g., on the know-how of knapping (see discussion in Snyder et al., 2022). Just as well, the possibility still remains and so triangulation with data from other species is additionally required. Non-human primates – untrained, and unenculturated – operate as an ideal control, due to their lack of copying abilities beyond the individual (see above) and greater certainty about past experiences in captive individuals (see also Bandini et al., 2022). And indeed, untrained and unenculturated individuals from some species of non-human primates show an ability to re-innovate knapping know-how. The clearest case comes from capuchin monkeys, who innovated all four early knapping techniques (Westergaard & Suomi, 1994, 1995b).<sup>5</sup> Further evidence comes from re-innovation of passive hammer technique by untrained, unenculturated orangutans (Motes-Rodrigo et al., 2022b). In summary, the indirect cultural transmission of know-how route can also be disregarded, meaning that knapping know-how is innovatable in the absence of know-how models.

Just as non-human apes have (minimal) culture (e. g., Whiten et al., 1999) and the culture of living humans is thoroughly documented, so too can we suspect that early toolmaking hominins were (at least, to some degree) cultural beings and that Oldowan knapping was (in some sense) cultural behavior (cf. Stout & Semaw, 2006, p. 308). However – from our theoretical perspective – Oldowan toolmaking and tool use were *minimal* cultural behaviors (cf. Snyder et al., 2022; Tennie et al., 2016, 2017, 2020a) – similar in principle to ape cultural behaviors today. Hominins, regardless of their phylogenetic position, would all have had some social learning capacities, but the

social learning capacities of early toolmaking hominins are unlikely to have included cultural transmission of know-how beyond the individual reach at the respective times and in the respective species. Non-copying social learning mechanisms like stimulus and local enhancement (Tennie et al., 2016, 2017; see also Mithen, 1996 on the Mode 1 Clactonian industry) and maybe triggering (*sensu* Sperber, 2000) would have been key to the ‘spread’<sup>6</sup> and stabilization of toolmaking re-innovations. These would have transmitted information like know-what (e. g., knappable rocks) and know-where (e. g., rocky outcrops and locations of carcasses), rather than the know-how, let alone copying-dependent know-how (see Bandini et al., 2020; Snyder et al., 2022; Tennie et al., 2020a). Cultural transmission of know-what and know-where (and triggering) would then have led – with greater likelihood than in their absence – to the subsequent development and expression of know-how on the individual level in affected members of hominin groups. Knapping behaviors would therefore have appeared to spread but were really only mediated indirectly (e. g., via know-what) and/or directly triggered (*sensu* Sperber, 2000; see also Buskell & Tennie, in press). In other words, social learning among hominins existed – and thus, their lives were cultural – but it essentially only affected the frequency of know-how that was in their individual reach (i. e., that was inside their ‘zone of latent solutions’; cf. Tennie et al. 2009, 2020; Bandini & Tennie, 2017). These hominins had cultures – but their cultures were bounded, and therefore, minimal.

All available lines of evidence would support the minimal culture model being the best (i. e., most parsimonious) among the current interpretations of hominin behavior before and during the Oldowan. Hundreds of thousands of years of technological stasis in the Oldowan, for example, can be best explained by a lack of cultural transmission of know-how (see Montrey & Schultz, 2020; Tennie et al., 2016, 2017, 2020; van Schaik et al., 2019). The same can be said for the – likely – multiple independent origins of the Oldowan (Braun et al., 2019; de la Torre, 2019; Hovers, 2012; Shea, 2017), because (for these hominins as well) the technology was likely ‘easy’ to invent – at least under the right circumstances (e. g., with appropriate motivation and raw materials). In the late Pliocene and early Pleistocene, the right circumstances were often met, in terms of hominin biology, cognition, and ecology, and consequently, there was the sud-

<sup>5</sup> Freehand hitting behavior in wild gorillas is superficially similar to freehand knapping technique and may therefore be informative on the individual development of toolmaking know-how by hominins (Masi et al., 2022).

<sup>6</sup> Here, it would be more appropriate to describe know-how as being catalyzed rather than spreading.

den appearance Oldowan assemblages across Africa in disconnected populations (see Acerbi et al., in press). In a similar vein, the minimal culture model also can explain the re-appearance of the Oldowan *sensu latu*, i. e., Eurasian Mode 1 technologies during later periods, even when and where there were more advanced technologies being produced in the same population or in other populations of the same species (Clark, 1963; Foley & Lahr, 2003; Parfitt et al., 2022; Semaw et al., 2020; Shea, 2013; Tennie et al., 2017; even in our recent experimental study, see Snyder et al., 2022).

Oldowan and later Mode 1 technologies are not unequivocal evidence for early cultural transmission of know-how in the hominin lineage – especially not for copying-dependent know-how (and its cultural evolution). Instead, we infer that, currently, a better explanation is the minimal culture model (Snyder et al., 2022; Tennie et al., 2016, 2017). Minimal cultural mechanisms, which can produce simple flaking behavior, likely continued to be present in later, related species (see point above) and, as a result, these minimal cultural capacities are still present in living modern humans. Just as with the re-innovation of ape tool use behaviors by human children (Neldner et al., 2020; Reindl et al., 2016), living humans (here, adults) can re-innovate early knapping techniques (the very same ones used by our Oldowan forebearers) when right circumstances are available (e. g., pertinent raw materials and motivation; Snyder et al., 2022). If Oldowan technology is explainable by minimal cultural capacities in living humans and extinct hominins, the question becomes: at what point in the archaeological record did the know-how of stone toolmaking exceed the individual reach and therewith become copying-dependent (see Tennie et al., 2016, 2017)? Future empirical research should follow a similar approach as we have applied, in order to identify which technology(-ies) are a better candidate for the origins of supra-individual know-how and the learning mechanisms by which it is produced: the cultural transmission of know-how via copying social learning.

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### References

- Acerbi, A., & Tennie, C. (2016): The role of redundant information in cultural transmission and cultural stabilization. *Journal of Comparative Psychology*, 130(1), 62.
- Acerbi, A., Snyder, W.D., & Tennie, C. (2022): The method of exclusion (still) cannot identify mechanisms of cultural inheritance. *Scientific Reports* 12, 21680.
- Ambrose, S.H. (2001): Paleolithic technology and human evolution. *Science*, 291(5509), 1748–1753.
- Arbilly, M., & Laland, K.N. (2014): The local enhancement conundrum: in search of the adaptive value of a social learning mechanism. *Theoretical Population Biology*, 91, 50–57.
- Backwell, L., & d’Errico, F. (2008): Early hominid bone tools from Drimolen, South Africa. *Journal of Archaeological Science*, 35(11), 2880–2894.
- Bandini, E., & Tennie, C. (2017): Spontaneous reoccurrence of “scooping”, a wild tool-use behaviour, in naïve chimpanzees. *PeerJ*, 5, e3814.
- Bandini, E., & Tennie, C. (2019): Individual acquisition of “stick pounding” behavior by naïve chimpanzees. *American Journal of Primatology*, e22987.
- Bandini, E., Motes-Rodrigo, A., Steele, M.P., Rutz, C., & Tennie, C. (2020): Examining the mechanisms underlying the acquisition of animal tool behaviour. *Biol. Lett.*, 16, 20200122.
- Bandini, E., Grossmann, J., Funk, M., Albiach-Serrano, A., & Tennie, C. (2021): Naïve orangutans (*Pongo abelii* and *Pongo pygmaeus*) individually acquire nut-cracking using hammer tools. *American Journal of Primatology*, 83(9), e23304.
- Bandini, E., Harrison, R.A., & Motes-Rodrigo, A. (2022): Examining the suitability of extant primates as models of hominin stone tool culture. *Humanities and Social Sciences Communications*, 9(1), 1–18.
- Barrett, B.J. (2019): Equifinality in empirical studies of cultural transmission. *Behavioural Processes*, 161, 129–138.
- Boyd, R. (2018): *A Different Kind of Animal: How Culture Transformed Our Species*. Princeton University Press.
- Boyd, R., & Richerson, P.J. (1988): *Culture and The Evolutionary Process*. University of Chicago press.
- Boyd, R., & Richerson, P.J. (1996): Why culture is common, but cultural evolution is rare. In: *Proceedings-British Academy* (Vol. 88, pp. 77–94). Oxford University Press Inc.
- Braun, D.R., Aldeias, V., Archer, W., Arrowsmith, J.R., Baraki, N., Campisano, C.J., Deino, A.L., DiMaggio, E.N., Dupont-Nivet, G., Engda, B., Feary, D.A., Garello, D.I., Kerfelew, Z., McPherron, S.P., Patterson, D.B., Reeves, J.S., Thompson, J.C., & Reed, K.E. (2019): Earliest known Oldowan artifacts at >2.58 Ma from Ledi-Geraru, Ethiopia, highlight early technological diversity. *Proceedings of the National Academy of Sciences*, 201820177.
- Buskell, A., & Tennie, C. (in press): Mere recurrence and cumulative culture at the margins. *The British Journal for the Philosophy of Science*.
- Cataldo, D.M., Migliano, A.B., & Vinicius, L. (2018): Speech, stone tool-making and the evolution of language. *PLOS ONE*, 13(1), e0191071.
- Clark, G. (1963). *World Prehistory: A New Outline*. Cambridge. Cambridge University Press.
- Clay, Z., & Tennie, C. (2018): Is Overimitation a Uniquely Human Phenomenon? Insights From Human Children as Compared to Bonobos. *Child Development*, 89(5), 1535–1544.

- Cueva-Temprana, A., Lombao, D., Soto, M., Itambu, M., Bushozi, P., Boivin, N., ... & Mercader, J. (2022): Oldowan Technology Amid Shifting Environments~ 2.03–1.83 Million Years Ago. *Frontiers in Ecology and Evolution*, 122.
- Davidson, I., & McGrew, W.C. (2005): Stone tools and the uniqueness of human culture. *Journal of the Royal Anthropological Institute*, 11(4), 793–817.
- Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., & Laland, K. N. (2012): Identification of the social and cognitive processes underlying human cumulative culture. *Science*, 335(6072), 1114–1118.
- Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E., & Kendal, R. L. (2013): Human cumulative culture: a comparative perspective. *Biological Reviews*, 89(2), 284–301.
- de la Torre, I. (2019): Searching for the emergence of stone tool making in eastern Africa. *Proceedings of the National Academy of Sciences*, 116(24), 11567–11569.
- d’Errico, F., & Backwell, L. R. (2003): Possible evidence of bone tool shaping by Swartkrans early hominids. *Journal of Archaeological Science*, 30(12), 1559–1576.
- Eerkens, J. W., & Lipo, C. P. (2005): Cultural transmission, copying errors, and the generation of variation in material culture and the archaeological record. *Journal of Anthropological Archaeology*, 24(4), 316–334.
- Eren, M. I., Lycett, S. J., & Tomonaga, M. (2020): Underestimating Kanzi? Exploring Kanzi–Oldowan comparisons in light of recent human stone tool replication. *Evolutionary Anthropology: Issues, News, and Reviews*, 29(6), 310–316.
- Foley, R., & Lahr, M. M. (2003): On stony ground: lithic technology, human evolution, and the emergence of culture. *Evolutionary Anthropology: Issues, News, and Reviews*, 12(3), 109–122.
- Galef, B. G. (1992): The question of animal culture. *Human Nature*, 3(2), 157–178.
- Haslam, M., Hernandez-Aguilar, A., Ling, V., Carvalho, S., De La Torre, I., DeStefano, A., ... & Warren, R. (2009): Primate archaeology. *Nature*, 460(7253), 339–344.
- Henrich, J. (2016): *The Secret of Our Success: How Culture Is Driving Human Evolution, Domesticating Our Species, and Making Us Smarter*. Princeton University Press.
- Henrich, J., Heine, S. J., & Norenzayan, A. (2010): The weirdest people in the world? *Behavioral and Brain Sciences*, 33(2–3), 61–83.
- Heyes, C. M. (1994): Social learning in animals: categories and mechanisms. *Biological Reviews*, 69(2), 207–231.
- Heyes, C. (2020): Culture. *Current Biology*, 30(20).
- Heyes, C. (2021): Imitation and culture: What gives? *Mind & Language*.
- Hovers, E. (2012): Invention, reinvention and innovation: the makings of Oldowan lithic technology. In: *Developments in Quaternary Sciences* (Vol. 16, pp. 51–68). Elsevier.
- Isaac, G. L. (1972): Early phases of human behaviour: models in Lower Palaeolithic archaeology. *Models in Archaeology*, 167–199.
- Isaac, G. L. (1984): The earliest archaeological traces. In: J. D. Clark (Ed.), *The Cambridge history of Africa* (Vol. 1, pp. 157–247). Cambridge: Cambridge University Press.
- Jelinek, A. J. (1977): The Lower Paleolithic: Current Evidence and Interpretations. *Annual Review of Anthropology*, 6, 11–32.
- Lombao, D., Guardiola, M., & Mosquera, M. (2017): Teaching to make stone tools: New experimental evidence supporting a technological hypothesis for the origins of language. *Scientific Reports*, 7(1), 14394.
- Lycett, S. J., & Gowlett, J. A. (2008): On questions surrounding the Acheulean ‘tradition’. *World Archaeology*, 40(3), 295–315.
- Lycett, S. J., Schillinger, K., Kempe, M., & Mesoudi, A. (2015): Learning in the Acheulean: experimental insights using handaxe form as a ‘model organism’. In: *Learning strategies and cultural evolution during the Palaeolithic* (pp. 155–166). Springer, Tokyo.
- Masi, S., Pouydebat, E., San-Galli, A., Meulman, E., Breuer, T., Reeves, J., & Tennie, C. (2022): Free hand hitting of stone-like objects in wild gorillas. *Scientific Reports*, 12(1), 1–10.
- Mithen, S. (1996): Social learning and cultural tradition: interpreting Early Palaeolithic technology. *The Archaeology of Human Ancestry: Power, Sex and Tradition*, 207–229.
- Moore, M. W., & Perston, Y. (2016): Experimental insights into the cognitive significance of early stone tools. *PLoS One*, 11, e0158803.
- Montrey, M., & Shultz, T. R. (2020): The evolution of high-fidelity social learning. *Proceedings of the Royal Society B*, 287(1928), 20200090.
- Morgan, T. J. H., Uomini, N. T., Rendell, L. E., Chouinard-Thuly, L., Street, S. E., Lewis, H. M., Cross, C. P., Evans, C., Kearney, R., de la Torre, I., Whiten, A., & Laland, K. N. (2015): Experimental evidence for the co-evolution of hominin tool-making teaching and language. *Nature Communications*, 6(1), 6029.
- Motes-Rodrigo, A., & Tennie, C. (2021): The Method of Local Restriction: In search of potential great ape culture-dependent forms. *Biological Reviews*, 96(4), 1441–1461.
- Motes-Rodrigo, A., Tennie, C., & Hernandez-Aguilar, R. A. (2022a): Bone-related behaviours of captive chimpanzees (*Pan troglodytes*) during two excavating experiments. *Primates*, 1–12.
- Motes-Rodrigo, A., Majlesi, P., Pickering, T. R., Laska, M., Axelsen, H., Minchin, T. C., ... & Hernandez-Aguilar, R. A. (2019): Chimpanzee extractive foraging with excavating tools: experimental modeling of the origins of human technology. *PLoS One*, 14(5), e0215644.
- Motes-Rodrigo, A., McPherron, S. P., Archer, W., Hernandez-Aguilar, R. A., & Tennie, C. (2022b): Experimental investigation of orangutans’ lithic percussive and sharp stone tool behaviours. *PLoS One*, 17(2), e0263343.
- Neadle, D., Allritz, M., & Tennie, C. (2017): Food cleaning in gorillas: social learning is a possibility but not a necessity. *PLoS One*, 12(12), e0188866.
- Neadle, D. L., Chappell, J., Clay, Z., & Tennie, C. (2021): Even under majority influence, great apes fail to copy novel actions. *OSF Preprints*. <https://doi.org/10.31219/osf.io/swt9b>
- Neldner, K., Reindl, E., Tennie, C., Grant, J., Tomaselli, K., & Nielsen, M. (2020): A cross-cultural investigation of young children’s spontaneous invention of tool use behaviours. *Royal Society Open Science*, 7(5), 192240.
- Parfitt, S. A., Lewis, M. D., & Bello, S. M. (2022): Taphonomic and technological analyses of Lower Palaeolithic bone tools from Clacton-on-Sea, UK. *Scientific Reports*, 12(1), 1–19.
- Pope, S. M., Taglialatela, J. P., Skiba, S. A., & Hopkins, W. D. (2018): Changes in frontoparietotemporal connectivity following do-as-I-do imitation training in chimpanzees (*Pan troglodytes*). *Journal of Cognitive Neuroscience*, 30(3), 421–431.
- Pradhan, G. R., Tennie, C., & van Schaik, C. P. (2012): Social organization and the evolution of cumulative technology

- in apes and hominins. *Journal of Human Evolution*, 63(1), 180–190.
- Putt, S.S., Wijekumar, S., Franciscus, R.G., & Spencer, J.P. (2017): The functional brain networks that underlie Early Stone Age tool manufacture. *Nature Human Behaviour*, 1(6), 0102.
- Reindl, E., Beck, S.R., Apperly, I.A., & Tennie, C. (2016): Young children spontaneously invent wild great apes' tool-use behaviours. *Proc. R. Soc. B*, 283, 20152402.
- Rolian, C., & Carvalho, S. (2017): Tool use and manufacture in the last common ancestor of *Pan* and *Homo*. In: M.N. Muller, R.W. Wrangham, & D.R. Pilbeam (Eds.), *Chimpanzees and human evolution* (pp. 602–644). The Belknap Press of Harvard University Press.
- Schick, K.D., & Toth, N. (1994): *Making silent stones speak: Human evolution and the dawn of technology*. Simon & Schuster.
- Schillinger, K., Mesoudi, A., & Lycett, S.J. (2014): Copying error and the cultural evolution of “additive” vs. “reductive” material traditions: an experimental assessment. *American Antiquity*, 79(1), 128–143.
- Schuppli, C., & van Schaik, C.P. (2019): Animal cultures: how we've only seen the tip of the iceberg. *Evolutionary Human Sciences*, 1.
- Semaw, S., Rogers, M.J., Quade, J., Renne, P.R., Butler, R.F., Dominguez-Rodrigo, M., ... & Simpson, S.W. (2003): 2.6-Million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *Journal of Human Evolution*, 45(2), 169–177.
- Semaw, S., Rogers, M.J., Simpson, S.W., Levin, N.E., Quade, J., Dunbar, N., ... & Everett, M. (2020): Co-occurrence of Acheulean and Oldowan artifacts with *Homo erectus* cranial fossils from Gona, Afar, Ethiopia. *Science Advances*, 6(10), eaaw4694.
- Shea, J.J. (2013): Lithic modes A–I: a new framework for describing global-scale variation in stone tool technology illustrated with evidence from the East Mediterranean Levant. *Journal of Archaeological Method and Theory*, 20(1), 151–186.
- Shea, J.J. (2017): Occasional, obligatory, and habitual stone tool use in hominin evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, 26(5), 200–217.
- Shipton, C. (2020): The unity of Acheulean culture. In: *Culture history and convergent evolution* (pp. 13–27). Springer, Cham.
- Snyder, W.D., Reeves, J.S., & Tennie, C. (2022): Early knapping techniques do not necessitate cultural transmission. *Science Advances*, 8(27), eabo2894.
- Sperber, D. (2000): An objection to the memetic approach to culture. In: R. Aunger (Ed.), *Darwinizing culture: the status of memetics as a science* (pp. 163–173). Oxford: Oxford University Press.
- Sterelny, K., & Hiscock, P. (in press): Cumulative Culture, Archaeology, and the Zone of Latent Solutions. *Current Anthropology*.
- Stout, D., & Chaminade, T. (2007): The evolutionary neuroscience of tool making. *Neuropsychologia*, 45(5), 1091–1100.
- Stout, D., & Chaminade, T. (2009): Making Tools and Making Sense: Complex, Intentional Behaviour in Human Evolution. *Cambridge Archaeological Journal*, 19(1), 85–96.
- Stout, D., & Hecht, E.E. (2017): Evolutionary neuroscience of cumulative culture. *Proceedings of the National Academy of Sciences*, 114(30), 7861–7868.
- Stout, D., & Semaw, S. (2006): Knapping skill of the earliest stone toolmakers: Insights from the study of modern human novices. In: N. Toth & K. Schick (Eds.), *The Oldowan: Case studies into the earliest Stone Age* (pp. 307–320). Gosport: Stone Age Institute Press.
- Stout, D., Semaw, S., Rogers, M.J., & Cauche, D. (2010): Technological variation in the earliest Oldowan from Gona, Afar, Ethiopia. *Journal of Human Evolution*, 58(6), 474–491.
- Stout, D., Rogers, M.J., Jaeggi, A.V., & Semaw, S. (2019): Archaeology and the Origins of Human Cumulative Culture: A Case Study from the Earliest Oldowan at Gona, Ethiopia. *Current Anthropology*, 60(3), 309–340.
- Tennie, C. (2019). Could nonhuman great apes also have cultural evolutionary psychology? *Behavioral and Brain Sciences*, 42.
- Tennie, C., Call, J. (in press): Unmotivated Subjects Cannot Provide Interpretable Data And Tasks With Sensitive Learning Periods Require Appropriately Aged Subjects A Commentary on Koops et al.'s “Field experiments find no evidence that chimpanzee nut cracking can be independently innovated.” *Animal Behavior and Cognition*.
- Tennie, C., Call, J., & Tomasello, M. (2009): Ratcheting up the ratchet: On the evolution of cumulative culture. *Phil. Trans. R. Soc. B*, 364, 2405–2415.
- Tennie, C., Call, J., & Tomasello, M. (2010): Evidence for emulation in chimpanzees in social settings using the floating peanut task. *PLoS One*, 5(5), e10544.
- Tennie, C., Call, J., & Tomasello, M. (2012): Untrained chimpanzees (*Pan troglodytes schweinfurthii*) fail to imitate novel actions. *PLoS One*. 2012;7(8):e41548.
- Tennie, C., Braun, D.R., Premo, L.S., & McPherron, S.P. (2016): The Island Test for Cumulative Culture in the Paleolithic. In: M.N. Haidle, N.J. Conard, & M. Bolus (Eds.), *The Nature of Culture* (pp. 121–133). Springer Netherlands.
- Tennie, C., Premo, L.S., Braun, D.R., & McPherron, S.P. (2017): Early Stone Tools and Cultural Transmission: Resetting the Null Hypothesis. *Current Anthropology*, 58(5), 652–672.
- Tennie, C., Bandini, E., van Schaik, C.P., & Hopper, L.M. (2020a): The zone of latent solutions and its relevance to understanding ape cultures. *Biology & Philosophy*, 35(5), 55.
- Tennie, C., Hopper, L.M., & van Schaik, C.P. (2020b): On the Origin of Cumulative Culture: Consideration of the Role of Copying in Culture-Dependent Traits and a Reappraisal of the Zone of Latent Solutions Hypothesis. In: *Chimpanzees in Context* (pp. 428–453). University of Chicago Press.
- Tomasello, M. (1999): The Human Adaptation for Culture. *Annual Review of Anthropology*, 28(1), 509–529.
- Tomasello, M. (2003): *The cultural origins of human cognition*. Harvard Univ. Press.
- Toth, N. (1985). The Oldowan reassessed: A close look at early stone artifacts. *Journal of Archaeological Science*, 12(2), 101–120.
- Toth, N., & Schick, K. (1994): Early stone industries and inferences regarding language and cognition. In: K.R. Gibson, & T. Ingold (Eds.), *Tools, language and cognition in human evolution* (pp. 346–362). Cambridge University Press.
- Toth, N., & Schick, K. (2009): The Oldowan: the tool making of early hominins and chimpanzees compared. *Annual Review of Anthropology*, 38, 289–305.
- Toth, N., & Schick, K. (2018): An overview of the cognitive implications of the Oldowan Industrial Complex. *Azania: Archaeological Research in Africa*, 53(1), 3–39.

- Toth, N., Schick, K. D., Savage-Rumbaugh, E. S., Sevcik, R. A., & Rumbaugh, D. M. (1993): Pan the Tool-Maker: Investigations into the Stone Tool-Making and Tool-Using Capabilities of a Bonobo (*Pan paniscus*). *Journal of Archaeological Science*, 20(1), 81–91.
- van Schaik, C. P., Pradhan, G. R., & Tennie, C. (2019): Teaching and curiosity: sequential drivers of cumulative cultural evolution in the hominin lineage. *Behavioral Ecology and Sociobiology*, 73(1), 1–11.
- Westergaard, G. C., & Suomi, S. J. (1993): Use of a tool-set by capuchin monkeys (*Cebus apella*). *Primates*, 34(4), 459–462.
- Westergaard, G. C., & Suomi, S. J. (1994): A simple stone-tool technology in monkeys. *Journal of Human Evolution*, 27(5), 399–404.
- Westergaard, G. C., & Suomi, S. J. (1995a): The manufacture and use of bamboo tools by monkeys: possible implications for the development of material culture among East Asian hominids. *Journal of Archaeological Science*, 22(5), 677–681.
- Westergaard, G. C., & Suomi, S. J. (1995b): The stone tools of capuchins (*Cebus apella*). *International Journal of Primatology*, 16(6), 1017–1024.
- Whiten, A. (2015): Experimental studies illuminate the cultural transmission of percussive technologies in *Homo* and *Pan*. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1682), 20140359.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., ... & Boesch, C. (1999): Cultures in chimpanzees. *Nature*, 399(6737), 682–685.
- Whiten, A., Horner, V., & Marshall-Pescini, S. (2003): Cultural panthropology. *Evolutionary Anthropology: Issues, News, and Reviews*, 12(2): 92–105.
- Wynn, T., & McGrew, W. C. (1989). An Ape's View of the Oldowan. *Man*, 24(3), 383.
- Wynn, T., Hernandez-Aguilar, R. A., Marchant, L. F., & McGrew, W. C. (2011). "An ape's view of the Oldowan" revisited. *Evolutionary Anthropology: Issues, News, and Reviews*, 20(5), 181–197.
- Zuberbühler, K., Gyga, L., Harley, N., & Kummer, H. (1996): Stimulus enhancement and spread of a spontaneous tool use in a colony of long-tailed macaques. *Primates*, 37(1), 1–12.

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