Homo neanderthalensis and the evolutionary origins of ritual in Homo sapiens

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Abstract

There is a large, if disparate, body of archaeological literature discussing specific instantia-

tions of symbolic material culture and the possibility of ritual practices in Neanderthal pop-

ulations. Despite this attention, however, no single synthesis exists which draws upon cog-

nitive, psychological, and cultural evolutionary theories of ritual. Here we review the evi-

dence for ritual-practice among now extinct Homo neanderthalensis, as well as the neces-

sary cognitive pre-conditions for such behaviour, in order to explore the evolution of ritual

in *Homo sapiens*. We suggest that the currently available archaeological evidence indicates

that Neanderthals may have utilised 'ritualisation' to increase the successful transmission

of technical knowledge across generations — providing an explanation for the technologi-

cal stability of the Middle Palaeolithic and attesting to a survival strategy differing from

near contemporary *Homo sapiens*.

Keywords: symbolism; Palaeolithic; Neanderthal; behaviour; cognition.

2

Introduction

Modern human lives are filled with rituals, from the secular act of blowing out candles on a birthday cake, to the overtly religious, such as performing Islamic salat. Rituals, owing to their ubiquity and embeddedness, can be prominent or invisible, and our engagement with them may be fleeting or profound. Today rituals serve a variety of purposes:

They bring people together to form coherent, co-operative groups (1, 2), they may serve signalling and trust functions (3-5), they can reduce individual or collective anxieties (6, 7), and they play a role in the recall and transmission of important cultural knowledge (8, 9).

While rituals in *Homo sapiens* appear ubiquitous today, it's not clear when they began to serve these roles in the evolutionary past of the genus *Homo*. As a first step towards exploring the extents of our common heritage of ritualised behaviours, here we review possible instances of ritual-like behaviour in our evolutionary cousins: *Homo neanderthalensis*.

Who were our cousins?

The common ancestor of hominins and chimpanzees existed around 6 million years ago; while *Homo sapiens*, and our relatives, the Neanderthals (*Homo neanderthalensis*) share a common ancestor who lived in the early Middle Pleistocene, 800-400 ka (10, 11). Though our chimpanzee relatives continue to exist (somewhat precariously), Neanderthals disappeared approximately 40,000-years-ago (12). Just as evaluation of chimpanzee cognition and behaviour can shed light on human origins, so too can comparisons between the archaeological record of near contemporary *Homo sapiens* and Neanderthals. What, then, do we know about the potential for ritual behaviours in our cousins? Let us first provide a sketch of what we know about their social and cognitive proclivities.

Having populated Europe and the Middle East between about 300,000 and 40,000 years BP, before being displaced by *Homo sapiens*, Neanderthals left an extensive — if patchy — record of their lifeways. Neanderthal groups employed various mobility strategies (13-15), and employed a formal stone technology which represents an increase in hierarchical complexity over that of their Acheulean forebears (16, 17). This stone technology was part of a wider techno-complex which included bone, claws, wood, shell, and adhesive components, with tools appearing to be more diverse and task-specific (in some cases) than those of the Acheulean (18-20).

Neanderthal hunting strategies involved coordinated effort (21). For example, at Mauran (dating to MIS 3) in the foothills of the French Pyrenees, there is evidence that Neanderthal groups corralled migratory bison into natural geographic traps where they were slaughtered *en masse*, butchered, and parts taken for consumption (22). This site was used for several hundred years, suggesting the maintenance of specialised, region specific techniques, through the transmission of adaptive cultural knowledge, and an understanding of collective intentionality (see also 23, 24).

The presence of interregional variation in Neanderthal biface traditions similarly indicates the transmission of cultural knowledge between generations (25), with the technological continuity of the Mousterian a feature of the Eurasian Middle Palaeolithic (26). This technological stability, relative to near contemporary *Homo sapiens*, is the subject of debate (27), with recent research suggesting that a predominance of high fidelity imitation without much experimentation in Neanderthal social learning may explain the technological stability (28, see also 29, 30, 31). Neanderthals, then, were expert hunter-gatherers liv-

ing in a variety of environments, who transmitted cultural knowledge over tens of thousands of years. But did they have the capacity for ritual, as we understand it in our own species?

Ritual and ritual actions

For the purposes of our endeavour here, we distinguish 'ritual' and 'ritualistic action', and acknowledge the challenges of applying contemporary standards and definitions that often rely on behaviour and belief to archaic contexts in which access to behaviour and belief can only be inferred. In defining ritual, we follow Hobson et al. (2018) in taking it to be: '(a) predefined sequences characterized by rigidity, formality, and repetition that are (b) embedded in a larger system of symbolism and meaning, [and] (c) contain elements that lack direct instrumental purpose' (p. 261). Element b necessarily requires an associated degree of community, shared knowledge and normativity. A 'ritualistic action' is, largely, the behavioural components of elements (a) and (c): It is an action which is repetitive, redundant, often rigidly or formally performed, and which is causally opaque and goal demoted (32-37). A ritualistic action is often an element of a larger ritual, but unlike rituals, can exist in symbolically impoverished contexts.

The above two terms, causal opacity and goal demotion, tie into element (c) regarding instrumental purpose. A causally opaque action is one in which the causal relationships between the action and the outcome are difficult for an observer to discern. For example, heating water over fire is causally transparent (it is possible to perceive how the transit of the property of heat from the fire serves to increase the temperature of the water); in contrast the process of heating water in a microwave is causally opaque (for most, how the temperature of water increases inside a box that does not, itself, get hot, is not intuitively

comprehendible). Notably, according to Whitehouse (38), ritual in humans is irretrievably causally opaque, meaning that causality in human rituals is not just unknown, but actually unknowable. An archetypical example of this is how the performative acts of intercessory prayer can causally facilitate a channel of communication, and why those actions – and not others – are superior. Not only is a causal answer not known, such an answer is unknowable. *Goal demotion* refers to the degree to which a naive observer is challenged in intuiting the motives and goals of the agent performing the action (6, 9, 32, 33). For example, lighting a candle in a dark room is *goal apparent* (a sensible and discernible goal is to illuminate the room), whereas lighting an unscented candle in an already lit room is *goal demoted* (the purpose of this action is elusive without context.

We further distinguish individualistic ritualistic actions from collective ritualistic actions. The former involve (by degrees) actions that are emancipated from otherwise instrumental purposes, which in the case of the latter, are extended to become formal, prescriptive, and stylised. In individuals, idiosyncratic individualistic ritualistic actions can arise through mistaken causal beliefs. Wearing underpants has utility, while wearing a specific pair for good luck is ritualistic (clearly removed by some degree from the purpose underpants are intended to serve, and formalised in the process). Such a belief need not be correct, shared, or symbolic: it merely requires performance. Similarly, repetitive, formal, and obligatory behaviours that can feature in Obsessive-Compulsive Disorder (such as turning a light-switch on and off 13 times) qualify as individualistic ritualistic actions: They are ritualistic, but lack 'sharedness' and symbolism.

It is also relevant to note that individual rituals need not be independent of, or in conflict with, collective rituals. Consider, *simpatias*: repetitive, causally opaque 'formulas' employed by Brazilians to resolve common problems (e.g., asthma, infidelity, bad luck etc). In one

study (39), novel simpatias that included a religious icon (e.g., an image of the Virgin Mary – a prominent feature of Brazilian Catholic belief systems) were rated as significantly more effective than those which did not. In this way, individualistic rituals that have unfolded to serve instrumental purposes can be seen to coexist with collective rituals and symbolism.

How individual ritualistic actions can transcend into collective rituals remains undetermined, but the distinction is useful in the context of archaic behaviour, where individual ritualistic actions (which are apparent across species) can be viewed as a necessary precursor for collective rituals. These definitions then allow for greater precision in inferring cognitive capacities. Consider a Western wedding: the predefined, rigid, formal, and repetitive elements typically involve walking down an aisle (flanked by a segregated audience broadly divided by affiliation), the statement and re-statement of specific vows, the exchange of rings, all done in the presence of a specific authority. Some aspects of this process could be dropped with little consequence (e.g., walking down the aisle), whereas omitting other aspects could render the ritual symbolically moot (e.g., failing to exchange rings) or legally invalid (e.g., the ceremony not being conducted by someone certified to do so). But what motive would a naive observer attribute in observing an exchange of identical rings, with the prescription they be worn on the fourth digit of the left hand? The condition of 'instrumental' purpose is important, but is best considered in the context of ritualistic behaviour where the system of symbolism and meaning are necessary components which serve a similar (if substitute) role as that of causal explanation.

Evidence for Neanderthal ritual

If we seek evidence for collective ritualistic actions, death-related behaviours are a good place to start. A recent review documented a range of death related behaviours,

across a diversity of primate species, that fall into three broad categories: carrying/dragging of corpses, defending the corpse (individually or as a group) and/or 'holding vigil' and apparent grieving (40). According to this review, many non-human primates display this range of behaviours in response to death. However, with regard to post-mortem treatment, grief, mourning and consoling, and other symbolic behaviours, they fall short of human standards (e.g., primates have rarely been observed consoling grieving group members). In many if not all cases, their behaviours are examples of individualistic ritual actions, rather than collective ritualistic actions (even if such individualistic actions are performed by conspecifics simultaneously – there is no documented or asserted evidence for shared symbolism). The question, then, is to what extent did Neanderthals display primate death-related behaviours, and to what extent did they 'exceed' them in a human-like way (thus providing evidence for ritual)?

Rituals for disposing of the dead are a significant part of the modern human experience, and intentional burials provide some of the clearest archaeological evidence for the presence of ritual. Chimpanzees have been known to place leafy branches on top of bodies of the deceased, though this behaviour is also performed for dead hetero-specifics, and might be a method for detecting movement (41). In hominins, intentional burial of the dead may date back to 400,000 BP — as suggested by the Iberian site of Sima de los Huesos (42) — although, currently, evidence is only strong for the last 150,000 years (43). Indeed, the earliest undisputed evidence for burial is attributed to Neanderthal contexts (43, 44). These burials typically occur in inhabited cave or rockshelter sites, which have been suggested to reflect an attachment to the dead and a desire to keep them physically and metaphorically close and safe after they have died (45). For example, at La Ferrassie (Dordogne, France) foetuses and young children were interred, possibly with grave goods (lithics) (46, 47).

It is important to note that an apparent preference for burying the dead within enclosed sites may simply reflect sampling bias — a phenomenon duly noted for Pleistocene records of symbolic behaviour (see 48). Nevertheless, the recurrent practice of multiple internments at Neanderthal sites, with over 20 individuals represented at some, such as Krapina, La Quina, and l'Hortus (43), indicates Neanderthal burial was in certain cases at least a repeated, normative, practice. In some instances, rituals are linked to specific places which may have evoked a sense of 'specialness'. The afore-mentioned sites stand out from other caves in yielding remains of unusually large numbers of individuals, suggesting that there might have been fixed points in the Neanderthal landscape where bodies were processed in mortuary ritual.

At Krapina, unusual incisions on a cranium are argued to evoke ritual treatment of the dead (49). Further, suggestions of Neanderthal grave goods or markers are present, (e.g., at La Ferrassie, Amud, Le Moustier, Dederiyeh I, La Chapelle-aux-Saint, La Quina), though unambiguous cases only appear in *Homo sapiens* (such as Skhul and Qafzeh and later, in the European Gravettian complexes; 50, 51, 52). Consequently, questions remain surrounding the intentions of — and involvement of ritual associated with — Neanderthal burial. Nonetheless, even if rituals were not a feature of Neanderthal burial, it appears that some of the socio-cognitive underpinnings of it were, including causal opacity (why keep a dead body close?) and normative action (repeated use of the same cave).

Other evidence which may shed light on Neanderthal propensity for ritual is the extensive record of utilised mineral pigments. It has long been argued that Neanderthals used red and black pigments for body painting (53-56), and evidence for Neanderthal ornamentation of the body is growing rapidly, with several clear cases of the use of feathers and claws of raptor and corvids emerging, as well as evidence for the wearing of shell beads and

pigment (57-60). This decoration of the body was arguably at least symbolic, and may also have involved ritual behaviours — though access to such an archaeologically invisible behaviour is thus far beyond us, as is determining how sophisticated the symbolism may have been. Was it part of a shared semi-doctrinal cosmological understanding of gods, or simply a way to capture attention to attract or intimidate conspecifics? A rare potential instance of Neanderthal rock art in Iberia lacks the formality of later Homo sapiens rock art in this region: H. sapiens hand stencils for example are widespread and usually occur in multiples unlike the isolated Neanderthal example, while Homo sapiens imagery is often formal and figurative rather than abstract (59, 61-63). The *Homo sapiens* hand stencils also have a unique property, in which many of the hands have multiple instances of phalange (digit section) amputation (ref). The authors suggest the removal may itself have been ritualistic, though it may also be the case that the hard-to-fake modification was an identity marker. In either case, similar behaviour in Neanderthals in not apparent, and clear documentation of collective ritualistic actions in Neanderthals is somewhat elusive; particularly if we accept Whitehouse's stipulation that collective rituals may be irretrievably causally opaque. What then, of individualistic ritualistic actions?

Ritualisation of culture transmission?

While showing greater tool innovation than their Acheulean forebears (29, 64), Neanderthal groups nonetheless maintained their material culture without significant change
in some key elements of lithic technology over tens and even hundreds of thousands of
years (refs). What features lead to this stability, and simultaneously, this lack of innovation?
We suggest one answer might be the use of ritualistic actions, incorporated into the transmission of cultural knowledge as part of the Neanderthal survival strategy.

When learning new skills or behaviours, one can embark on a protracted trial-and-error expedition. Modern *Homo sapiens* tend not to do this. Rather, we observe others and copy them. Infants can learn how to use novel objects in this way from the middle of their first year (65, 66). By two years of age, learning by observing others intensifies to the extent that children will copy obviously causally irrelevant actions, in what has come to be known as over-imitation (67-69).

For some authors, the foundations of over-imitation can be found in lithic constructions of the Acheulean (29-31). Critical is that many aspects of Acheulean stone tool construction involve processes in which outcomes are hidden from and/or are counter-intuitive with regard to intended outcomes (e.g., when manufacturing a biface to remove mass from one surface one needs to strike on the opposite surface) — which is likely to make the intentions of the action goal demoted (what purpose did the act serve), and – at least to some extent – causally opaque (in what manner did this action causally produce the overall outcome; (70). This requirement renders unlikely that the propagation of this technological process was achieved via individualistic, independent invention, or other processes of social learning (e.g., emulation).

Over-imitation is increasingly considered the most compelling way in which the mind (whether that of a modern *Homo sapiens* child or now-extinct hominins) shows social and cognitive preparedness to engage in ritual (23, 28, 30, 71). In over-imitation, the sequence of modelled actions include those that are causally irrelevant (e.g., wiping a stick across the top of an unopened box) and the inference to an intention which is unknown or unavailable (e.g., it is unclear why a stick would be used to prise open a box's lid when one's fingers would do). There are some distinctions: Most commonly, in over-imitation the focus is an external object (in experimental settings, typically a box of some kind) and involves

only a demonstrator and lone observer, whereas ritualistic actions do not always involve objects and are frequently performed in the service of group identification and group bonding (2, 72). (Though such actions would, by definition, leave no material record). Nonetheless, as Nielsen and colleagues have argued (34), in over-imitation, causal opacity and goal demotion synergistically function to yield unique markers indicating that particular actions are ritualistic, in turn leading them to be reproduced with a starkly increased frequency from actions that do not share these features.

Indeed, ritualistic actions tend to beget an imitative response, in which human children and adults are predisposed to copy the entire procedure even though they may recognize some aspects of the action as entirely functionally redundant. The Levallois technology employed by Neanderthals involves more hierarchically removed steps and chains than most Acheulean knapping sequences (16), so the need to surmount causal opacity becomes even more salient. The implication here is that by the time Neanderthals appeared on the palaeolandscape, they were over-imitators some aspects of cultural transmission (most visible to us in lithic technology) and thus, capable of engaging in ritual behaviour. Importantly, over-imitative actions employed during knapping may be causally opaque and initially unknown, but may ultimately be knowable. That is, through extensive engagement and faithful repetition of the construction process, it is feasible that redundant actions can be identified. In the case of lithic technology, modern experts can explicitly state the purpose of actions several places removed from the ultimate goal in a hierarchical structure (16). In this sense ritualistic actions (in contrast to Whitehouse's conception of ritual) are not irretrievably causally opaque, and may potentially serve as a point of distinction for Neanderthal and *Homo sapiens* ritual behaviour. Regardless, as engagement with individualistic ritualistic actions increases, there is a platform for them to be converted into collective ritualistic actions. In this, children become critical.

Hawcroft and Dennell (73) argue that, given Neanderthals spent less time as juveniles, both relatively and absolutely compared to *Homo sapiens*, learning the prerequisite technological and social skills for adult life would have required the adoption of directed instructional learning where subadults acquire existing knowledge by imitating their elders, rather than through exploratory, experience-based learning. Just like *Homo sapiens* children, Neanderthal neonates were born vulnerable and underwent significant brain growth as they matured (74, 75). Overall, Palaeolithic *Homo sapiens* juveniles appear to have experienced less stress during their childhood than their Neanderthal counterparts, who had greater juvenile mortality (76). Debate remains around whether a significant difference in the rate of maturation to adulthood was experienced by Neanderthals (77-80), though it does appear that patterns of Neanderthal biological and cognitive growth are subtly different from those of contemporary and later *Homo sapiens*.

Neanderthals had a faster maturation rate and consequently a shorter childhood than *Homo sapiens* (8o). The significance of a relatively brief childhood and a faster rate of growth, may imply a lesser 'volume' of cultural information to acquire. *Homo sapiens* have a childhood lasting until aged 8, followed by 4 years of juvenility (81). By contrast (and for reference), chimpanzees transition from their juvenile phase into adolescence after seven years. During these seven years, chimpanzees, while capable of learning cultural information, appear limited to acquiring techniques for nut-cracking, termite fishing, and other comparatively simple, adaptively-utilitarian behaviours. It is beyond the scope of the present paper to go into detail, but nonetheless it is worth noting that there are suggestions

that the delayed maturation rate of *Homo sapiens* in comparison to Neanderthals reflects the need to acquire more, and more diverse social information, as evinced by strategies such as engaging in experimental and fantasy play in the former (82). Indeed, such fantasy play may be a key building block for appreciating the opaque causality of ritual in adulthood.

The idea of fantasy play highlights another key point. There are profound neural connections between the cerebellum and the parietal and frontal lobes (refs), an interconnectivity that suggests the cerebellum may aid in the process of creative thinking (83, 84); a cognitive prerequisite of fantasy play. The principal morphological differences were that *H. sapiens* had relatively larger parietal lobes and a particularly large cerebellum in comparison to Neanderthals (refs). According to Wynn, Overmann and Coolidge (83), this brain restructuring meant Neanderthals were very experienced in cognitively managing pragmatic situations through a strong focus on objects and actions while *H. sapiens* are less attentive to details but more able to develop creative solutions and plastically modify their behaviour according to needs (84, 85). A shift away from a more functional to a more creative engagement with objects potentially paved the way for an expansion in symbolic thinking and with it a key building block for appreciating the opaque causality of ritual in adulthood.

Homo sapiens — as a species — also appears to have maintained a large cultural corpus by sustaining large social networks, in which expertise is both widely shared and occasionally diffuse (86). Neanderthal populations, on the other hand, are argued to have been smaller and more widely dispersed than subsequent Upper Palaeolithic *H. sapiens* (86-89). One possible solution for maintaining a cultural corpus might have been reinforcing the

teaching of key life skills using ritualistic actions (i.e., causally opaque and goal demoted actions)— which may have proven itself more dependable in the Neanderthal social context. By embedding ritualistic actions alongside corresponding information, individuals can be less likely to question the authority with which it is given. Neanderthal children, under this assumption, may have been recipients of knowledge which was a high fidelity copy of that acquired by their parents and other community members. If modern evidence is applicable, this interpretation would represent an efficient solution, as ritualistic actions tend to arouse over-imitation responses, which themselves may also be more memorable (9), and which may suppress innovation and change. Prevailing views are that modern human children over-imitate primarily to satisfy social motivations, whether they be for reasons of affiliation or to satisfy a pull towards normativity (23). Our speculation here is that Neanderthals may have over-imitated solely to satisfy skill acquisition motivations. By this line of reasoning, ritualistic actions may have been present among the Neanderthals, as the cognitive faculties and corresponding behaviors evolved to serve functional purposes. Only in *Homo* sapiens were these same faculties and behaviors co-opted to serve social purposes. This shift between ritualistic action and collective ritual is likely to mark a shift from apparently causally opaque to irretrievably causally opaque, and from individualistic or dyadic to collective(WHITEHOUSE REF).. Indeed, it may have been that the larger group sizes of H. sapiens necessitated the development of stronger social motivations to strengthen in-group cohesion.

There is another aspect to group size that is relevant here, particularly if ritual behaviour is to not only develop, but sustain in such a way that it leaves detectable traces. We already noted that Neanderthal group sizes may have been small and widely spread across the Neanderthal territory. This low density population could be a likely explanation for the

whether ritualistic, individual, or collective - (like any other topic subject to archaeological scrutiny) require a sufficiently large population size of individuals engaging in a particular category of behaviour, or a sufficiently large number of cases practiced across time, to increase the likelihood of discovery. Though speculative in the historic context, it may be the case that the more individuals who engage in a specific behaviour, the more likely it is for that behaviour to propagate. Not only would this provide a greater number of cases that may leave a record; it also is self-sustaining, as such a tendency acts as a prophylactic against loss – the greater the number of members of a community who practice something, the less likely it is for that behaviour to be lost in the face of a catastrophic event (go-g2). Our argument is thus that Neanderthals were a ritual animal – capable of individual ritual actions, though not collective in the sense that they shared symbolism of cosmology - but that there weren't enough of them in each individual community for reliable traces of such behaviour to remain in the archaeological record.

Conclusion

Neanderthals were a co-operative, social, intelligent, tool-using species, which shared recent common heritage with our own lineage and likely displayed a propensity for over-imitation, and by implication, a capacity for cognition associated with ritualistic action. Yet the evidence that rituals (larger, shared, complexes of symbolic action and beliefs) featured in their lives is neither widespread nor compelling. By the line of reasoning set out here, the lack of evidence for ritual surrounding symbolic material culture in the Neanderthal record but long-standing continuity within their complex lithic technology may indicate that ritual

behaviour was utilised in a narrower way than by near contemporary and modern *Homo sapiens*. Neanderthals' use of ritual and ritualised actions was likely focused on reinforcing the faithful transmission of technical knowledge across generations under conditions of a relatively short childhood and relatively small social groups. In *Homo sapiens* ritual may have initially functioned in a similar way but, underpinned by an enhanced role for the cerebellum in cognition, was later exapted for reinforcing expansive and diffuse social networks; perhaps in response to the advent of complex projectile technology. Such an interpretation would indicate that ritual in *Homo* is not a 'one size fits all' behaviour — but a social technique which can be moulded or applied differently across species. Thus, claims for collective rituals (corresponding with the psychological and anthropological understanding of cultural rituals) in Neanderthal may be too rich, while a more precise characterization of ritualized action (also corresponding to psychological and anthropological definitions) might be more useful and more easily defended.

References

- Wilson M. Rituals of Kinship among the Nyakyusa. London: Oxford University Press;
 1957.
- 2. Whitehouse H. Modes of religiosity: a cognitive theory of religious transmission. Walnut Creek, CA: AltaMira; 2004.
- 3. Irons W. Religion as a hard-to-fake sign of commitment. In: Nesse RM, editor.
 Russell Sage Foundation series on trust Evolution and the capacity for commitment. 3. New
 York, NY: Russell Sage Foundation; 2001. p. 290-309.

- 4. Watanabe JM, Smuts BB. Explaining religion without explaining it away: Trust, truth, and the evolution of cooperation in Roy A. Rappaport's "The Obvious Aspects of Ritual". American Anthropologist. 1999;101:98-112.
- 5. Henrich J. The evolution of costly displays, cooperation and religion: Credibility enhancing displays and their implications for cultural evolution. Evolution and Human Behavior. 2009;30:244-60.
- 6. Boyer P, Liénard P. Ritual behavior in obsessive and normal individuals: Moderating anxiety and reorganizing the flow of action. Current Directions in Psychological Science. 2008;17:291-4.
- 7. Lang M, Krátký J, Shaver JH, Jerotijević D, Xygalatas D. Effects of anxiety on spontaneous ritualized behavior. Current Biology. 2015;25:1892-7.
- 8. De Simini F. Of gods and books: Ritual and knowledge transmission in the manuscript cultures of premodern India. Berlin, Boston: De Gruyter; 2016.
- 9. Kapitány R, Kavanagh C, Whitehouse H, Nielsen M. Examining memory for ritualized gesture in complex causal sequences. Cognition. 2018;181:46-57.
- 10. Endicott P, Ho SY, Stringer C. Using genetic evidence to evaluate four palaeoanthropological hypotheses for the timing of Neanderthal and modern human origins. Journal of Human Evolution. 2010;59:87-95.
- 11. Scally A, Durbin R. Revising the human mutation rate: implications for understanding human evolution. Nature Reviews Genetics. 2012;13:745.
- Higham T, Douka K, Wood R, Ramsey CB, Brock F, Basell L, et al. The timing and spatiotemporal patterning of Neanderthal disappearance. Nature. 2014;512:306.
- 13. Conard NJ. Settlement Dynamics of the Middle Paleolithic and Middle Stone Age.
 Tübingen.: Kerns Verlag; 2001.

- 14. Hovers E. Territorial behaviour in the Middle Paleolithic of the Southern Levant. In: Conard NJ, editor. Settlement dynamics of the Middle Paleolithic and Middle Stone Age. Tübingen: Kerns Verlag; 2001. p. 123-52.
- 15. Richter J. Social memory among late Neanderthals. In: Orschiedt J, Weniger G-C, editors. Neanderthals and Modern Humans-Discussing the Transition: Central and Eastern Europefrom 50,000-30,000 BP Mettman: Neanderthal Museum; 2000. p. 123-32.
- 16. Muller A, Clarkson C, Shipton C. Measuring behavioural and cognitive complexity in lithic technology throughout human evolution. Journal of Anthropological Archaeology. 2017;48:166-80.
- 17. Wynn T, Coolidge FL. The expert Neandertal mind. Journal of Human Evolution. 2004;46:467-87.
- 18. Boëda E, Bonilauri S, Connan J, Jarvie D, Mercier N, Tobey M, et al. Middle Palaeolithic bitumen use at Umm el Tlel around 70 000 BP. Antiquity. 2008;82:853-61.
- 19. Shimelmitz R, Bisson M, Weinstein-Evron M, Kuhn SL. Handaxe manufacture and re-sharpening throughout the Lower Paleolithic sequence of Tabun Cave. Quaternary International. 2017;428:118-31.
- 20. Zaidner Y. Adaptive flexibility of Oldowan Hominins: Secondary use of flakes at Bizat Ruhama, Israel. PLoS ONE. 2013;8:e66851.
- 21. Costamagno S, Meignen L, Beauval C, Bernard V, Bruno M. Les Pradelles (Marillac-le-Franc, France): a Mousterian reindeer hunting camp? . Journal of Anthropological Archaeology. 2006;25:466–84.
- 22. Farizy C, David F, Jaubert J. Hommes et bisons du Paleolithique moyen a Mauran.

 Paris: CNRS; 1994.

- Nielsen M. The human social mind and the inextricability of science and religion. . In: Henley TB, Rossano MJ, Kardas EP, editors. Handbook of Cognitive Archeology:

 Psychology in Prehistory New York and London: Routledge; 2019. p. 296-310.
- 24. Shipton C. Three stages in the evolution of human cognition normativity, recursion, and abstraction. In: Henley TB, Rossano MJ, Kardas EP, editors. Handbook of Cognitive Archeology: Psychology in Prehistory New York and London: Routledge; 2019. p. 153-74.
- 25. Ruebens K. Regional behaviour among late Neanderthal groups in Western Europe: a comparative assessment of late Middle Palaeolithic bifacial tool variability. Journal of Human Evolution. 2013;65:341-62.
- de la Torre I, Martínez-Moreno J, Mora R. Change and stasis in the Iberian Middle Paleolithic: considerations on the significance of Mousterian technological variability.

 Current Anthropology. 2013;54:320-36.
- 27. Akazawa T, Nishiaki Y, Aoki K. Dynamics of Learning in Neanderthals and Modern Humans, Volume 1, Cultural Perspectives. Tokyo: Springer Japan; 2013.
- 28. Langley MC, Benítez-Burraco A, Kempe V. Playing with language, creating complexity: Has play contributed to the evolution of complex language? submitted.
- 29. Nielsen M. Imitation, pretend play and childhood: Essential elements in the evolution of human culture? Journal of Comparative Psychology. 2012;126:170-81.
- 30. Rossano MJ. Cognitive fluidity and Acheulean over-imitation. Cambridge Archaeological Journal. 2017;27:495-509.
- 31. Shipton C, Nielsen M. Before cumulative culture: The evolutionary origins of overimitation and shared intentionality. Human Nature. 2015;26:331-45.
- 32. Kapitány R, Nielsen M. Adopting the ritual stance: The role of opacity and context in ritual and everyday actions. Cognition. 2015;145:13-29.

- 33. Kapitány R, Nielsen M. The ritual stance and the precaution system: The role of goal-demotion and opacity in ritual and everyday actions. Religion, Brain & Behavior. 2017;7:27-42.
- Nielsen M, Tomaselli K, Kapitány R. The influence of goal demotion on children's reproduction of ritual behavior. Evolution and Human Behavior. 2018;39:343-8.
- 35. Liénard P, Boyer P. Whence collective rituals? A cultural selection model of ritualized behavior. American Anthropologist. 2006;108:814-27.
- 36. Legare CH, Wen NJ, Herrmann PA, Whitehouse H. Imitative flexibility and the development of cultural learning. Cognition. 2015;142:351-61.
- 37. Watson-Jones RE, Legare CH, Whitehouse H, Clegg JM. Task-specific effects of ostracism on imitative fidelity in early childhood. Evolution and Human Behavior. 2014;35:204-10.
- 38. Whitehouse H. The coexistence problem in psychology, anthropology, and evolutionary theory. Human Development. 2011;54:191–9.
- 39. Legare CH, Souza A. Evaluating ritual efficacy: Evidence from the supernatural. Cognition. 2012;124:1-15.
- 40. Gonçalves A, Carvalho S. Death among primates: a critical review of non-human primate interactions towards their dead and dying. Biological Reviews. 2019;94:1502-29.
- 41. Boesch C. Wild cultures: A comparison between chimpanzee and human cultures. Cambridge: Cambridge University Press; 2012.
- Carbonell E, Mosquera M. The emergence of a symbolic behaviour: The Sepulchral pit of Sima de los Huesos, Sierra de Atapuera, Burgos, Spain. Comptes Rendus Palevol. 2006; 5:155-60.
- 43. Pettitt P. The Palaeolithic origins of burial. London. : Routledge; 2011.

- Langley MC, Clarkson C, Ulm S. Behavioural complexity in Eurasian Neanderthal populations: A chronological examination of the archaeological evidence. Cambridge Archaeological Journal. 2008;18:289-307.
- 45. Stiner MC. Love and death in the Stone Age: What constitutes first evidence of mortuary treatment of the human body? Biological Theory. 2017;4:248–61.
- 46. Capitan L, Peyrony D. Deux squelettes humaines au milieu des foyers de l'époque Moustérienne. Revue de l'École d'Anthropologie. 1909;19:402-9.
- 47. Capitan L, Peyrony D. Station préhistorique de la Ferrassie. Revue Anthropologique. 1912;22:29-50.
- 48. Langley MC, Clarkson C, Ulm S. Symbolic expression in Sahul, Sunda, and Wallacea. Quaternary Science Reviews. 2019;221:105883.
- 49. Frayer DW, Orschiedt J, Cook J, Russell MD, Radov J. Krapina 3: Cut marks and ritual the behavior? Periodicum Biologorum. 2006;108:519–24.
- 50. Bar-Yosef Mayer DE, Vandermeersch B, Bar-Yosef O. Modern Behavior of Anatomically Modern Humans: Shells and ochre from Qafzeh Cave, Israel. Journal of Human Evolution. 2009;56:307–14.
- Garrod DAE, Bate DMA. The stone age of Mount Carmel. Oxford: Clarendon Press;1937.
- 52. Formicola V, Buzhilova A. Double child burial from Sunghir (Russia): Pathology and inferences for Upper Paleolithic funerary practices. American Journal of Physical Anthropology. 2004;124:189-98.
- 53. Bordes F. Stratigraphie du Loess et évolution des industries Paléolithiques dans l'Ouest du Bassin de Paris. L'Anthropologie. 1952;56:405-52.

- 54. Kuhn SL, Stiner MC. Body ornamentation as information technology: towards an understanding of the significance of early beads. In: Mellars P, Boyle K, Bar-Yosef O, Stringer C, editors. Rethinking the human revolution. Cambridge: McDonald Institute for Archaeological Research; 2007. p. 45–54.
- 55. Kuhn SL, Stiner MC. Paleolithic ornaments: Implications for cognition, demography, and identity. Diogenes. 2007;214:40–8.
- 56. Zilhão J, Angelucci DE, Badal-García E, d'Errico F, Daniel F, Dayet L, et al. Symbolic use of marine shells and mineral pigments by Iberian Neandertals. Proceedings of the National Academy of Science. 2010;107:1023-8.
- 57. Finlayson C, Brown K, Blasco R, Rosell J, Negro JJ, Bortolotti GR, et al. Birds of a feather: Neanderthal exploitation of raptors and corvids. PLoS ONE. 2012;7:e45927.
- 58. Morin E, Laroulandie V. Presumed symbolic use of diurnal raptors by Neanderthals. PLoS ONE. 2012;7:1–5.
- 59. Hoffmann DL, Standish CD, Garcia-Diez M, Pettitt PB, Milton JA, Zilhão J, et al. U-Th dating of carbonate crusts reveals Neandertal origin of Iberian cave art. Science 2018;359:912-5.
- 6o. Peresani M, Fiore I, Gala M, Romandini M, Tagliacozzo A. Late Neandertals and the intentional removal of feathers as evidenced from bird bone taphonomy at Fumane Cave 44 ky B.P., Italy. Proceedings of the National Academy of Science. 2011;108:3888–93.
- 61. García-Diez M, Garrido D, Hoffmann DL, Pettitt P, Pike A, Zilhão J. The chronology of hand stencils in European Palaeolithic rock art: implications of new U-series results from El Castillo Cave (Cantabria, Spain). Journal of Anthropological Sciences. 2015;93:135-52.

- 62. Rodriguez-Vidal J, d'Errico F, Pacheco FG, Blasco R, Rosell J, Jennings RP, et al. A rock engraving made by Neanderthals in Gibraltar. Proceedings of the National Academy of Sciences. 2014;111:13301–6.
- 63. Lewis-Williams D. Mind in the cave. London: Thames and Hudson; 2002.
- 64. Shipton C. A million years of hominin sociality and cognition: Acheulean bifaces in the Hunsgi-Baichbal Valley, India. Oxford: Archaeopress (British Archaeological Reports); 2013.
- 65. Barr R, Dowden A, Hayne H. Developmental changes in deferred imitation by 6- to 24-month-old infants. Infant Behaviour and Development. 1996;19:159-71.
- 66. Meltzoff AN. Infant imitation and memory: Nine-month-olds in immediate and deferred tests. Child Development. 1988;59:217-25.
- 67. Horner V, Whiten A. Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). Animal Cognition. 2005;8:164-81.
- 68. Lyons DE, Young AG, Keil FC. The hidden structure of overimitation. Proceedings of the National Academy of Sciences, USA. 2007;104:19751-6.
- 69. Nielsen M. Copying actions and copying outcomes: Social learning through the second year. Developmental Psychology. 2006;42:555-65.
- 70. Shipton C. The evolution of social transmission in the Acheulean. In: Overmann K, Coolidge F, editors. Squeezing minds from stones: Cognitive archaeology and the evolution of the human mind. New York: Oxford University Press; 2019. p. 332-54.
- 71. Nielsen M. The social glue of cumulative culture and ritual behavior. Child Development Perspectives. 2018;12:264-8.

- 72. Wen NJ, Herrmann PA, Legare CH. Ritual increases children's affiliation with ingroup members. Evolution & Human Behaviour. 2016;37:54-60.
- 73. Hawcroft J, Denell R. Neandertal cognitive life history and its implications for material culture. In: Derevenski JS, editor. Children and material culture. New York: Thames and Hudson; 2000. p. 89-99.
- 74. Neubauer S, Hublin J-J, Gunz P. The evolution of modern human brain shape. Science Advances. 2018;24:eaao5961.
- Ponce de León M, Golovanova L, Doronichev V, Romanova G, Akazawa T, Kondo O, et al. Neanderthal brain size at birth provides insights into the evolution of human life history. Proceedings of the National Academy of Science. 2008;105:13764–8.
- 76. Soffer O. Ancestral lifeways in Eurasia The Middle and Upper Paleolithic Records. In: Nitecki MH, Nitecki DV, editors. Origins of anatomically modern humans. Boston: Springer; 1994. p. 101-19.
- 77. Guatelli-Steinberg D, Reid DJ, Bishop TA, Larsen CS. Anterior tooth growth periods in Neandertals were comparable to those of modern humans. Proceedings of the National Academy of Sciences 2005;102:14197–202.
- 78. Macchiarelli R, Bondioli L, Debenath A, Mazurier A, Tournepiche J-F, Birch W, et al. How Neanderthal molar teeth grew. Nature. 2006;444:748–51.
- 79. Ramiez-Rossi FV, Bermudez de Castro JM. Surprisingly rapid growth in Neanderthals. Nature. 2004;428:936–9.
- 8o. Smith TM, Tafforeau P, Reid DJ, Pouech J, Lazzari V, Zermeno JP, et al. Dental evidence for ontogenic differences between modern humans and Neanderthals.

 Proceedings of the National Academy of Science. 2010;107:20923–8.

- 81. Locke JL, Bogin B. Language and life history: A new perspective on the development and evolution of human language. Behavioral and Brain Sciences. 2006;29:259-325.
- 82. Nowell A. Childhood, play and the evolution of cultural capacity in Neanderthals and modern humans. In: M. H, N. C, M. B, editors. The nature of culture Vertebrate paleobiology and paleoanthropology. Dordrecht: Springer; 2016. p. 87-97.
- 83. Wynn T, Overmann KA, Coolidge FL. The false dichotomy: a refutation of the Neandertal indistinguishability claim Journal of Anthropological Sciences 2016;94:201-21
- 84. Wynn T, Coolidge FL. The role of expert technical cognition in human evolution. In: Henley TB, Rossano MJ, Kardas EP, editors. Handbook of cognitive archaeology: Psychology in pre-history. London: Routledge Press; 2019. p. 261-84.
- 85. Di Paolo LD, Di Vincenzo F. Emulation, (over)imitation and social creation of cultural information. In: Di Paolo LD, Di Vincenzo F, De Petrillo F, editors. The evolution of primate social cognition Springer; 2018. p. 267-82.
- 86. Gamble C. The Palaeolithic societies of Europe. Cambridge: Cambridge University Press; 1999.
- 87. Conard NJ. The demise of the Neanderthal cultural niche and the beginning of the Upper Paleolithic in Southwestern Germany. In: Conard NJ, Richter J, editors. Neanderthal lifeways, subsistence and technology: One hundred fifty years of Neanderthal study.

 London: Springer; 2011. p. 223–40.
- 88. Féblot-Augustins J. La circulation des matières premières au Paléolithique. Liège: ERAUL; 1997.
- 89. Bocquet-Appel JP, Degioanni A. Neanderthal demographic estimates. Current Anthropology. 2013;54:S202-S13.

- 90. Derex M, Beugin MP, Godelle B, Raymond M. Experimental evidence for the influence of group size on cultural complexity. Nature. 2013;503:389.
- 91. Henrich J. Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses—the Tasmanian case. American Antiquity. 2004;69:197-214.
- 92. Powell A, Shennan S, Thomas MG. Late Pleistocene demography and the appearance of modern human behavior. Science. 2009;324:1298-301.