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# Drawings of Representational Images by Upper Paleolithic Humans and their Absence in Neanderthals Reflect Historical Differences in Hunting Wary Game

Richard G. Coss

## Abstract

One characteristic of the transition from the Middle Paleolithic to the Upper Paleolithic in Europe was the emergence of representational charcoal drawings and engravings by Aurignacian and Gravettian artists. European Neanderthals never engaged in representational drawing during the Middle and Early Upper Paleolithic, a property that might reflect less developed visuomotor coordination. This article postulates a causal relationship between an evolved ability of anatomically modern humans to throw spears accurately while hunting and their ability to draw representational images from working memory. Unlike Neanderthals, archaic and anatomically modern humans in sub-Saharan Africa adopted longer-range hunting practices using hand-cast spears as a compensation for the emergence of increasingly wary game. For Neanderthals, paleoclimatic fluctuations likely precluded consistent hunting of cold-adapted game, a property making game more approachable for close-range hunting with thrusting spears. As evidence of less historical wariness of humans, many of the species hunted by Neanderthals were eventually domesticated. Due to strong sources of natural selection on archaic and anatomically modern humans for effective hunting, the parietal cortex that integrates visual imagery and motor coordination expanded progressively, yielding the globular shape of the human cranium that is not evident in Neanderthals. To characterize how the cognitive properties employed for throwing spears and drawing line work are similar, the Upper Paleolithic drawings of animals in Chauvet cave, France, are discussed in the speculative context of how these artists engaged simultaneously in overt attention to guide their hand movements and covert attention to their mental images during the drawing process.

**Keywords:** anatomically modern humans, Chauvet cave art, representational drawing, Neanderthals, overt and covert attention, predator–prey arms race, spear throwing and thrusting

## INTRODUCTION

One of the important and highly controversial issues in archaeology is interpreting how advancements in lithic technologies during the transition from the Middle Stone Age (MSA) to the Late Stone Age (LSA) in southern Africa about 70 ka (thousand years ago) is indicative of the enhanced cognitive capabilities of anatomically modern *Homo sapiens* (AMH).

This article focuses on one unique property of this advancement—the drawing of recognizable images on cave walls by AMH newly arrived to Europe. This artistic ability contrasts markedly with its absence in Eurasian Neanderthals (*H. neanderthalensis*). To address this issue, I will review the archaeological evidence showing progressive technological advances by AMH and the relative stability of Middle to Early Upper Paleolithic Neanderthal technology.

Although neurobiological study of how visual imagery is translated into artistic expression is in its early stages of enquiry, I will speculate on the different types of neurological constraints that might have restricted Neanderthal artistic ability.

To construct a model of how visual imagery was expressed in complex drawings by AMH, but not Neanderthals, the first section of this article reviews the important role of hunting game that required advanced visuomotor coordination. I will argue that the ecological challenges of hunting progressively wary game in sub-Saharan Africa for speculatively more than 500,000 years reflected the effects of a multispecies “arms race” of predator–prey interactions. Successfully evasive behavior by prey and successful hominin hunting practices acted as strong sources of natural selection, enhancing prey wariness that led to the counteracting adoption of long-range projectiles. Prior to the arrival of AMH in Europe ~40 ka, the large game hunted by Neanderthals would not have experienced the same intensity and duration of natural selection from hominin hunting as that experienced by sub-Saharan African game. As such, European game presented less complex hunting challenges that promoted strategic hunting innovations.

The second section reviews studies of visuomotor imagery employed in athletic activities relevant to hunting, such as using visual imagery in event rehearsal. I will then bridge relevant empirical studies of visuomotor imagery, several of which employed brain imaging, with anecdotal observations of artistic practices. The overall conceptual framework of this article provides an evolutionary explanation of why hunting less challenging game never fostered Neanderthal artistic abilities. This construct is contrasted with how hunting wary game by AMH employed advanced forms of visuomotor imagery that could be co-opted for other creative activities, including the drawing of recognizable images.

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## HUMAN HUNTING HYPOTHESIS

### Cognitive Arms Race of Human Ancestors and their Prey

Hunting game for the energetic properties of meat has likely had a long evolutionary history in the human lineage prior to hominins evolving obligate bipedalism. It probably originated as cooperative hunting using arboreal tactics similar to those employed by common chimpanzees (*Pan troglodytes*) hunting red colobus (*Colobus badius*) monkeys (Boesch 1994).

With the advent of bipedalism (Richmond and Jungers 2008) more than 6 Ma (million years ago) followed by the earliest fossil evidence of long legs in *H. erectus* ~1.8 Ma, the putative ability to run down small or disabled prey to exhaustion (Bramble and Lieberman 2004) provided the initial source of natural selection on these prey for their inclusion of hominins into their guild of predators. A long history of hunting in this manner might have initiated the first selective sweep of cognitive adaptations in relatively small prey in which foraging bipeds were no longer perceived as nonthreatening agents. Because this selective sweep would be distributed spatially and temporally across numerous species, recognition by prey that *H. erectus* was dangerous would indubitably have been slow in the ecological time frame. Nevertheless, it would eventually engender a multispecies arms race in which prey could anticipate potential danger from hominins via their distinct perceptual features, such as body odor, dark skin, upright bipedal gait, and vocal emissions. The cognitive ability of terrestrial prey to recognize the facing orientation of hominins would already have been established earlier because recognition of two facing eyes is essential for assessing the intentions of other predators (Coss and Goldthwaite 1995). Coincident with the increasing wariness of smaller prey that *H. erectus* was dangerous, the reciprocally greater difficulty in capturing prey by *H. erectus* very likely acted as a major source of selection

for enhanced social cooperation, communication, and technological innovations in hunting.

Since the focus of this article is identifying the cognitive factors that support the ability to draw that differentiated AMH and Neanderthals, I will focus on the perceptual-cognitive aspects of visuomotor imagery employed for hunting that are also useful for drawing. The ability to employ visual imagery is very important in assessing prey behavior while preparing an attack and organizing the action patterns to carry out the attack. This ability requires the anticipation of prey defensive responses in a manner analogous to how “mirror neurons” are activated when one observes the action of another conspecific, thus recreating a preparatory pattern of neural activity to replicate this action (Buccino et al. 2001). Natural selection from predation has also shaped in some prey the heterospecific analog of a mirror-neuron system. For example, there are numerous daytime observations during game drives in grassland habitat of foraging antelope, zebras, and warthogs appearing to ignore resting lions at relatively close distances (Brubaker and Coss 2015). This form of heterospecific threat assessment can be interpreted within the Theory of Mind framework, notably “second-order intentionality” in which an assessor believes that other individuals have beliefs and desires (Dennett 1983). Visual imagery could play an important role in this form of hominin assessment of heterospecific intentions which could extend more generally into anticipating the utility of nearby sites for processing kills that afforded protection from scavenging carnivores (Domínguez-Rodrigo 2001). Due to the phylogenetic breadth of mirror-neuron and adjunct motor-imagery systems in related primates, it is reasonable to argue that the common *H. erectus* ancestor of AMH and Neanderthals more than 800 ka (Green et al. 2010) was similarly capable in this domain.

Anecdotal reports of human endangerment by African wildlife inspired the Human Hunting Hypothesis, which focused initially on

developing an evolutionary model to explain why African bush elephants (*Loxodonta africana*) were more consistently dangerous to humans than Asian elephants (*Elephas maximus*). The primary argument was that Asian elephants experienced less consistent hunting from archaic humans (presumably *H. heidelbergensis*, see Sankhyan et al. 2012) in South Asia “until modern humans colonized southern Asia with their well-honed lithic traditions, developed originally for hunting reclusive African game” (Thuppil and Coss 2012, 178). Following the arrival of AMH in Central Asia ~40 ka, large megafauna, such as ancestral horses (*Equus caballus*), experienced human hunting for a period hypothesized as insufficient in duration to promote the evolution of antihuman behavior (Brubaker and Coss 2015).

### Habituation as a Contextual Process Useful for Human Hunting

In developing my argument about the sources of natural selection from hunting that shaped modern cognition relevant to drawing, I have expanded the construct of the Human Hunting Hypothesis to include European megafauna hunted by Neanderthals. A major component of this hypothesis is the differential ability of a particular species to habituate completely to humans; complete habituation to humans is defined herein as the behavioral context in which humans become ecologically irrelevant as predictors of danger when viewed repeatedly in nonthreatening situations.

For species with a long history of terrestrial predators, evolved antipredator responses can be modulated by short-term habituation that fosters the ability of prey to forage near predators if there are no threatening consequences. In the context of daily exposure to benign humans for long periods, wild horses (*E. c. ferus*) at the Assateague National Seashore, an island near the eastern shore of Maryland, can undergo complete habituation to humans as evidenced by their grazing inattentively within

touching distances of beachgoers. Repeated exposure to an environmental attribute without an important consequence engenders continuous perceptual updating with learning that this particular attribute does not have predictive properties and thus can be ignored. However, with multiple episodes of preexposure without consequences, the attention-regulating properties of habituation lead to “latent inhibition” that retards learning that this attribute is a reliable predictor of an important consequence (Lubow and Moore 1959). Latent inhibition by prey exhibiting short-term habituation to a predator previously in view is likely to engender a slower flight-reaction time when the predator charges suddenly from cover. Such ambush attacks from concealment might have been employed as a hunting tactic by both AMH and Neanderthals for prey that had habituated previously to human presence. In species without a natural aversion to humans, latent inhibition can buffer the effects of repeated human harassment, leading to crop-raiding pests. For example, archaeological evidence in Borneo suggests that the bearded pig (*Sus barbatus*) and barking deer (*Muntiacus spp.*) were hunted persistently in Borneo by AMH for at least 40,000 years (Barker et al. 2007). Rather than being highly vigilant near human settlements, both species raid crops repeatedly despite consistent human harassment (Fredriksson 2005). Such assertive behavior suggests that the duration of natural selection from hunting was insufficient to promote in these species cognitive changes in which humans are innately recognized as predators.

The aforementioned model of historically inconsistent hunting of large game in Central Asia, leading to their ability to habituate well to humans, was tested experimentally by comparing the flight-initiation distances of plains zebras (*E. quagga*) to a person approaching steadily on foot (Brubaker and Coss 2015). Zebras in eastern and southern Africa living near settlements with high exposure to humans were compared with zebras living far from settlements with low

human exposure. Wild horses from Nevada with similar high and low human-exposure levels were selected for comparative study. Prior to domestication ~5.5 ka, ancestral horses adapted to cold climatic conditions in Central Asia are speculated to have been hunted only episodically by Late Archaic hominins (Neanderthals and Denisovans) during warmer interstadial and interglacial periods until the arrival of AMH about 40 ka. Despite domestication, wild horses with low exposure to humans exhibited an average flight distance (146 m) even larger than that of plain zebras (105 m) with low exposure to humans, a property indicating that domestication has not blunted horse antipredator behavior. As predicted, horses from high human-exposure areas exhibited a much larger degree of habituation than similarly exposed plains zebras, yielding an average flight distance of 17 m compared with 37 m for plains zebras. This longer zebra flight distance is just outside the effective range of poisoned arrows shot by Hazda and San hunter-gatherers in eastern and southern Africa (Brubaker and Coss 2015). The flight distances of impala (*Aepyceros melampus*) and greater kudu (*Tragelaphus strepsiceros*) are also longer than poison-arrow range (Tarakini et al. 2014, 80). As mentioned previously, wild horses habituate readily to benign humans and can be adopted out quickly to private care following roundups by the U.S. Bureau of Land Management or other wildlife management agencies. Plains zebras have never been domesticated despite repeated attempts, the context of which suggest that they “might be adaptively constrained in habituating completely to humans, a process making them unmanageable for domestication” (Brubaker and Coss 2015, 374). Again, it is reasonable to suggest that extinct European caballoid horses (*E. ferus gallicus*), like their aforementioned modern counterpart, were capable of habituating to humans moving about at a distance, but would be very cautious when approached directly on foot in full view. As discussed further below, the inattentiveness of horses to nondangerous

ungulates, such as reindeer (*Rangifer tarandus*) and bison (*Bison priscus*), might have been exploited by Neanderthals and later by AMH using animal skins as subterfuge.

### Advances in Archaic and Modern Human Hunting Technologies

In this section, I will focus on the effects of the predator–prey arms race from the AMH perspective in sub-Saharan Africa and how it might have enhanced perceptual-motor coordination useful for drawing cave art. This brain-enhancement process will be contrasted with the different hunting challenges faced by Neanderthals, arguing that the cold-adapted mammalian prey hunted by Neanderthals had not evolved the same degree of antihuman behavior as sub-Saharan African species. I will contrast this conjecture with the advancement in hunting technology exhibited by early AMH in southern Africa to cope with the increasing wariness of humans by a diverse number of prey species.

### Close-Range Hunting Tactics by Neanderthals

Middle Pleistocene (~300 ka) wooden spears pointed at both ends, ranging in length from 1.8 m to 2.5 m, were discovered at a late *H. heidelbergensis* or early Neanderthal occupation site in Schöningen near Helinstedt, Germany (Thieme 1997; Conard et al. 2015; Schoch et al. 2015). Spears of this type might have been used to hunt horses (butchered at this site) at close range. The thick shape of these spears coupled with strike-force simulations suggest that they were likely used as bimanual thrusting spears rather than hand-cast ones (Schmitt, Churchill, and Hylander 2003). Examination of Neanderthal shoulder morphology and muscle insertion sites lends further supports to the argument that Neanderthals applied underhand thrusting forces for penetrating game with spears at close range. Nevertheless, this “Spear Thrusting Hypothesis” is controversial. The alternative explanation for Neanderthal

shoulder morphology is that the repetitive scraping of hides requires even more muscle action than spear thrusting, and such intensive activity might account for shoulder remodeling (Shaw et al. 2012). It is reasonable to argue in the context of this study that Neanderthal hide-scraping ability could have been applied to scraping figurative designs on the walls of caves and rock shelters, as was done by Upper Paleolithic AMH, but there is no current evidence that they ever engaged in this activity.

According to Bent Sørensen, the Neanderthals had high mobility during the warmer Eem interglacial period and concentrated on procuring mostly meat from large game (Sørensen 2009). The species hunted frequently were horses and reindeer (Grayson and Delpech 2002). Larger, more challenging game would have included red deer (*Cervus elaphus*), bison (*Bison bonasus*), woolly rhinoceros (*Coelodonta antiquitatis*), and woolly mammoth (*Mammuthus primigenius*). Among these species, reindeer might have been the easiest to hunt because current research indicates that their flight distances are seasonally variable (as close as 22 m prior to seasonal hunting). Importantly, wild reindeer reduce their flight distance about 6 m when approached repeatedly on foot the same day (Reimers et al. 2009). Genetic analysis suggests that wild reindeer, like wild horses that can be easily tamed and bred, probably habituated rapidly to captive management when introduced to domestic herds (Røed et al. 2008). Red deer are also amenable to farming, and wild red deer habituate well to human presence if they are not confined immediately (Goddard, Gordon, and Hamilton 1996).

If unhabituated reindeer hunted by Neanderthals exhibited similar flight distances as modern reindeer, Neanderthals must have employed stealthy hunting tactics to attack game at close range, either from cover or approaching them slowly in open habitat to engender habituation. The bulky animal skins they wore for keeping warm could have disguised their body shapes deceptively with the familiar appearances



of nondangerous species. Animal disguises are especially useful for hunting species with long flight distances. As apparent in their rock art, San hunter-gatherers in South Africa have had a long history of wearing deceptive animal disguises to approach prey to within poison-arrow range (Thackeray 1983). There is also skeletal evidence that killing large game up close was clearly dangerous for Neanderthal hunters and possibly involved wrestling by several hunters to stabilize floundering game for more spear penetrations. This idea is supported by evidence that some Neanderthals experienced traumatic injuries to the neck and head not unlike those of injured rodeo performers (Berger and Trinkaus 1995), and the Neanderthal genome shows positive selection for fast blood clotting to limit blood loss during injury (Simonti et al. 2016).

### Longer-Range Hunting Practices of Anatomically Modern Humans

More than 1 million years ago, meat procured by *H. erectus* through killing small animals and scavenging larger carcasses was processed using early Acheulian biface tools employed as scrapers, picks, and robust hand axes. More advanced large-flake Acheulian tools began to appear in East Africa ~1 million years ago, and in India and southern Europe, the latter exhibiting a temporal discontinuity due to the intensification of high-latitude glacial cycles affecting human occupation (Sharon 2010).

The next major technological change by African hominins began during the last half of the Middle Pleistocene, characterized ~500 ka by fluctuating episodes of manufacturing prepared core flake and blade tools in eastern and southern Africa (Johnson and McBrearty 2010; Wilkins and Chazan 2012), where blades were possibly used as tips of hand-delivered spears (Wilkins et al. 2012). The presence of cleavers suggests a gradual functional shift from Acheulian to early MSA technologies. This widespread geographic emergence of MSA technology was preceded by changes in

the intensity and phase of the Indian monsoon, leading to a faunal turnover in eastern and southern Africa resulting from range contraction, migration, and extinction due to increased aridity and expanding grasslands (deMenocal 2004; Faith and Behrensmeier 2013). The extinction of several species with specialized diets led Richard Potts to develop his “Variability Selection Hypothesis,” arguing that paleoclimatic fluctuations generated ecological challenges to hominins that were disruptive, engendering differential selection for greater hominin behavioral flexibility (Potts 1998). The Human Hunting Hypothesis discussed in this section pinpoints a more explicit source of natural selection shaping human cognitive capabilities—the historic filtering out of unsuccessful hunter-gatherer groups in sub-Saharan Africa that were less capable of coping with the difficulty of hunting wary game in open habitat.

Prior to the emergence of drier habitat during the Middle Pleistocene, Acheulian hunters in Ethiopia would, presumably, have had much less difficulty hunting large game that failed to perceive them as predatory threats. As seasonal rainfall changed in northeast Africa, species like the Nubian ass (*E. africanus africanus*), which adapted well to arid conditions, would have experienced prolonged relaxed selection from hominin hunters (Rabinovich, Gaudzinski-Windheuser, and Goren-Inbar 2008) and large felid predators like lions (*Panthera leo*) that depended on daily sources to water. The Nubian ass is the only African species that was later domesticated (Orlando 2015), possibly by early Saharan herders more than 5 ka, thereby becoming the donkey (*E. asinus*). Unlike sub-Saharan ungulates that coevolved with hominins, the Nubian ass appears more curious than fearful when approached on foot, a level of boldness that has led to its endangerment by poachers. Genetic evidence suggests that wild stock was recruited repeatedly to expand managed groups in a process similar to that of goats (Kimura et al. 2010).



Such repeated introductions presumably reflect the ease in which Nubian asses habituated well to humans. In contrast, there is no evidence to my knowledge of any wild-caught sub-Saharan ungulates habituating completely to humans the way horses and donkeys do. The eland (*Taurotragus oryx*), a species hunted for a considerable period of time as shown in scenes from southern African rock art (Thackeray 2005), does habituate to humans under benign care, but these timid antelope can become dangerous when cornered. Despite numerous domestication attempts, a well-funded international team concluded that the eland was not a good candidate for domestication in Kenya (Wirtu 2004, 87).

Sub-Saharan ungulates exhibit a common suite of defensive behaviors after detecting approaching humans on foot that typically include head-up alert postures, alarm vocalizations (e.g., snorting), tail-flicking, foot-stamping, stotting (e.g., Thomson's gazelles, *Gazella thomsonii*), and evasive flight (Caro 1994). A complementary observation that Thomson's gazelles recognize the human body form as dangerous was reported by Fritz Walther (1969). When Walther stepped into full view of a nearby gazelle after being visually occluded by his vehicle, the gazelle fled immediately. Such observation of human recognition is complemented by experimental study in which springbok (*Antidorcas marsupialis*) skin disguises yielded a reliably shorter average flight distance to human approaches than undisguised approaches (Thackeray 1983). Following flight to a safe distance from a person approaching on foot, Grevy's zebras (*E. grevyi*) may fan out defensively as if anticipating a simultaneous attack from several predators, including human hunters (Brubaker and Coss 2016).

Rather than fleeing, several larger mammals will engage in defensive mobbing of humans, like that observed when lions attack individuals in herds of Cape buffalo (*Syncerus caffer*). Humans suddenly encountering Cape buffalo on foot are greatly endangered, and guides

consistently warn tourists on walking safaris to maintain long distances from these animals. Along with Cape buffalo, hippos (*Hippopotamus amphibious*) are considered by some tour guides as perhaps the most dangerous African species because of their stealthy mobbing tactic of capsizing small boats (Penkunas, Coss, and Shultz 2014, 34). Like Asian elephants, bush elephants can attack without warning, a process augmented by learning which groups of humans are dangerous by using odor cues (Soltis et al. 2014).

There is still a debate about whether hunting was a prominent activity during the Middle Pleistocene, because assemblages of large game, such as hippos, suids, equids, giraffes, and bovids at butchering sites, do not reveal the methods of game procurement by *H. erectus* that could have involved intentional hunting or carcass scavenging. Evidence of carcass processing is unambiguous when bones and Acheulian stone tools are found together, as was evident for a hippopotamus (*Hippopotamus cf. amphibious*) butchered in Ethiopia (Gallotti et al. 2010). Nevertheless, one important attribute indicative of consistent hunting by *H. erectus* is the repeated processing of complete carcasses at the same site (Endicott, Ho, and Stringer 2010).

The aforementioned faunal turnover 400 to 500 ka in eastern Africa due to changes in seasonal rainfall (Faith and Behrensmeyer 2013) and spread of open grasslands with grazing species adapted to drier habitat restricted the suitable hunting of archaic *H. sapiens* to game pathways where water was available. Analyses of the impact scars (microfractures) of ~279 ka MSA points in Ethiopia are consistent with experimental evidence of the forces produced by hand-cast projectiles (Sahle et al. 2013). South African MSA faunal assemblages at kill-butchery sites and occupation sites in rock shelters provide evidence of the sizes and range of species hunted by early AMH at a site older than 115 ka (Wurz 2002). At Klaisie River Mouth, Richard Klein (1976) examined the frequency

of mammals of different sizes, ranging from small blue duikers (*Philantomba monticola*), medium-sized species like plains zebras, and large species represented by the Cape buffalo and extinct giant buffalo (*Pelorovis antiquus*). The tactic of face-to-face hunting with spears is suggested by the discovery of a giant buffalo vertebra with a stone point embedded at a low angle (Milo 1998). In contrast, hunting of prey evolutionarily naïve to humans must have been easy because there are abundant bones of Cape fur seals (*Arctocephalus pusillus*) and penguins dated at the Eem interglacial ~125 ka when elevated sea level allowed easier access to aquatic sources of meat (Klein 1976). More recent MSA faunal assemblages associated with the Howiesons Poort Industry in Sibudu Cave, South Africa, provide evidence that a moderate number of plains zebras were hunted by AMH in southern Africa between 62 and 65 ka. Species with a larger presence in Sibudu Cave assemblages are the Cape buffalo, steenbok (*Raphicerus campestris*), and bushpig (*Potamochoerus larvatus*). Interestingly, the diminutive blue duiker dominates the assemblages, indicating a concentrated effort at hunting this skittish forest-living species (Wadley 2008). Conversely, the grey duiker (*Sylvicapra grimmia*) is infrequent, a finding that might reflect the challenges of hunting a wary species in open habitat.

The Howiesons Poort Industry at Sibudu Cave overlies the Still Bay Industry, providing the opportunity to evaluate changes in hunting technology at two intervals separated by 5,000 to 8,000 years. As pre-Howiesons Poort technology, the Still Bay points exhibit advanced manufacturing techniques, using hard and soft (wood or bone) hammers for knapping, heat treatment before flaking, and pressure flaking to produce serrated edges (Lombard et al. 2010; Henshilwood 2012). Pressure flaking in particular made bifacial lanceolate-shaped points remarkably similar in appearance to much later European Solutrean points made by AMH. Further evidence of new functional

insights within the Still Bay Industry is found in Blombos Cave with ages between 70 and 77 ka. Some of the points show evidence of having been hafted axially as weapon tips (Villa et al. 2009). An important innovation of the later Howiesons Poort Industry was the manufacturing of backed points possibly used as projectile tips (Pargeter 2007; Lombard 2011). The viscosity of plant-gum adhesives employed for mounting these tips required well-controlled temperature regulation (Wadley, Hodgskiss, and Grant 2009). More importantly from the standpoint of hunting innovations, some of the backed quartz microliths and the bone points in the Howiesons Poort assemblage might represent the earliest use of bow and arrow (Blackwell, d'Errico, and Wadley 2008; Lombard 2011).

The South African Still Bay and Howiesons Poort Industries characterize the use of projectile technology that would allow effective hunting of large, dangerous game by early AMH at relatively safe distances (Shea 2006). The widespread adoption of Howiesons Poort microlith technology along the South African coast and in places with higher rainfall illustrates their hunting utility. Along with the development of advanced projectiles, other artifacts, such as engraved ochre and perforated shells for adornment, indicate an emerging sense of symbolic thinking and appraisal of beauty (Henshilwood and d'Errico 2011). Irrespective of these notable innovations, Still Bay and Howiesons Poort Industries were historically transient, and these industries are separated by an interval of low and variable rainfall that impacted game and edible plant availability (Wurz 2013). It seems reasonable to suggest that the advanced cognitive capabilities that fostered these industries were already present in other AMH populations in eastern and northeastern Africa and contributed to the dispersal of AMH from Africa into Eurasia ~70 to 80 ka during a humid interval (cf. Blome et al. 2012; Mellars et al. 2013; Groucutt et al. 2015; Clarkson et al. 2017). Research on six sub-Saharan hunter-gatherer genomes shows that they share a common

ancestry distinct from agriculturalist populations; the highest genetic diversity is most evident in the click-speaking ≠Khomani and Namibian Bushmen, suggesting a southern rather than eastern African origin for the AMH population that left Africa (Henn et al. 2011).

Considering that the founding populations entering Eurasia during the late MSA would have had the same cognitive capabilities as their sub-Saharan counterparts, the next section examines how visuomotor coordination for hunting wary game could have been co-opted for making well-illustrated cave drawings of animals. Before proceeding, there is one conundrum that needs to be addressed—the ~30-ka delay in the expression of representational rock art by African AMH (Vogelsang et al. 2010) and its appearance in divergent AMH populations dispersing to Eurasia and Australia (Powell, Shennan, and Thomas 2009). Ecological factors associated with hunting might have contributed to this delay. For African AMH, one possibility was the advent of poison-arrow hunting (d'Errico et al. 2012) that increased the efficiency of game procurement, even though tracking large, slowly dying animals could be time-consuming and energetically costly. Nevertheless, it is reasonable to suggest that an increase in hunting efficiency coupled with sharing dried meat and storable plant foods allowed more time to conceptualize various types of causal inferences with spiritual components that promoted representational drawing (see Solomon 2008). The congruent reduction of hunting effort in AMH encountering less wary European game and completely human-naïve game in Australia might have promoted representational art similarly (Moore and Brumm 2005; Roberts and Brook 2010; Clarkson et al. 2017).

Since the act of drawing enhances observational skills, perhaps these drawings were useful for conceptualizing hunts, evaluating game attentiveness, selecting vulnerable body areas as targets, and fostering group cohesiveness via spiritual ceremonies. To evaluate AMH ability to draw and its absence in Neanderthals,

I will speculate on how visuomotor imagery facilitated the expression of highly advanced drawings at one cave site, Chauvet cave in Vallon-Pont-d'Arc, Ardèche, France. The charcoal drawings of animals in this cave are among the oldest in Europe, with radiocarbon dates of about 32 ka near the beginning of the Upper Paleolithic (Cuzange et al. 2007). Chauvet cave was occupied during two periods separated by 5,000 years. Both periods exhibit cave art that provides insight into how visual imagery was transformed into targeted arm movements during drawing, analogous to the imagery employed when hunters assessed the trajectories of spears about to be thrown at animal targets.

### The Perceptual Relationship between Drawing and Spear Throwing

The dispersal of AMH across Europe signifies the transition from the Middle Paleolithic that lasted about 200,000 years to the Upper Paleolithic. Paul Mellars (2005, 13) lists a series of technological innovations that appeared abruptly in the Early Upper Paleolithic, the most relevant for this article being the complex and varied art forms (engraving, sculptures, cave paintings). Mellars also questions whether Neanderthals contributed to any substantial Upper Paleolithic innovations. And the long period of the Middle Paleolithic technology in Europe suggests relative stability in Neanderthal hunting practices constrained by their low subpopulation densities affecting the cultural transmission of information (Powell, Shennan, and Thomas 2009). Nevertheless, Neanderthals were capable tool makers, using precision-knapping with mostly their right hands (Uomini 2011; Villa and Roebroeks 2014). Repetitive arm motions similar to those used for scraping hides were used to engrave eight somewhat regularly spaced lines on the floor of Gorham's Cave, Gibraltar, dated ~39 ka (Rodríguez-Vidal et al. 2014). Attributed to Neanderthals, this engraving is the first known for an inhabited area of a cave. About the same age, a bird bone

with regularly spaced notches associated with the Châtelperronian stone industry was found at the Grotte du Renne, Arcy-sur-Cure, France (d'Errico et al. 1998). I am not surprised that Neanderthals were capable of engraving regularly spaced patterns since stone knapping generates some degree of visual-pattern regularity. Parallel lines were also engraved by AMH on ochre at Klaisies River Mouth and Blombos Cave -75 to 100 ka, and ostrich shells show regularly spaced engravings at Howiesons Poort levels at Diepkloof Rock Shelter (d'Errico and Henshilwood 2011; Mellars et al. 2013, 10701). Even more impressively, a much older (-430 to 540 ka) example of equally spaced parallel and zig-zag lines engraved on a fossil shell was found in Indonesia and presumably made by *H. erectus* (Joordens et al. 2015). It must be noted here that perception of pattern regularity, such as cross-hatching and ladder-like designs (Coss 2003), has had a long ecologically important history in the primate lineage because it has been useful for the rapid detection of snake scales and scale patterns of potentially dangerous snakes (Meno, Coss, and Perry 2013; Isbell and Etting 2017).

### CONSTRAINTS ON NEANDERTHAL DRAWING

Evidence of complex tool fabrication and very rare pattern-engraving activity by Neanderthals suggests that their lack of drawing representational images is not based on any decrement in small, visually guided motor movements needed for tool fabrication and spear-tip hafting. My conjecture is that Neanderthals could mentally visualize previously seen animals from working memory, but they were unable to translate these mental images effectively into the coordinated hand-movement patterns required for drawing.

Exteriorizing mental images by drawing them requires the integration of three mental processes: (1) the ability to generate vivid and relatively coherent static and dynamic images from working memory based on actual experiences; (2) the ability to rearrange

these mental images into novel combinations and generate entirely novel images; (3) the ability to focus attention overtly on specific features of these mental images to initiate the line drawing while simultaneously attending covertly to other features of the mental image for stopping the drawing action. As typically studied experimentally, covert attention is the process of shifting attention from a visually fixated target to a peripheral (nonfoveal) cue without moving the eyes in that direction (see Kelley et al. 2008). Rather than uncoupling attention to a peripheral cue from a visually fixated one, the act of drawing requires expanded attention to peripheral parts of the mental image during visually fixated guidance of the drawing hand.

The inability of Neanderthals to draw recognizable images would not be costly for survival because the evolutionary changes in Neanderthal brain organization and plasticity (Wynn, Overmann, and Coolidge 2016) appear to have achieved a steady state due to stabilizing selection (Siegal and Bergman 2002) sufficiently well-adapted for coping with the complexity of environmental challenges Neanderthals faced. With further respect to Neanderthal brain evolution, the pattern of morphological transformations from neonatal to adult endocranial shapes in modern humans and Neanderthals is similar, but Neanderthals typically had longer brain cases with larger brain volumes (Neubauer 2014). Unlike AMH, Neanderthal skulls never underwent a globularization (dorsal and lateral cranial bulging) transformation. Based on endocranial differences that include older *H. Heidelbergensis*, Bruner, Manzi, and Arsuaga (2003) conclude that AMH and Neanderthal brain development exhibited distinct ontogenetic growth trajectories, notably the early increase in dorsal brain volume that induced AMH cranial globularization of infant skulls. This increase in AMH cranial globularity implies that their parietal cortex was larger than that of Neanderthals (Bruner and Iriki 2016).

The parietal cortex is the integrative nexus of prefrontal, somatosensory, and visual cortices, and a smaller Neanderthal parietal cortex might explain the absence of drawing abilities. Drawing is a visually creative process, especially for the expression of new ideas (Fish and Scrivener 1990). One way to pinpoint the contribution of the parietal cortex during a creative act is using functional magnetic resonance imaging (fMRI) to study the redirection of blood flow in tiny capillaries as a proxy signal of neuronal activity. In a study of design decision-making, design majors with two years of training and nondesign majors were asked to imagine new pen designs while looking at pen images from inside an fMRI scanner (Kowatari et al. 2009). Subjects then drew their pen designs after brain scanning. Analysis revealed that both expert and novice designers showed elevated left to right activity of the prefrontal cortex coupled with suppression of activity most strongly in the left parietal cortex. Nondesign majors with the most original pen designs showed more left parietal cortex suppression than novices with less creative designs. These researchers make the conjecture that prefrontal inhibition of the left parietal cortex reduced any interference on novel imagery generation by prefrontal cortex. In a different study (Mechelli et al. 2004), subjects in an fMRI scanner viewed faces, houses, and chairs and then imagined them. Brain activity was different for the viewed and imagined images, with the process of viewing images activating mostly early visual cortex (areas 17 or 18) due to the low cognitive load. Similar to the previous study, the generation of “vivid” imagery of faces, houses, and chairs elevated neural activity in both the prefrontal cortex, interpreted as the content-sensitive brain area for developing mental images, and the superior parietal cortex as the brain area mediating attention to the imagined images. During the visual-imagery task, the precuneus, a postero-medial brain region in the posterior parietal cortex, was similarly activated. Along with the dorsal premotor cortex, the precuneus is

considered an important area involved in visuospatial imagery (Oshio et al. 2010). It plays an essential role in the visual guidance of hand movements, also coordinated by the cerebellum (Gowen and Miall 2007). The precuneus makes extensive subcortical and cortical projections, notably to the prefrontal and parietotemporal association areas that integrate visual, auditory, and somatosensory information (Cavanna and Trimble 2006). Compared with the flatter Neanderthal brain cases, the evolutionary enlargement of the precuneus is thought to have been a contributor to AMH cranial globularity (Bruner et al. 2016).

A summarizing point relevant to drawing imagined images is that the posterior parietal cortex is involved in the retrieval of mental images from prefrontal cortex and it integrates visual input and motor activity that involve regulation of attention and hand-eye coordination (Orban et al. 2006). The same visuospatial and ocularmotor networks revealed by fMRI are activated when subjects overtly and covertly attend to targets on a computer screen, although overt attention has much stronger activating properties (Beauchamp et al. 2001). As will be emphasized in the analysis of Chauvet cave drawings, overt and covert attention to mental images during the drawing process can be viewed as analogous to attending overtly and covertly to real objects (Posner 1980).

What would have been the ecological circumstances that promoted AMH parietal expansion? Viewed from the assertions of the Human Hunting Hypothesis, the killing of elusive African game required extensive experience observing animal behavior, especially subtle changes in the vigilance of focal animals in herds where multiple individuals might have been vigilant simultaneously. Upright head and ear orientations, indicating an immediate change in monitoring their surroundings (Beauchamp 2015, 39), would prompt hunters to decide whether they had been detected and whether to continue their hunt. Mirror neurons assessing the actions of another species

as found in macaque monkeys (Buccino et al. 2004) would play a critical role in evaluating whether hunters were detected by game. For European game that would have a higher degree of habituation potential to human presence, both Neanderthals and later Aurignacian hunters would have likely engaged in similar decision-making for initiating and terminating hunts. Cognitive differences would emerge in how hunting was carried out. Through repeated experience, spear throwing at game by Aurignacian hunters would have entailed careful targeting of vulnerable body areas coupled with possible mental rehearsal of spear trajectory and impact. Close-range spear thrusting by ambushing Neanderthals would have also likely entailed mental rehearsal of spear-thrusting action coupled with complex group coordination for applying multiple spear thrusts to subdue large game.

Another facet of hunting is anticipating the direction prey will take during evasive running and the contingencies that might emerge as animals in groups panic during an attack. Attacking coyotes appear to anticipate the direction ground squirrels run and have been observed to take shortcuts to capture them before they reach their burrows. In cooperative human hunting, also observed in lions (Stander 1992), one or more hunters approaching game can act as a distraction, inducing a predictable pattern of prey retreat in the direction of ambush sites. Similar tactics might have been employed much earlier in coordinated group hunting by *H. erectus*. There is no reason to consider that Neanderthals would have been deficient in employing mental imagery for coordinating group activity to deal with evasive prey or for close-range spear thrusting. Nevertheless, it is reasonable to argue that, historically, overhead spear throwing by AMH involved much greater vividness in imagining the trajectory spears would take to reach their targets.

Spear throwing has biomechanical and perceptual properties similar to baseball

and dart throwing and can employ mental-imagery rehearsal to enhance performance. For dart throwing, the immediate feedback of targeting results complements the mental practice of throwing darts with eyes closed by imagining the “feel” of the darts, sight of the target, and hearing the darts hit the target (Mendoza and Wichman 1978). Mental-practice improvements might result from the repeated activation of mirror neurons in premotor cortex if the imagery process simulates watching others perform the same tasks. In a related study, subjects with eyes closed and little body movement engaged in multiple trials of imagining that they threw a soft baseball covered with Velcro at a target of concentric rings. This imagery practice was followed by tossing the baseball. Subjects who imagined the action of baseball throwing were consistently better throughout a seven-inning testing period than individuals who threw the baseball without imagery practice (Surburg, Porretta, and Sutlive 1995). Driskell, Copper, and Moran (1994, 489) suggest, however, “that the effect of mental practice was stronger the more the task required cognitive activities.” That is, a well-developed mental plan based on previous experience allows more effective mental practice because of schematic knowledge of the physical task. Actual knowledge of the task results is thought to act as reinforcement, allowing motor-pattern modification. However, in a study of beanbag tossing at a target, subjects imagining the entire beanbag toss without making any body movements still showed subsequent tossing improvements. This finding illustrates that mental playbacks alone can enhance motor memory of the sequence of tossing movements in the absence of direct feedback (Zecker 1982). An important attribute of mental rehearsal is learning the appropriate sequence of movements. Errors in motor-skill learning guided by visual coordination can affect imagery rehearsal because they interfere



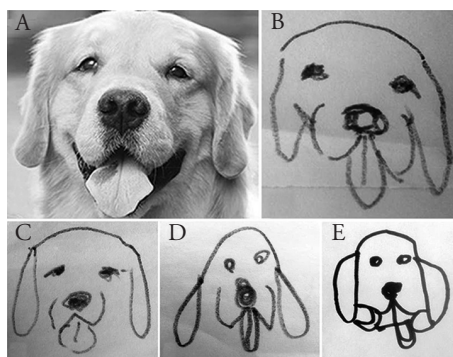
with learning correct action sequences. Overlearning a motor task induces automaticity in motor coordination that overrides any interference from the visual modality (Rémy et al. 2010).

### Visuomotor Imagery and Drawing Automaticity

The expression of representational drawings by young children (Baker and Kellogg 1967) indicates the presence of neural circuits operating early in development capable of fostering the ability to draw. Rapid learning of sequential hand movements using pen and pencils to create images can occur with one episode of drawing. In my early academic career as a teacher in a university art department, I taught a basic undergraduate drawing course for design majors. In the introductory part of the course emphasizing visualization, I capitalized on the effects of visuomotor imagery to accelerate students' drawing performances. This was accomplished by sitting next to the students, taking their hands, holding their pencils with my left hand (for right-handed students), and then making repetitive counterclockwise circular movements of circles and multiple ellipses simulating the sequential photographic frames of a flipping coin. If students' hands were not relaxed, I could make errors in these circular and elliptical drawings that students repeated (sometime for hours) until corrected by another bout of hand-guided drawing.

Another way to accelerate drawing was having students trace professional architectural illustrations, a process that yielded motor movements of sketching surface textures and vegetation that had a professional appearance and transferred well to drawing actual buildings and landscape vegetation. I have used this hand-guiding technique multiple times with different children, and in one very precocious case, a 21-month-old toddler (my son, Craig) drew a circular face with two dots for eyes and two horizontal lines as arms. As a

demonstration for this article, I took the hand of a boy (age 4 years 11 months) and drew an image of a dog seen on the screen of an iPad Mini. The boy's attention was more focused on my hand guiding his relaxed hand than looking at the image of the dog being drawn. Without further instruction, the child proceeded to trace the hand-guided drawing and then he quickly drew the dog by himself. He then redrew a reasonable facsimile of the dog nine days later and retained some drawing automaticity four months later (figure 1). This demonstration shows how a young child can draw a realistic-looking animal with the rapid induction of visuomotor memory.



**FIGURE 1** Progression of drawings by Connor McMillan: A. Photograph of dog model. B. Hand-guided drawing in which Connor's right hand is relaxed and the author moves Connor's hand to outline the dog's head, beginning with the dog's forehead. C. Connor's tracing of drawing B with paper overlay. D. Connor's uninstructed drawing shows visuomotor automaticity when his drawing starts with the dog's forehead. E. Connor's drawing nine days later also begins with the dog's forehead. Drawings are 7 to 8 cm wide.

### Analyses of Animal Drawings in Chauvet Cave

Chauvet cave had two periods of occupation, one during the Aurignacian period ~32 ka and another during the Gravettian period ~27 ka

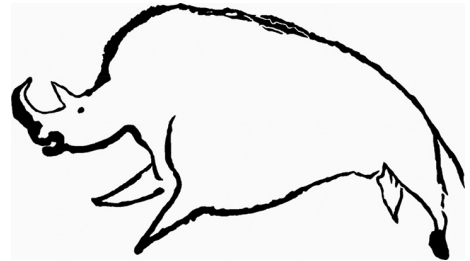


(Cuzange et al. 2007). I will focus my analysis on individual drawings and discuss composite drawings of adjacent animals in the context of drawing automaticity, presumably by the same artist. To evaluate the drawing process used by these artists, I examined animal images in Chauvet cave published on the Web and as illustrations in articles and books. My most relevant source was the 2011 film *Cave of Forgotten Dreams* (Werner Herzog, director), which presented dynamic, well-illuminated views of the drawings and cave-wall surfaces. Shifts of camera location and lighting revealed variation in the application of charcoal and insight into the sequence of drawing actions. Video still frames of these drawings were then used to create the animal images described herein. Many of the drawings and engravings were centered near eye level and were sized vertically and horizontally to accommodate the left-to-right or right-to-left reach of artists' hands holding charcoal sticks.

The orientation of animal heads and level of drawing detail entailing greater mental-image vividness might reveal the artists' handedness. In a study of forced-choice recognition of two side-by-side faces flipped to face opposite directions, the right-facing heads were more likely to be remembered correctly by left-handed subjects and left-facing heads were more likely to be remembered correctly by right-handed subjects. Congruent with this finding, greater numbers of right-handed subjects drew left-facing faces and left-handed subjects drew right-facing faces, an effect that appears to be face specific and not evident for recognizing other objects or for drawing left- or right-facing bicycles (Martin and Jones 1999).

Close-up photographs of the charcoal drawings prompted educated guesses about how visual imagery was employed during the drawing process under hazy torchlight. None of the animals are facing the artists directly (frontal views) or have their heads turned toward the artist where both eyes were drawn.

This observation of profile (side-view) drawing is important because, if the visual imagery employed in drawing was based on scenes from nature, then some of the animals drawn should have their heads facing the artist with both eyes in view. Lack of frontal views of animals might reflect the vividness of the hunting experience in which dead and butchered animals on their sides were inspected closely. A more reasonable explanation is that side views of animals present more species-recognizable cues for the artists and audiences. Although not facing directly, several drawings depict animals turned obliquely toward the artists in perspective (figures 2 and 3). Still, the abundance of side views of animals suggests that they were easier to draw and possibly preferred for ritual purpose or teaching because side views more clearly depict vulnerable body areas for targeting with spears and arrows (Guthrie 2006, 94).



**FIGURE 2** Perspective drawing of woolly rhinoceros (*Coelodonta antiquitatis*) in Chauvet cave by presumably a right-handed artist. Drawing is based on a video still frame from the movie *Cave of Forgotten Dreams* (Peter Zeitlinger, photography director). Rhinoceros contours were extracted by tracing the inner and outer edges of well-defined charcoal lines. The artist conceivably projected the mental image of the rhinoceros at a three-dimensional oblique angle and then started drawing the horn to visually anchor the drawing. It is reasonable to posit that the artist drew the rhinoceros's shoulder and back before drawing the limbs, using serial bouts of overt attention at the mental image to coordinate hand movements. The eye probably was positioned last to give life to the drawing metaphorically.



**FIGURE 3** Perspective drawing of cave lion (*Panthera spelaea*) head from the movie *Cave of Forgotten Dreams*. The lion's nose might have been the anchoring point for initiating the sweeping line characterizing the forehead and neck by presumably a left-handed artist. The asymmetric nose and ear positions indicate that the artist was visualizing the lion in three dimensions. The eye and whisker spots were possibly added last to complete the drawing.

Based on video scenes of people standing near the drawings, the heights and widths of the drawings reflect eye-level positioning of standing artists who would have been able to draw entire animals without moving laterally. Some of the charcoal line work is delicate, suggesting that Aurignacian and Gravettian artists used pointed sticks with burnt tips as drawing implements. Shading of the drawings to enhance the illusion of three-dimensional animal bodies might have employed the pelage of animal skins for smearing applied charcoal repeatedly. In some drawings, scraping of the cave wall enhanced the contrast of the charcoal outlines of animal heads and eyes. Charcoal shading near the eyes of horses, contrasted by unshaded light-brown eye-rings (similar to the light-brown eye-rings of Przewalski's horses), might reflect natural facial-pattern variation in these extinct horses.

Many of the animals appear to have been drawn using large sequential sweeps of the hands, a process employed in contemporary

student drawing exercises labeled as “contour drawing” in which the artist looks at the object being drawn and creates an outline of its shape without lifting the pencil off the page. In blind contour drawing, the artists must not look at their drawings until they are finished (Hobart 2005). In the latter process, visuomotor imagery predominates, and prepubescent children can be quite adept in making outline drawings that resemble the objects or models viewed (Pariser 1979). Due to the presence of long continuous lines in some animal drawings in Chauvet cave, I consider them the equivalent of contour drawings.

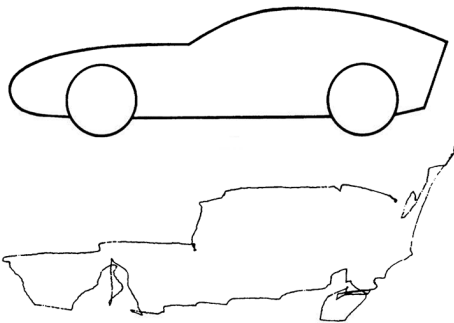
The process of making a continuous line in a contour drawing while looking at the model involves covert attention directed at the line's stopping point without taking the eyes off the model. More specifically, the drawing can be completed while maintaining visual fixation of the starting point on the model, or the artist can visually trace the contours of the model while guiding her or his hand movements covertly. When the artist draws the model and alternates back and forth in transferring his or her visual image of the model to paper, the dynamic feedback of viewing changes in hand position allows rapid anticipatory adjustments in hand position. This alternation between looking at the model and looking at the hand does not necessarily disrupt the mental image transferred to paper. As an example of covert and overt attention directed at an imagined image, I had the opportunity to demonstrate for the American space program the accuracy of an early eye-tracking device that employed electro-oculography (Coss 1969). I first imagined a fastback sports car and then “projected this mental image on the screen” one meter in front of me. By stabilizing my mental image of the car (~1 m width), I could visually trace its outline and wheels with one uninterrupted sequence of saccades (figure 4). This example shows direct exteriorization of mental imagery without manual feedback. Analogous to contour drawing, accurate overarm spear throwing

would employ intense visual fixation of the target combined with kinesthetic feedback of arm position and covert monitoring of the spear tip. Further discussion of the role of covert attention at real and imagined images appears in Laeng and Teodorescu (2002).

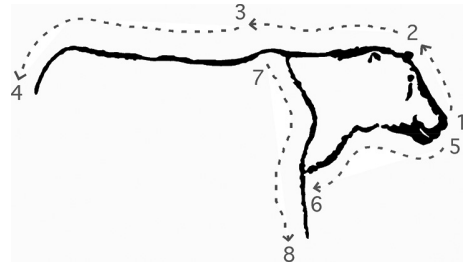
Several Chauvet cave drawings of animals provide subtle indices of the direction of arm motion as the artist projected his or her mental imagery on the cave wall and traced essential contours with few interruptions in hand motion. Figure 5 depicts a contour drawing of a cave lion (*Panthera spelaea*) with an attentive posture. Note the vertical stripe below the eye similar to that of African cheetahs (*Acinonyx jubatus*). Several lion drawings depict eye patterns typical of all extant *Panthera*, such as dark vertical eye bars and whitish patches below the dark lower eyelids. An exception is the absence of the whitish chins typical of *Panthera*. On the whole, the anatomical detail of the lion drawings is remarkable and likely reflects the perceptual salience of lions and its influence on visual imagery. In two recent studies of lion salience, images of target lions in visual arrays of antelope, engendered faster detection times by children and adults than target antelope

in visual arrays of lions (Penkunas and Coss 2013). A follow-up eye-tracking study of adults using the same experimental protocol showed that lions prompted faster eye saccades to lion targets than antelope targets (Yorzinski et al. 2014).

The similarities of adjacent drawings of bovids, horses, and lions suggest that the process of visual imagery in drawing might have been subordinated by visuomotor imagery enhanced by previous drawings of the same animal species. Several drawings of animal heads exhibit nearly identical head contours (figure 6) and could have been made successively within hours to weeks by the same artist. The aforementioned example of hand-guided drawing by a child that yielded drawing automaticity (sometimes referred to as “canonical drawing,” see Willats 1977) is very typical of young children. As posited by Karmiloff-Smith (1990, 74) with respect to children drawing houses, “an already compiled house-drawing procedure is run off fast and automatically and, although repeated drawings may involve minor changes at the level of denotation (e.g., addition of a door knob, an extra window), initially they do not involve changes in sequential order.”



**FIGURE 4** Drawing of imagined fastback sports car using electro-oculography and X-Y plotter. The imagined car (above) was mentally stabilized on a screen and then the contours were visually scanned (below), starting with the upper rear deck and traveling counterclockwise to complete the drawing in approximately 6 seconds.



**FIGURE 5** Contour drawing of a cave lion from the movie *Cave of Forgotten Dreams* by a likely left-handed artist. Numbered dashed lines are an attempt to show the starting and stopping sequences of hand movements in which the artist used overt attention to guide the drawing action. The numbered arrowheads theoretically characterize sequential bouts of covert attention at the mental image for planning each drawing movement.

Similarities in the adjacent drawings of Aurignacian and Gravettian artists would not reflect age-related perceptual constraints in children because these artists could clearly visualize and draw animals in three dimensions. The closely packed drawings of rhinoceroses depicted as a series of seven long upsweeping horns and three aurochs (*Bos primigenius*) with virtually identical curvilinear horns might reflect the spatial limitations of smooth cave-wall surfaces and possible symbolic references to the grouping behavior of ungulate herds under threat. Some groups of horses and rhinoceroses appear to be grazing inattentively, whereas all the lions appear to be vigilant.

Although drawing automaticity is defined by highly repetitious line work influenced by visuomotor imagery, drawing standardization exemplifies the larger framework of an artistic style (Sackett 1977). Besides the influence of visuomotor imagery, the standardization of many animal drawings, including the absence of frontal views, might simply reflect the artist's frequent exposure to the previous drawings of other artists coupled with social reinforcement of the artist's own drawings. From this standpoint, style can be viewed as a social process in which frequently seen two-dimensional contour features (lineaments) in design and art become

preferred aesthetically, and social reinforcement promotes the standardization of these "canonical lineaments" (Coss 2005).

The standardization of the closely packed drawings (notably lions and horses) might reflect an urgency to complete the drawings quickly due to environmental constraints, such as the noxious inhalation of torchlight smoke and smoke produced during the production of fresh charcoal. In light of this speculation, it must be noted that modern humans exhibit a genetic adaptation to counter smoke toxicity that is not present in Neanderthals and Asian Denisovans (Hubbard et al. 2016). Another time constraint might have been a buildup of carbon dioxide emitted from the roots of surface vegetation that restricted the time frame for the film crew during the production of *Cave of Forgotten Dreams*.

From a neurobiological perspective, drawing standardization is a higher-order cognitive process involving the interplay of pattern recognition while viewing actual objects, visual imagery from working memory of similar-looking objects, and visuomotor imagery from previous drawing activity. As mentioned previously in the comparison of design majors and non-design majors, neural activity in the left parietal cortex was suppressed when students engaged in greater design innovation (Kowatari et al. 2009). In some studies, visual imagery enhances neural activity in early visual cortex that routes topographically organized visual features for assembly into recognizable Gestalts in the inferior temporal lobe and image manipulation in prefrontal cortex. Projections back to early visual cortex are thought to aid the reassembly of the original visual experience, but this imagery reassembly does not necessarily engender the conscious experience of visual imagery (Kosslyn and Thompson 2003). Nevertheless, visual input during a drawing task coordinated by parietal cortex might have distractive properties during imagery generation by working memory in prefrontal cortex (Sauseng et al. 2005). Automaticity in drawing using tightly



**FIGURE 6** Drawings of adjacent heads of cave bears (*Ursus spelaeus*) from the movie *Cave of Forgotten Dreams*, possibly done successively by the same artist, who appears to be right handed. The two heads have been aligned at the same angle to compare the nose-to-forehead contours that are remarkable similar and possibly indicate drawing automaticity.

coupled visuomotor imagery would likely reduce bottom-up interference with higher-order imagery generation, allowing the roaming of covert attention over the mental image for planning the next drawing action.

## CONCLUSION

The focus of this article has been how hunting wary African game engendered evolutionary changes in AMH brain organization that fostered the ability to draw representational images, an aptitude never expressed by Neanderthals. Such artistic exteriorization of visual thinking allowed others to participate in the artist's

visualization process. There are enormous social implications in this ability to share mental images with group members. Deep within Chauvet cave, the realistic-looking animals viewed in the animated context of flickering torchlight and shifting shadows indubitably enhanced the emotions of perceivers (see Verpooten and Nelissen 2010). Clusters of cave lions with heads and eyes outlined by scraped reflective surfaces and the provocative horns of aurochs and rhinoceroses must have provided dramatic experiences to the successive Aurignacian and Gravettian cave occupants. We will never know how this drama was interpreted symbolically and its implications for group cohesiveness.

## WORKS CITED

- Blackwell, Lucinda, Francesco d'Errico, and Lyn Wadley. 2008. "Middle Stone Age Bone Tools from the Howiesons Poort Layers, Sibudu Cave, South Africa." *Journal of Archaeological Science* 35 (6): 1566–80. <http://dx.doi.org/10.1016/j.jas.2007.11.006>.
- Baker, Harry, and Rhoda Kellogg. 1967. "A Developmental Study of Children's Scribbles." *Pediatrics* 40 (3): 382–89.
- Barker, Graeme, Huw Barton, Michael Bird, Patrick Daly, Ipoi Datan, Alan Dykes et al. 2007. "The 'Human Revolution' in Lowland Tropical Southeast Asia: The Antiquity and Behavior of Anatomically Modern Humans at Niah Cave (Sarawak, Borneo)." *Journal of Human Evolution* 52 (3): 243–61. <http://dx.doi.org/10.1016/j.jhevol.2006.08.011>.
- Beauchamp, Guy. 2015. *Animal Vigilance: Monitoring Predators and Competitors*. Amsterdam: Academic Press.
- Beauchamp, Michael S., Laurent Petit, Timothy M. Ellmore, John Ingeholm, and James V. Haxby. 2001. "A Parametric fMRI Study of Overt and Covert Shifts of Visuospatial Attention." *NeuroImage* 14 (2): 310–21. <http://europepmc.org/abstract/med/11467905>.
- Berger, Thomas D., and Erik Trinkaus. 1995. "Patterns of Trauma among the Neandertals." *Journal of Archaeological Science* 22 (6): 841–52. [http://dx.doi.org/10.1016/0305-4403\(95\)90013-6](http://dx.doi.org/10.1016/0305-4403(95)90013-6).
- Blome, Margaret Whiting, Andrew S. Cohen, Christian A. Tryon, Alison S. Brooks, and Joellen Russell. 2012. "The Environmental Context for the Origins of Modern Human Diversity: A Synthesis of Regional Variability in African Climate 150,000–30,000 Years Ago." *Journal of Human Evolution* 62 (5): 563–92. <https://doi.org/10.1016/j.jhevol.2012.01.011>.
- Boesch, Christophe. 1994. "Chimpanzee-Red Colobus Monkeys: A Predator-Prey System." *Animal Behaviour* 47 (5): 1135–48. <http://dx.doi.org/10.1006/anbe.1994.1152>.
- Bramble, Dennis M., and Daniel E. Lieberman. 2004. "Endurance Running and the Evolution of *Homo*." *Nature* 432: 345–52. doi:10.1038/nature03052.
- Brubaker, Alexali S., and Richard G. Coss. 2015. "Evolutionary Constraints on Equid Domestication: Comparison of Flight Initiation Distances of Wild Horses (*Equus caballus ferus*) and Plains Zebras (*Equus quagga*)." *Journal of Comparative Psychology* 129 (4): 366–76. doi.org/10.1037/a0039677.
- \_\_\_\_\_. 2016. "Effects of Single- and Mixed Species Group Composition on the Flight Initiation Distances of Plains and Grevy's Zebras." *Ethology* 122 (7): 531–41. <http://dx.doi:10.1111/eth.12500>.
- Bruner, Emiliano, and Atsushi Iriki. 2016. "Extending Mind, Visuospatial Integration, and the Evolution of the Parietal Lobes in the Human Genus." *Quaternary International* 405 (Part A): 98–110. <http://dx.doi.org/10.1016/j.quaint.2015.05.019>.

- Bruner, Emiliano, Giorgio Manzi and Juan Luis Arsuaga. 2003. "Encephalization and Allometric Trajectories in the Genus Homo: Evidence from the Neandertal and Modern Lineages." *Proceedings of the National Academy of Sciences USA* 100 (26): 15335–40. doi:10.1073/pnas.2536671100.
- Bruner, Emiliano, Todd M. Preuss, Xu Chen, and James K. Rilling. 2017. "Evidence for Expansion of the Precuneus in Human Evolution." *Brain Structure and Function* 222 (2): 1053–60, doi:10.1007/s00429-015-1172-y.
- Buccino, G., F. Binkofski, G. R. Fink, L. Fadiga, L. Fogassi, V. Gallese et al. 2001. "Action Observation Activates Premotor and Parietal Areas in a Somatotopic Manner: An fMRI study." *European Journal of Neuroscience* 13 (2): 400–404. doi:10.1111/j.1460-9568.2001.01385.x.
- Buccino, Giovanni, Fausta Lui, Nicola Canessa, Ilaria Patteri, Giovanna Lagravinese, Francesca Benuzzi et al. 2004. "Neural Circuits Involved in the Recognition of Actions Performed by Nonconspicuous: An fMRI Study." *Journal of Cognitive Neuroscience* 16 (1): 114–26. doi:10.1162/089892904322755601.
- Caro, T. M. 1994. "Ungulate Antipredator Behaviour: Preliminary and Comparative Data from African Bovids." *Behaviour* 128 (3): 189–228. doi:10.1163/156853994X00262.
- Cavanna, Andrea E., and Michael R. Trimble. 2006. "The Precuneus: A Review of Its Functional Anatomy and Behavioural Correlates." *Brain* 129 (3): 564–83. <https://doi.org/10.1093/brain/awl004>.
- Clarkson, Chris, Zenobia Jacobs, Ben Marwick, Richard Fullagar, Lynley Wallis, Mike Smith et al. 2017. "Human Occupation of Northern Australia by 65,000 Years Ago." *Nature* 547:306–10. doi:10.1038/nature22968.
- Conard, Nicholas J., Jordi Serangeli, Utz Böhner, Britt M. Starkovich, Christopher E. Miller, Brigitte Urban, and Thijs Van Kolfschoten. 2015. "Excavations at Schöningen and Paradigm Shifts in Human Evolution." *Journal of Human Evolution* 89 (12): 1–17. <http://dx.doi.org/10.1016/j.jhevol.2015.10.003>.
- Coss, Richard G. 1969. "Electro-oculography: Drawing with the Eye." *Leonardo* 2 (4): 399–401. <http://www.jstor.org/stable/1572123>.
- . 2003. "The Role of Evolved Perceptual Biases in Art and Design." In *Evolutionary Aesthetics*, edited by Eckart Voland and Karl Grammer, 69–130. Heidelberg: Springer-Verlag.
- . 2005. "Constraints on Innovation: The Role of Pattern Recognition in the Graphic Arts." In *Environmental Awareness—Evolutionary, Aesthetic, and Social Perspectives*, edited by Richard G. Coss, 403–18. Dubuque, IA: Kendall/Hunt.
- Coss, Richard G., and Ronald O. Goldthwaite. 1995. "The Persistence of Old Designs for Perception." In *Perspectives in Ethology 11: Behavioral Design*, edited by Nicholas S. Thompson, 83–148. New York: Plenum.
- Cuzange, Marie-Thérèse, Emmanuelle Delqué-Količ, Tomasz Goslar, Pieter Meiert Grootes, Tom Higham, Evelyne Kaltnecker et al. 2007. "Radiocarbon Intercomparison Program for Chauvet Cave." *Radiocarbon* 49 (2): 339–47. <https://doi.org/10.1017/S0033822200042272>.
- d'Errico, Francesco, Lucinda Blackwell, Paola Villa, Ilaria Degano, Jeannette J. Lucejko, Marion K. Bamford, et al. 2012. "Early Evidence of San Material Culture Represented by Organic Artifacts from Border Cave, South Africa." *Proceedings of the National Academy of Sciences USA* 109 (33): 13214–19. <http://dx.doi.org/10.1073/pnas.1204213109>.
- d'Errico, Francesco, and Christopher S. Henshilwood. 2011. "The Origin of Symbolically Mediated Behavior, From Antagonistic Scenarios to a Unified Research Strategy." In *Homo Symbolicus: The Dawn of Language, Imagination and Spirituality*, edited by Christopher S. Henshilwood and Francesco d'Errico, 49–73. Amsterdam: Benjamins.
- d'Errico, Francesco, Joao Zilhão, Michèle Julien, Dominique Baffier, and Jacques Pelegrin. 1998. "Neanderthal Acculturation in Western Europe? A Critical Review of the Evidence and Its Interpretation." *The Neanderthal Problem and the Evolution of Human Behavior*, special issue, *Current Anthropology* 39 (S1): S1–S44. doi:10.1086/204689.
- deMenocal, Peter B. 2004. "African Climate Change and Faunal Evolution During the Pliocene-Pleistocene." *Earth and Planetary Science Letters* 220 (1–2): 3–24. [http://dx.doi.org/10.1016/S0012-821X\(04\)00003-2](http://dx.doi.org/10.1016/S0012-821X(04)00003-2).
- Dennett, Daniel C. 1983. "Intentional Systems in Cognitive Ethology: The 'Panglossian Paradigm' Defended." *Behavioral and Brain Sciences* 6 (3): 343–90.
- Domínguez-Rodrigo, Manuel. 2001. "A Study of Carnivore Competition in Riparian and Open Habitats of Modern Savannas and Its Implications for Hominid Behavioral Modeling." *Journal of Human Evolution* 40 (2): 77–98. doi:10.1006/jhev.2000.0441.



- Driskell, James E., Carolyn Copper, and Aidan Moran. 1994. "Does Mental Practice Enhance Performance?" *Journal of Applied Psychology* 79 (4): 481–92. <http://dx.doi.org/10.1037/0021-9010.79.4.481>.
- Endicott, Phillip, Simon Y. W. Ho, and Chris Stringer. 2010. "Using Genetic Evidence to Evaluate Four Palaeoanthropological Hypotheses for the Timing of Neanderthal and Modern Human Origins." *Journal of Human Evolution* 59 (1): 87–95. <http://dx.doi.org/10.1016/j.jhevol.2010.04.005>.
- Faith, J. Tyler, and Anna K. Behrensmeyer. 2013. "Climate Change and Faunal Turnover: Testing the Mechanics of the Turnover-Pulse Hypothesis with South African Fossil Data." *Paleobiology* 39 (4): 609–27. <http://dx.doi.org/10.1666/12043>.
- Fish, Jonathan, and Stephen Scrivener. 1990. "Amplifying the Mind's Eye: Sketching and Visual Cognition." *Leonardo* 23 (1): 117–26. <http://www.jstor.org/stable/1578475>.
- Fredriksson, Gabriella. 2005. "Human–Sun Bear Conflicts in East Kalimantan, Indonesian Borneo." *Ursus* 16 (1): 130–37. [http://dx.doi.org/10.2192/1537-6176\(2005\)016\[0130:HBCIEK\]2.0.CO;2](http://dx.doi.org/10.2192/1537-6176(2005)016[0130:HBCIEK]2.0.CO;2).
- Gallotti, Rosalia, Carmine Collina, Jean-Paul Raynal, Guy Kieffer, Denis Geraads, and Marcello Piperno. 2010. "The Early Middle Pleistocene Site of Gombore II (Melka Kunture, Upper Awash, Ethiopia) and the Issue of Acheulean Bifacial Shaping Strategies." *African Archaeology Review* 27 (4): 291–322. doi:10.1007/s10437-010-9083-z.
- Goddard, P. J., I. J. Gordon, and W. J. Hamilton. 1996. "The Effect of Post-Capture Management Strategy on the Welfare and Productivity of Wild Red Deer (*Cervus elaphus*) Hinds Introduced to Farming Systems." *Animal Science* 63 (2): 315–27. doi:10.1017/S1357729800014879.
- Gowen, E., and R. C. Miall. 2007. "Differentiation between External and Internal Cuing: An fMRI Study Comparing Tracing with Drawing." *NeuroImage* 36 (2): 396–410. doi:10.1016/j.neuroimage.2007.03.005.
- Grayson, Donald K., and Françoise Delpech. 2002. "Specialized Early Upper Palaeolithic Hunters in Southwestern France?" *Journal of Archaeological Science* 29 (12): 1439–49. <http://dx.doi.org/10.1006/jasc.2002.0806>.
- Green, Richard E., Johannes Krause, Adrian W. Briggs, Tomislav Maricic, Udo Stenzel, Martin Kircher et al. 2010. "A Draft Sequence of the Neanderthal Genome." *Science* 328 (5979): 710–22. doi:10.1126/science.1188021.
- Groucutt, Huw S., Eleanor M. L. Scerri, Laura Lewis, Laine Clark-Balzan, James Blinkhorn, Richard P. Jennings et al. 2015. "Stone Tool Assemblages and Models for the Dispersal of *Homo sapiens* out of Africa." *Quaternary International* 382:8–30. <http://dx.doi.org/10.1016/j.quaint.2015.01.039>.
- Guthrie, R. Dale. 2006. *The Nature of Paleolithic Art*. Chicago: University of Chicago Press.
- Henn, Brenna M., Christopher R. Gignoux, Matthew Jobin, Julie M. Granka, J. M. Macpherson, Jeffrey M. Kidd et al. 2011. "Hunter-gatherer Genomic Diversity Suggests a Southern African Origin for Modern Humans." *Proceedings of the National Academy of Sciences USA* 108 (13): 5154–62. doi:10.1073/pnas.1017511108.
- Henshilwood, Christopher S. 2012. "Late Pleistocene Techno-traditions in Southern Africa: A Review of the Still Bay and Howiesons Poort, c. 75–59 ka." *Journal of World Prehistory* 25 (3): 205–37. doi:10.1007/s10963-012-9060-3.s.
- Henshilwood, Christopher S., and Francesco d'Errico. 2011. "Middle Stone Age Engravings and Their Significance to the Debate on the Emergence of Symbolic Material Culture." In *Homo Symbolicus: The Dawn of Language, Imagination and Spirituality*, edited by Christopher S. Henshilwood and Francesco d'Errico, 75–96. Amsterdam: Benjamins.
- Hobart, April. 2005. "Sketching in Nature: Journaling Helps Students Develop Observation Skills and a Deep Appreciation of Nature." *The Science Teacher* 72 (1): 30–34. <http://search.proquest.com/openview/938c0662d7df7cddb-fa9a389d4247950/1?pq-origsite=gscholar&cbl=40590>.
- Hubbard, Troy D., Iain A. Murray, William H. Bisson, Alexis P. Sullivan, Aswathy Sebastian, George H. Perry et al. 2016. "Divergent Ah Receptor Ligand Selectivity during Hominin Evolution." *Molecular Biology and Evolution* 33 (10): 2648–58. doi:10.1093/molbev/msw143.
- Isbell, Lynne A., and Stephanie F. Etting. 2017. "Scales Drive Detection, Attention, and Memory of Snakes in Wild Vervet Monkeys (*Chlorocebus pygerythrus*)." *Primates* 58 (1): 121–29. doi:10.1007/s10329-016-0562-y.
- Johnson, Cara Roue, and Sally McBrearty. 2010. "500,000-Year-Old Blades from the Kapthurin Formation, Kenya." *Journal of Human Evolution* 58 (2): 193–200. doi:10.1016/j.jhevol.2009.10.001.
- Joordens, Josephine C. A., Francesco d'Errico, Frank P. Wesselingh, Stephen Munro, John de Vos, Jakob Wallinga et al. 2015. "*Homo erectus* at Trinil on Java used Shells for Tool Production and Engraving." *Nature* 518: 228–31. doi:10.1038/nature13962.



- Karmiloff-Smith, Annette. 1990. "Constraints on Representational Change: Evidence from Children's Drawing." *Cognition* 34 (1): 57–83. [http://dx.doi.org/10.1016/0010-0277\(90\)90031-E](http://dx.doi.org/10.1016/0010-0277(90)90031-E).
- Kelley, Todd A., John T. Serences, Barry Giesbrecht, and Steven Yantis. 2008. "Cortical Mechanisms for Shifting and Holding Visuospatial Attention." *Cerebral Cortex* 18 (1): 114–25. doi:10.1093/cercor/bhm036.
- Kimura, Birgitta, Fiona B. Marshall, Shanyuan Chen, Sonia Rosenbom, Patricia D. Moehلمان et al. 2010. "Ancient DNA from Nubian and Somali Wild Ass Provides Insights into Donkey Ancestry and Domestication." *Proceedings of the Royal Society B: Biological Sciences* 278 (1702): 50–57. doi:10.1098/rspb.2010.0708.
- Klein, Richard G. 1976. "The Mammalian Fauna of the Klasies River Mouth Sites, Southern Cape Province, South Africa." *South African Archaeological Bulletin* 31 (123/124): 75–98. doi:10.2307/3887730.
- Kosslyn, Stephen M., and William L. Thompson. 2003. "When Is Early Visual Cortex Activated during Visual Mental Imagery?" *Psychological Bulletin* 129 (5): 723–46. <http://dx.doi.org/10.1037/0033-2909.129.5.723>.
- Kowatari, Yasuyuki, Seung Hee Lee, Hiromi Yamamura, Yusuke Nagamori, Pierre Levy, Shigeru Yamane et al. 2009. "Neural Networks Involved in Artistic Creativity." *Human Brain Mapping* 30 (5): 1678–90. doi:10.1002/hbm.20633.
- Laeng, Bruno, and Dinu-Stefan Teodorescu. 2002. "Eye Scanpaths during Visual Imagery Reenact Those of Perception of the Same Visual Scene." *Cognitive Science* 26 (2): 207–31. [http://dx.doi.org/10.1016/S0364-0213\(01\)00065-9](http://dx.doi.org/10.1016/S0364-0213(01)00065-9).
- Lombard, Marlize. 2011. "Quartz-tipped Arrows Older than 60 ka: Further Use-trace Evidence from Sibudu, KwaZulu-Natal, South Africa." *Journal of Archaeological Science* 38 (8): 1918–30. <http://dx.doi.org/10.1016/j.jas.2011.04.001>.
- Lombard, Marlize, Lyn Wadley, Zenobia Jacobs, Moleboheng Mohapi, and Richard G. Roberts. 2010. "Still Bay and Serrated Points from Umhlatuzana Rock Shelter, KwaZulu-Natal, South Africa." *Journal of Archaeological Science* 37 (7): 1773–84. <http://dx.doi.org/10.1016/j.jas.2010.02.015>.
- Lubow, R. E., and A. U. Moore. 1959. "Latent Inhibition: The Effect of Non-Reinforced Preexposure to the Conditional Stimulus." *Journal of Comparative and Physiological Psychology* 52:415–19.
- Martin, Maryanne, and Gregory V. Jones. 1999. "Motor Imagery Theory of a Contralateral Handedness Effect in Recognition Memory: Toward a Chiral Psychology of Cognition." *Journal of Experimental Psychology: General* 128 (3): 265–82. <http://dx.doi.org/10.1037/0096-3445.128.3.265>.
- Mechelli, Andrea, Cathy J. Price, Karl J. Friston, and Almit Ishai. 2004. "Where Bottom-up Meets Top-down: Neuronal Interactions during Perception and Imagery." *Cerebral Cortex* 14 (11): 1256–65. <https://doi.org/10.1093/cercor/bhh087>.
- Mellars, Paul. 2005. "The Impossible Coincidence. A Single-Species Model for the Origins of Modern Human Behavior in Europe." *Evolutionary Anthropology* 14 (1): 12–27. doi:10.1002/evan.20037.
- Mellars, Paul, Kevin C. Gori, Martin Carr, Pedro A. Soares, and Martin B. Richards. 2013. "Genetic and Archaeological Perspectives on the Initial Modern Human Colonization of Southern Asia." *Proceedings of the National Academy of Sciences USA* 110 (26): 10699–704. doi:10.1073/pnas.1306043110.
- Mendoza, Dwight, and Harvey Wichman. 1978. "'Inner' Darts: Effects of Mental Practice on Performance of Dart Throwing." *Perceptual and Motor Skills* 47 (3): 1195–99. <http://journals.sagepub.com/doi/abs/10.2466/pms.1978.47.3f.1195>.
- Meno, Whitney, Richard G. Coss, and Susan Perry. 2013. "Development of Snake-directed Antipredator Behavior by Wild White-faced Capuchin Monkeys: I. Snake-species Discrimination." *American Journal of Primatology* 75 (3): 281–91. doi:10.1002/ajp.22106.
- Milo, Richard G. 1998. "Evidence for Hominid Predation at Klasies River Mouth, South Africa, and Its Implications for the Behaviour of Early Modern Humans." *Journal of Archaeological Science* 25 (2): 99–133. <http://dx.doi.org/10.1006/jasc.1997.0233>.
- Moore, Mark W., and Adam R. Brumm. 2005. "Symbolic Revolutions and the Australian Archaeological Record." *Cambridge Archaeological Journal* 15 (2): 157–75. <https://doi.org/10.1017/S0959774305000089>.
- Neubauer, Simon. 2014. "Endocasts: Possibilities and Limitations for the Interpretation of Human Brain Evolution." *Brain Behavior and Evolution* 84 (2): 117–34. doi:10.1159/000365276.
- Orban, Guy A., Kristl Claeys, Koen Nelissen, Ruth Smans, Stefan Sunaert, James T. Todd et al. 2006. "Mapping the Parietal Cortex of Human and Non-human Primates." *Neuropsychologia* 44 (13): 2647–67. <http://dx.doi.org/10.1016/j.neuropsychologia.2005.11.001>.
- Orlando, Ludovic. 2015. "Equids." *Current Biology* 25 (20): R965–R979. <http://dx.doi.org/10.1016/j.cub.2015.09.005>.

- Oshio, Ritz, Satoshi Tanaka, Norihiro Sadato, Masahiro Sokabe, Takashi Hanakawa, and Manabu Honda. 2010. "Differential Effect of Double-pulse TMS Applied to Dorsal Premotor Cortex and Precuneus during Internal Operation of Visuospatial Information." *NeuroImage* 49 (1): 1108–15. doi:10.1016/j.neuroimage.2009.07.034.
- Pargeter, Justin. 2007. "Howiesons Poort Segments as Hunting Weapons: Experiments with Replicated Projectiles." *South African Archaeological Bulletin* 62 (186): 147–53. <http://www.jstor.org/stable/20474970>.
- Pariser, David A. 1979. "Two Methods of Teaching Drawing Skills." *Studies in Art Education* 20 (3): 30–42.
- Penkunas, Michael J., and Richard G. Coss. 2013. "Rapid Detection of Visually Provocative Animals by Preschool Children and Adults." *Journal of Experimental Child Psychology* 114 (4): 527–36. <http://dx.doi.org/10.1016/j.jecp.2012.10.001>.
- Penkunas, Michael J., Richard G. Coss, and Susanne Shultz. 2014. "Risk Assessment by British Children and Adults." *International Journal of Psychological Studies* 6 (3): 32–43. <http://dx.doi.org/10.5539/ijps.v6n3p32>.
- Posner, Michael I. 1980. "Orienting of Attention." *Quarterly Journal of Experimental Psychology* 32 (1): 3–25. <http://dx.doi.org/10.1080/0033558008248231>.
- Potts, Richard. 1998. "Variability Selection in Hominid Evolution." *Evolutionary Anthropology: Issues, News, and Reviews* 7 (3): 81–96. doi:10.1002/(SICI)1520-6505(1998)7:3<81::AID-EVAN3>3.0.CO;2-A.
- Powell, Adam, Stephen Shennan, and Mark G. Thomas. 2009. "Late Pleistocene Demography and the Appearance of Modern Human Behavior." *Science* 324 (5932): 1298–1301. doi:10.1126/science.1170165.
- Rabinovich, Rivka, Sabine Gaudzinski-Windheuser, and Naama Goren-Inbar. 2008. "Systematic Butchering of Fallow Deer (*Dama*) at the Early Middle Pleistocene Acheulian Site of Gesher Benot Ya'aqov (Israel)." *Journal of Human Evolution* 54 (1): 134–49. <http://dx.doi.org/10.1016/j.jhevol.2007.07.007>.
- Reimers, Eigil, Leif E. Loe, Sindre Eftestøl, Jonathan E. Colman, and Bjørn Dahle. 2009. "Effects of Hunting on Response Behaviours of Wild Reindeer." *Journal of Wildlife Management* 73 (6): 844–51. <http://dx.doi.org/10.2193/2008-133>.
- Rémy, Florence, Nicole Wenderoth, Karen Lipkens, and Stephan P. Swinnen. 2010. "Dual-task Interference during Initial Learning of a New Motor Task Results from Competition for the Same Brain Areas." *Neuropsychologia* 48 (9): 2517–27. <http://dx.doi.org/10.1016/j.neuropsychologia.2010.04.026>.
- Richmond, Brian G., and William L. Jungers. 2008. "*Orrorin tugenensis* Femoral Morphology and the Evolution of Hominin Bipedalism." *Science* 319 (5870): 1662–65. doi:10.1126/science.1154197.
- Roberts, Richard G., and Barry W. Brook. 2010. "And Then There Were None?" *Science* 327 (5964): 420–22. doi:10.1126/science.1185517.
- Rodríguez-Vidal, Joaquín, Francesco d'Errico, Francisco Giles Pacheco, Ruth Blasco, Jordi Rosell, Richard P. Jennings et al. 2014. "A Rock Engraving Made by Neanderthals in Gibraltar." *Proceedings of the National Academy of Sciences USA* 111 (37): 13301–6. doi:10.1073/pnas.1411529111.
- Røed, Knut H., Øystein Flagstad, Mauri Nieminen, Øystein Holand, Mark J. Dwyer, Nils Røv, and Carles Vilà. 2008. "Genetic Analyses Reveal Independent Domestication Origins of Eurasian Reindeer." *Proceedings of the Royal Society B: Biological Sciences* 175: 1849–55. doi:10.1098/rspb.2008.0332.
- Sackett, James R. 1977. "The Meaning of Style in Archaeology: A General Model." *American Antiquity* 42 (3): 369–80. <http://www.jstor.org/stable/279062>.
- Sahle, Yonatan, W. Karl Huchings, David R. Braun, Judith C. Sealy, Leah E. Morgan, Agazi Negash, and Alemmal Atnafu. 2013. "Earliest Stone-Tipped Projectiles from the Ethiopian Rift Date to >279,000 Years Ago." *PLOS ONE* 8 (1): e78092. doi:10.1371/journal.pone.0078092.
- Sankhyan, Anek, Giani L. Badam, Laxmi N. Dewangan, Sheuli Chakraborty, Shashi Prabha, Suwendu Kundu et al. 2012. "New Postcranial Hominin Fossils from the Central Narmada Valley, India." *Advances in Anthropology* 2 (3): 125–31. <http://dx.doi.org/10.4236/aa.2012.23015>.
- Sauseng, Paul, Wolfgang Klimesch, Michael Doppelmayr, Thomas Pecherstorfer, Roman Freunberger, and Simon Hanslmayr. 2005. "EEG Alpha Synchronization and Functional Coupling during Top-Down Processing in a Working Memory Task." *Human Brain Mapping* 26 (2): 148–55. doi:10.1002/hbm.20150.
- Schmitt, Daniel, Steven E. Churchill, and William L. Hylander. 2003. "Experimental Evidence Concerning Spear Use in Neandertals and Early Modern Humans." *Journal of Archaeological Science* 30 (1): 103–14. <http://dx.doi.org/10.1006/jasc.2001.0814>.

- Schoch, Werner H., Gerlinde Bigga, Utz Böhner, Pascale Richter, and Thomas Terberger. 2015. "New Insights on the Wooden Weapons from the Paleolithic Site of Schöningen." *Journal of Human Evolution* 89 (12): 214–25. <http://dx.doi.org/10.1016/j.jhevol.2015.08.004>.
- Sharon, Gonen. 2010. "Large Flake Acheulian." *Quaternary International* 223–224: 226–33. <http://dx.doi.org/10.1016/j.quaint.2009.11.023>.
- Shaw, Colin N., Cory L. Hofmann, Michael D. Petraglia, Jay T. Stock, and Jinger S. Gottschall. 2012. "Neandertal Humeri May Reflect Adaptation to Scraping Tasks, but Not Spear Thrusting." *PLOS ONE* 7 (7): e40349. doi:10.1371/journal.pone.0040349.
- Shea, John J. 2006. "The Origins of Lithic Projectile Point Technology: Evidence from Africa, the Levant, and Europe." *Journal of Archaeological Science* 33 (6): 823–46. <http://dx.doi.org/10.1016/j.jas.2005.10.015>.
- Siegal, Mark L., and Aviv Bergman. 2002. "Waddington's Canalization Revisited: Developmental Stability and Evolution." *Proceedings of the National Academy of Sciences USA* 99 (16): 10528–32. doi:10.1073/pnas.102303999.
- Simonti, Corinne N., Benjamin Vernot, Lisa Bastarache, Erwin Bottinger, David S. Carrell, Rex L. Chisholm et al. 2016. "The Phenotypic Legacy of Admixture between Modern Humans and Neandertals." *Science* 351 (6274): 737–41. doi:10.1126/science.aad2149.
- Solomon, Anne. 2008. "Myths, Making and Consciousness: Differences and Dynamics in San Rock Arts." *Current Anthropology* 49 (1): 59–86. <http://www.journals.uchicago.edu/doi/abs/10.1086/523677>.
- Soltis, Joseph, Lucy E. King, Iain Douglas-Hamilton, Fritz Vollrath, and Anne Savage. 2014. "African Elephant Alarm Calls Distinguish between Threats from Humans and Bees." *PLOS ONE* 9 (2): e89403. doi:10.1371/journal.pone.0089403.
- Sørensen, Bent. 2009. "Energy Use by Eem Neanderthals." *Journal of Archaeological Science* 36 (10): 2201–5. <http://dx.doi.org/10.1016/j.jas.2009.06.003>.
- Stander, P. E. 1992. "Cooperative Hunting in Lions: The Role of the Individual!" *Behavioral Ecology and Sociobiology* 29 (6): 445–54. doi:10.1007/BF00170175.
- Surburg, Paul R., David L. Porretta, and Vins Sutlive. 1995. "Use of Imagery Practice for Improving a Motor Skill." *Adapted Physical Activity Quarterly* 12 (3): 217–27. <http://dx.doi.org/10.1123/apaq.12.3.217>.
- Tarakini, Tawanda, William-Georges Crosmary, Hervé Fritz, and Peter Mundy. 2014. "Flight Behavioural Responses to Sport Hunting by Two African Herbivores." *South African Journal of Wildlife Research* 44 (1): 76–83. <http://ir.nust.ac.za/xmlui/handle/123456789/551>.
- Thackeray, J. F. 1983. "Disguises, Animal Behaviour and Concepts of Control in Relation to Rock Art of Southern Africa." *South African Archaeological Bulletin Goodwin Series* 4 (June): 38–43. doi:10.2307/3858102.
- . 2005. "Eland, Hunters and Concepts of 'Sympathetic Control': Expressed in Southern African Rock Art." *Cambridge Archaeological Journal* 15 (1): 27–34. doi:10.1017/S0959774305000028.
- Thieme, Hartmut. 1997. "Lower Palaeolithic Hunting Spears from Germany." *Nature* 385 (6619): 807–10. <http://search.proquest.com/openview/937866fd839797d393ce5e31c047de86/1?pq-origsite=gscholar&cbl=40569>.
- Thuppil, Vivek, and Richard G. Coss. 2012. "Using Threatening Sounds as a Conservation Tool: Evolutionary Bases for Better Managing Human-Elephant Conflict in India within the Existing Legal Framework." *Journal of International Wildlife Law & Policy* 15:167–85. <http://dx.doi.org/10.1080/13880292.2012.678794>.
- Uomini, Natalie T. 2011. "Handedness in Neanderthals." In *Neanderthal Lifeways, Subsistence and Technology: One Hundred Fifty Years of Neanderthal Study*, edited by N. J. Conard and J. Richter, 139–54. Vertebrate Paleobiology and Paleoanthropology. Heidelberg: Springer Science+Business Media B.V.
- Verpooten, Jan, and Mark Nelissen. 2010. "Sensory Exploitation and Cultural Transmission: The Late Emergence of Iconic Representations in Human Evolution." *Theory in Biosciences* 129 (2): 211–21. doi:10.1007/s12064-010-0095-7.
- Villa, Paolo, and Will Roebroeks. 2014. "Neandertal Demise: An Archaeological Analysis of the Modern Human Superiority Complex." *PLOS ONE* 9 (4): e96424. doi:10.1371/journal.pone.0096424.
- Villa, Paola, Marie Soressi, Christopher S. Henshilwood, and Vincent Mourre. 2009. "The Still Bay Points of Blombos Cave (South Africa)." *Journal of Archaeological Science* 36 (2): 441–60. <http://dx.doi.org/10.1016/j.jas.2008.09.028>.
- Vogelsang, Ralf, Jürgen Richter, Zenobia Jacobs, Barbara Eichhorn, Veerle Linseele, and Richard G. Roberts. 2010. "New Excavations of Middle Stone Age Deposits at Apollo 11 Rockshelter, Namibia: Stratigraphy, Archaeology, Chronology and Past Environments." *Journal of African Archaeology* 8 (2): 185–218. doi:10.3213/1612-1651-10170.

- Wadley, Lyn. 2008. "The Howieson's Poort Industry of Sibudu Cave." *South African Archaeological Society Goodwin Series* 10 (December): 123–32. <http://www.jstor.org/stable/40650023>.
- Wadley, Lyn, Tamaryn Hodgskiss, and Michael Grant. 2009. "Implications for Complex Cognition from the Hafting of Tools with Compound Adhesives in the Middle Stone Age, South Africa." *Proceedings of the National Academy of Sciences USA* 106 (24): 9590–94. doi:10.1073/pnas.09009571106.
- Walther, Fritz R. 1969. "Flight Behaviour and Avoidance of Predators in Thomson's Gazelle (*Gazella Thomsoni* Guenther 1884)." *Behaviour* 34 (3):184–221. <http://dx.doi.org/10.1163/156853969X00053>.
- Wilkins, Jayne, and Michael Chazan. 2012. "Blade Production ~500 Thousand Years Ago at Kathu Pan 1, South Africa: Support for a Multiple Origins Hypothesis for Early Middle Pleistocene Blade Technologies." *Journal of Archaeological Science* 39 (6): 1883–1900. <http://dx.doi.org/10.1016/j.jas.2012.01.031>.
- Wilkins, Jayne, Benjamin J. Schoville, Kyle S. Brown, and Michael Chazan. 2012. "Evidence for Early Hafted Hunting Technology." *Science* 338 (6109): 942–46. doi:10.1126/science.1227608.
- Willats, John. 1977. "How Children Learn to Draw Realistic Pictures." *Quarterly Journal of Experimental Psychology* 29 (3): 367–82. <http://dx.doi.org/10.1080/14640747708400614>.
- Wirtu, Gemechu. 2004. "Developing Embryo Technologies for the Eland Antelope (*Taurotragus oryx*)." Ph.D. diss., Louisiana State University. [http://etd.lsu.edu/docs/available/etd-04152004-102159/unrestricted/Wirtu\\_dis.pdf](http://etd.lsu.edu/docs/available/etd-04152004-102159/unrestricted/Wirtu_dis.pdf).
- Wurz, Sarah. 2002. "Variability in the Middle Stone Age Lithic Sequence, 115,000–60,000 Years Ago at Klasies River, South Africa." *Journal of Archaeological Science* 29 (9): 1001–15. <http://dx.doi.org/10.1006/jasc.2001.0799>.
- \_\_\_\_\_. 2013. "Technological Trends in the Middle Stone Age of South Africa between MIS 7 and MIS 3." *Current Anthropology* 54 (S8): S305–S319. doi:10.1086/673283.
- Wynn, Thomas, Karenleigh A. Overmann, and Frederick L. Coolidge. 2016. "The False Dichotomy: A Refutation of the Neandertal Indistinguishability Claim." *Journal of Anthropological Sciences* 94: 201–21. doi:10.4436/jass.94022.
- Yorzinski, Jessica L., Michael J. Penkunas, Michael L. Platt, and Richard G. Coss. 2014. "Dangerous Animals Capture and Maintain Attention in Humans." *Evolutionary Psychology* 12 (3): 534–48. <http://journals.sagepub.com/doi/abs/10.1177/147470491401200304>.
- Zecker, Steven G. 1982. "Mental Practice and Knowledge of Results in the Learning of a Perceptual Motor Skill." *Journal of Sport Psychology* 4 (1): 52–63. <http://dx.doi.org/10.1123/jsp.4.1.52>.