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Processes of Visuospatial Attention and Working Memory



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Timothy Hodgson
Editor

Processes of Visuospatial Attention and Working Memory

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Preface

When I was first approached to edit a volume on visuospatial attention and working memory, I was not only honoured and excited but also daunted by the proposed topic's scope. Consider just the brain structures involved in visuospatial attention and working memory for example: the mid-brain and brainstem centres that control eye movements; the cortical visual pathways in the occipital, parietal and temporal lobes that process object features and locations; through to the lateral and medial frontal lobes of the cerebral cortex and basal ganglia which mediate top-down control over perception and action and maintain information in memory across delays.

To address the challenge, I began by defining the aims of the project in more detail and started to identify features that I thought would make the book distinctive. Firstly, it was decided that the volume should focus on research which addressed processes and mechanisms and that the inclusion of chapters with clinical relevance was also essential. I wanted the volume to bridge a gap I felt existed between research into the control of overt shifts in attention (eye movements) and research into covert attention (paying attention out of the corner of the eye). I also felt no attempt had been made to date to cover evolutionary and developmental perspectives on the topic and so this would be good to attempt. Finally, the book needed to be as international as possible and not just include people whose research I already knew. Following some more thought, many literature searches and much reading, I came up with a "wish list" of authors and chapter topics. In the summer of 2017, I began sending out e-mails and to my surprise the majority of authors responded enthusiastically to my invitation to contribute chapters straight away!

Part I of the book comprises four chapters which focus on *Evolution and Development*. Land's opening chapter outlines an important perspective on how gaze shifting eye movements (saccades) evolved. Surprisingly, cross species comparisons suggest that saccades did not evolve to shift the point of gaze, but to hold the eye stable as the fast phase of the compensatory eye movements that accompany head rotation (nystagmus). That the production and manipulation of stone tools by our ancestors might be key to the evolution of human visuospatial attention and working memory is the implication of the chapter by Bruner and colleagues. The

expansion of the medial parietal lobes and precuneus region of the cerebral cortex within the fossil record combined with contemporary neuroimaging evidence is used to argue that enhanced integration of information in working memory was a key factor driving evolution of human cognitive capacities. Following on from these two chapters, it is intriguing to consider how ontology might mimic phylogeny when reading Johnson's contribution, which presents a comprehensive overview of research into how visuospatial attention develops in children. Comparative studies of spatial working memory in humans, children and non-human species are described in De Lillo's chapter. A unique feature of the human capacity to remember spatial locations seems to be the ability to strategically chunk multiple locations in a sequence and encode them as holistic shapes and patterns.

Part II comprises the main body of the book and contains a series of chapters representing a snapshot of contemporary research into *Processes, Mechanisms and Models* in the field. Common themes running through this section are interactions between memory and attention and the extent to which past events influence attention, perception and action in the present. Liesefeld and colleagues outline their dimensional weighting account of trial-by-trial interactions in visual search, whilst Parr and Friston present an active inference framework which successfully models eye movement scan paths by combining memory for what has been seen at a location with predictions regarding what will be seen if one looks there again. Bahami et al. review neurophysiological studies of working memory and selective attention in the prefrontal cortex and the role played by dopamine. Aagten-Murphy and Bays then present a comprehensive review of studies that have examined how information is integrated across saccades and the conditions under which changes to a visual scene are perceived during saccades. The next chapter by Chen and Hutchinson describes how long-term memory influences attention, whilst Laflamme and Enns continue the theme of interactions between memory, perception and attention with new findings from the "superstitious perception" task. Elliot and Coleman's chapter argues that certain types of neural oscillatory activity may be important in selecting objects for action and anticipating future events. Hunt and colleagues address an important long-standing debate in the field, the relationship between covert attention and eye movements. Their chapter suggests that whilst oculomotor programming and covert attention are closely associated, the two processes are not strictly equivalent. Finally in this section, Macaluso's chapter raises the important question of how results obtained in the laboratory apply in the real world, assessing the current state and future opportunities for neuroimaging studies of visuospatial attention in natural visual scenes.

The five chapters in *Part III* present topics of clinical relevance dealing with patient-based research in *Neuropsychology and Neuropsychiatry*. Smith and Archibald consider patients with progressive supranuclear palsy, a condition that can be confused for Parkinson's disease in its early stage, which is characterised by attentional impairments confined to the vertical axis. Zokai and Husain summarise research using delayed reproduction working memory tasks to examine dissociable mechanism underlying deficits in Alzheimer's and Parkinson's patients, whilst Park

and Ichinose give an account of working memory impairments in schizophrenia, showing how abnormalities in this group are likely to arise due to attentional and perceptual problems affecting memory encoding. Pennington and Klaus revisit dopamine's role in attention and working memory reviewing recent findings of clinically relevant epigenetic interactions between environmental stressors and genes involved in dopamine transmission. The contribution from my own group on eye movements in neuropsychological tasks comes last and includes an updated version of a model of eye movement control in complex tasks originally presented by Land. Thus, our chapter links back to the opening contribution on the evolution of saccades by Land and therefore seemed a fitting place to end the volume.

I would like to thank all the contributing authors, series editor Thomas Barnes, Alamelu Damodharan and rest of the production team at Springer for all their time and patience with the project. I believe the resulting volume represents a very personal and original survey of a wide and complex field, and I hope you will agree the finished book has been well worth the wait!

Lincoln, UK
July 2019

Timothy Hodgson

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Part I
Evolution and Development

The Evolution of Gaze Shifting Eye Movements



Michael F. Land

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Abstract In animals with good eyesight most eye movements consist of saccades, which rapidly shift the direction of the eye's axis, and intervals between the saccades (fixations) in which gaze is kept stationary relative to the surroundings. This stability is needed to prevent motion blur, and it is achieved by reflexes which counter-rotate the eye when the head moves. This saccade-and-fixate strategy arose early in fish evolution, when the original function of saccades was to re-centre the eye as the fish turned. In primates, and other foveate vertebrates, saccades took on the new function of directing the fovea to objects of interest in the surroundings. Among invertebrates the same saccade-and-fixate pattern is seen, especially in insects, crustaceans and cephalopod molluscs.

Keywords Fixation · Invertebrates · Saccade · Stabilising reflexes · Vertebrates

1 Saccades and Fixations: A Universal Pairing

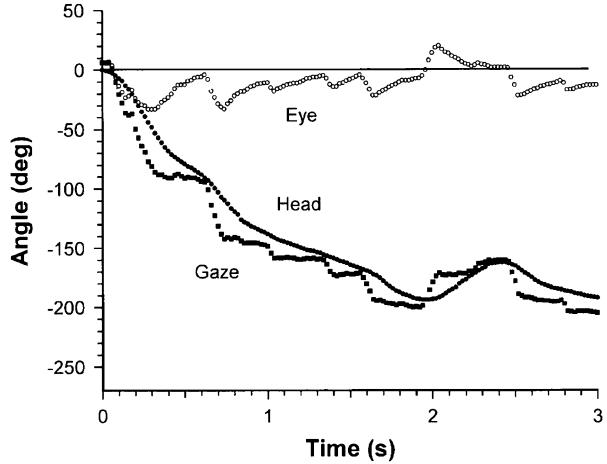
In humans, all other vertebrates, and in invertebrates with good eyesight, there is one pattern of eye movements that is almost universal: the pairing of fast gaze-shifting movements (saccades) with periods of stable gaze (fixations). In humans there are other types of eye movement – pursuit and vergence – but our usual method of

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Fig. 1 The author's left eye, looking round a room. The eyes perform saccades and between these compensate for head movements. Gaze (eye + head) moves in a series of discrete fixations, around the direction of the moving head. From Land and Tatler (2009). Note the similarity to Fig. 2



interrogating the surroundings is by using saccades to move our high-resolution foveas around the scene in a series of fixations (Fig. 1).

It seems natural for us to think of saccades, primarily, as movements that shift our direction of acute vision, but this is not how they began. Gordon Walls, in a landmark article, provided an outline of the way that fixations and saccades came about in vertebrates (Walls 1962). As he puts it, the origin of eye movements ‘... lies in the need to keep an image fixed on the retina, not in the need to scan the surroundings’. By the Ordovician period, at least 450 mya, the first fishes already had a reflex in which rotations of the head during swimming evoked compensatory movements of the eyes. This, the vestibulo-ocular reflex (VOR), was brought about by signals from the ampullae or semicircular canals of the vestibular system, and its function was to keep the image still with respect to the surroundings, in spite of movements of the head. At the same time, or slightly later, a second reflex evolved, which took retinal motion signals and fed them back negatively to the eye muscles via the optic tectum. This optokinetic reflex (OKR) also functioned to clamp the image to the surroundings. The need for this double image-stabilising system can be attributed to the fact that vertebrate photoreceptors are slow, cones taking 20 ms or more to respond fully to a change in intensity (Friedburg et al. 2004), so that if the eyes moved passively with the head, the image would be degraded by motion blur. We know from studies on human vision that blurring starts to occur when the image moves across the retina at speeds greater than about 1 degree per second, so compensatory eye movements are essential for clear vision, especially at higher spatial frequencies. These eye movements are continuous, and equal or at least proportional to the disturbance caused by the natural motion of the head, or imposed by an experimenter.

What then happens when a fish makes a turn? If the reflexes are operating as they should, the eyes will become trapped at the limit of their range, and a mechanism is needed to return them to a central point in the orbit. In practice, fish tend to make

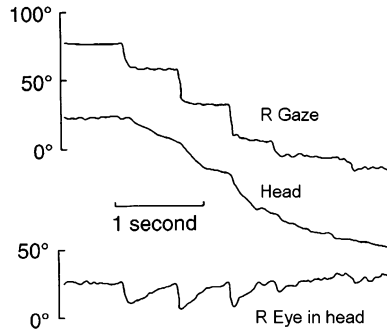


Fig. 2 Records of the eye, head and gaze movements of a goldfish making a turn. The eyes make saccades, but between these their movements are equal and opposite to those of the head. This results in gaze moving in a series of rotationally stable fixations. Goldfish lack a fovea, so the gaze shifts are more a necessary consequence of making a turn than a need to redirect a region of higher resolution. Redrawn from Easter et al. (1974)

these recentring movements early in a turn rather than when the eyes hit a backstop (Fig. 2). These movements need to be fast, since vision will not be possible or desirable during the reset, and this seems to be where the need for saccades originated. To quote Walls again: ‘even in the lowest fishes, we see a good reason for saccadic eye movements to be as quick as they notoriously are’. In clinical practice, these reflex movements in humans have become known as ‘slow phases’ and ‘flick backs’ or ‘fast phases’ and together referred to as ‘nystagmus’. But they are actually the ancient raw material from which almost all normal movements are derived.

2 Variations in Vertebrates

In some species of most vertebrate classes, this ‘saccade and fixate’ system has been adapted for a second use, namely, for targeting particular objects in the surroundings for more detailed scrutiny. Where this has evolved, it is always associated with a region of high resolution on the retina, either an area of elevated retinal ganglion cell density, as in a cat, or a smaller distinct fovea, as in a pipefish, chameleon, hawk or primate (Land 2015). These targeting movements do not occur in vertebrates with more uniform retinæ, such as goldfish, toads and rabbits: here the appearance of a novel object does not provoke a saccade. The ability to target objects also requires the ability to hold them on a high-resolution area or fovea, and this has led, in humans and other primates, to further oculomotor refinements. These include the ability to fixate and to track moving objects smoothly. Tracking usually means that the reflexes which keep the overall image stationary (VOR and OKN) have to be suspended or modified, so that the eye can move with the target and allow the background to drift (e.g. if you track your moving finger, while observing the background, you can appreciate the destructiveness of motion blur). In primates

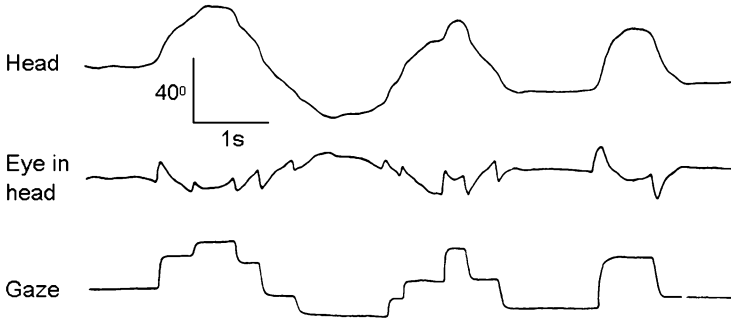


Fig. 3 Head, eye and gaze movements of a rabbit tracking the hand of an observer. Unlike primates, the target is tracked with the head, while the eyes make nystagmus-like saccades and compensatory movements, resulting in steplike gaze shifts. Modified from Collewijn (1977)

tracking extends to the third dimension, so that the foveas of the two eyes can converge on a single object independent of its distance. In mammals with lateral eyes, objects are tracked, but with the head rather than the eyes. Figure 3 shows a rabbit tracking the experimenter's hand with head movements. The eyes remain locked to the background, making a series of saccades and compensatory movements, so that gaze follows the head in a series of discrete fixations that do not directly follow the target, as they would in humans.

In humans, a saccade may be attracted to objects that are novel or otherwise 'eye-catching', but more commonly they are made to objects from which information is needed for the execution of a task, for example, to the spoon needed to stir the coffee or the nail that will be hit with a hammer (Land and Tatler 2009). This implies that the saccadic system has swift access to memories of where things are in the surroundings and information about their identities. Even when the eyes are not involved in information collection, they show the same pattern of saccades and fixations, at a rate of about three per second (Fig. 1).

In vertebrates with necks, head movements add to eye movements in determining the sizes of saccades. Heads have more inertia than eyes, so the contributions of the head need to be managed so that they do not slow up the gaze shifts. In small saccades ($<40^\circ$) in primates, eye movement contributes most to the gaze shift, with head movement adding to both the speed and amplitude of the saccade, while gaze-stabilising reflexes are temporarily turned off (Fig. 4a). When the predetermined end-point of the gaze change is reached, VOR is turned on, and the eyes move in the opposite direction, exactly counteracting the ongoing head movement and establishing fixation. For smaller saccades the head contributes about 30% to the gaze change. For larger saccades the eyes reach a 'backstop', and, with VOR still turned off, gaze is carried entirely by the head until the gaze end-point is reached, when VOR is re-established (rectangle, Fig. 4b).

The situation in birds is different. Having light heads and flexible necks, the contribution of head movement to gaze shifts is much higher than in mammals, and it is these head movements that make smaller birds seem so busy and vigilant. In

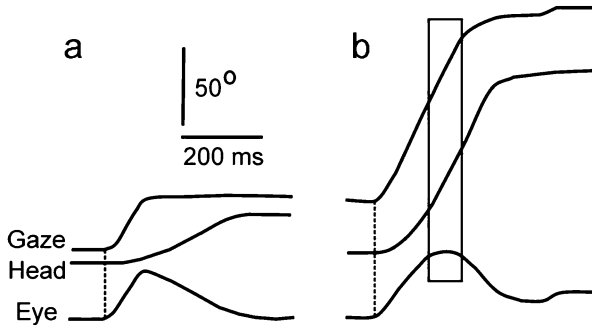


Fig. 4 Eye and head movements during a small (a) and large (b) combined saccade. Note that in (b) VOR remains turned off as the head completes the movement (rectangle) and recommences when the end-point is reached. Redrawn from Guitton (1992)

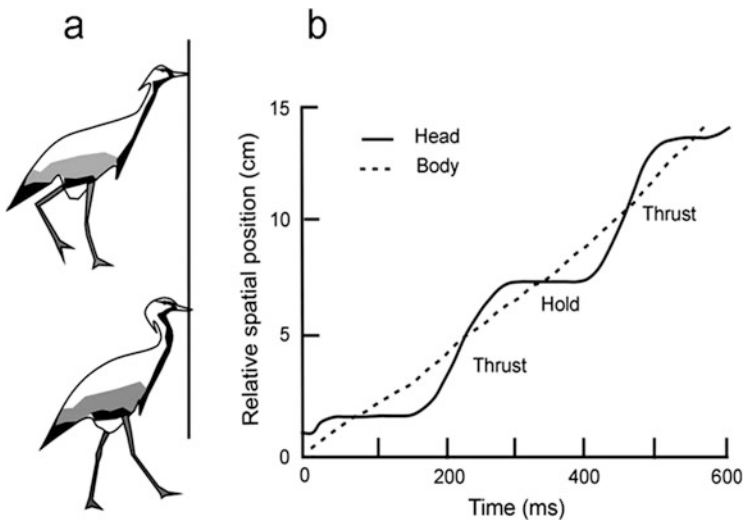
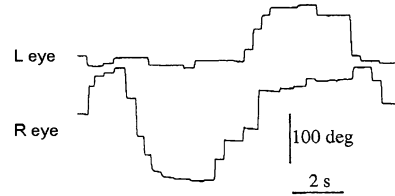


Fig. 5 Translational ‘saccades’ made by a demoiselle crane (a) and a pigeon (b). During the ‘hold’ phases, the head remains still in space (held by an optokinetic mechanism) and then moves forward during the ‘thrust’ phase. The body motion continues throughout. (a) Redrawn from photographs by Necker (2007) and (b) records from Frost (1978)

peahens, the head contribution to large gaze shifts ($>40^\circ$) is almost 90%; although with smaller gaze shifts, this reduces to about 60% (Yorzinski et al. 2015).

Many ground-feeding birds also make what may be called ‘translational saccades’ while walking. The head moves forward, and then stabilises, as the body continues to walk under the stationary head (Fig. 5). The function of this ‘head-bobbing’ seems to be similar to that of rotational saccade and fixate behaviour: to allow the view to the side to be held temporarily stationary on the retina while not preventing forward motion.

Fig. 6 Asynchronous saccades made by the two eyes of a chameleon, recorded with search coils. Adapted from Ott (2001)



The extent to which the two eyes are yoked during saccades varies considerably across vertebrates. In primates, the eyes are synchronised in timing, and their movements have the same amplitude; in other mammals the eyes are synchronised, but the movement amplitudes are more variable. At the other extreme, chameleon eyes are entirely independent in both the timing and amplitude of saccades (Fig. 6), until the moment preceding a strike, when they both point forwards. Seahorses and pipefish, which, like chameleons, have distinct foveas, have similarly asynchronous saccades. One particularly remarkable fish, the sandlance (*Limnichthyes fasciatus*), differs from all other vertebrates in that, following each saccade, the eye is not held still but drifts back towards a central position (Pettigrew et al. 1999).

3 Saccades and Fixations Outside the Vertebrates

The logic of Walls' argument – that the main function of eye movements is to keep the image still on the retina – should apply equally to those invertebrates that have good eyesight. This means the arthropods, especially crustaceans and insects, and cephalopod molluscs. Figure 7 shows a record of a rock crab, moving in a curvilinear path. Like the goldfish (Fig. 2), the eyes make fast saccadic eye movements with slow movements between them that compensate for body rotations. These slow movements result in periods of stationary gaze. Like vertebrates, crabs have a powerful optokinetic reflex and also the equivalent of a vestibular system that measures body rotation. Clearly, the saccade and fixate strategy is not just an idiosyncrasy of the vertebrate oculomotor system.

Insects too employ saccades and fixations. The situation here is different as the eyes are part of the head, so gaze stability has to be achieved by neck movements to compensate for rotations of the body. Figure 8a shows the head and body of a walking stalk-eyed fly, turning through a right angle. The head makes two saccades, at 120 ms and just before 400 ms, but before and between these movements, the head angle does not change. Flying flies behave rather similarly. In an impressive study, Schilstra and van Hateren (1998) recorded from both the head and thorax of flying blowflies with miniature search coils. Figure 8b shows that both the body and head rotate jerkily, but the head moves faster, and there is compensation for the slower body rotation (head on thorax), resulting in crisp changes of gaze (head).

Hoverflies have such fine control of their body angle during flight that they dispense with neck movements. The result is that 'saccades' appear as rapid changes

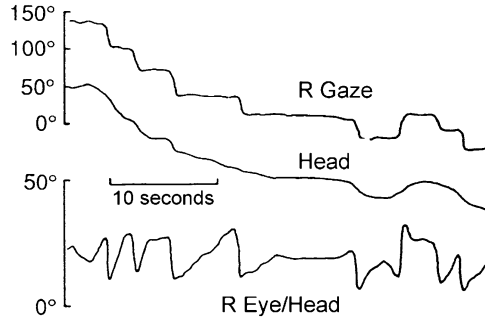


Fig. 7 Gaze, head and eye movements of a rock crab walking on a curved path. As with the goldfish (Fig. 2), the role of eye movements is twofold: to make gaze-shifting saccades and to compensate for movements of the head. Note that the eye/head scale is magnified. Redrawn from Paul et al. (1990)

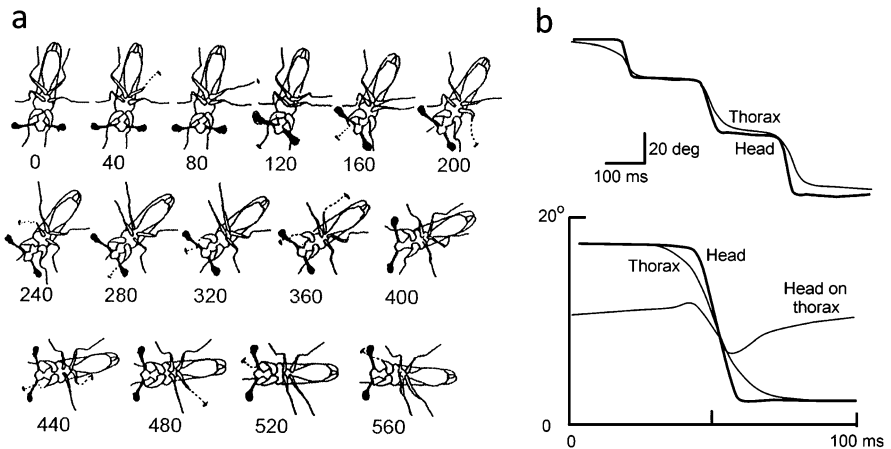


Fig. 8 (a) Stalk-eyed fly walking through a right angle on a glass plate. It makes two saccades (at 120 and 380 ms), with fixations in between (redrawn from an unpublished film by W Wickler and U Seibt). (b) Three saccadic turns made by a flying blowfly (top) showing the steplike rotations of the head in space and slower movements of the body. Below is a detail of a single saccade, showing the counterrotation of the head on the thorax. Both adapted from Schilstra and van Hateren (1998)

in orientation of the whole body, with ‘fixations’ between them in which translational flight continues but body angle is held constant (Collett and Land 1975). Interestingly, males have a frontal region of higher resolution, not present in females, and they use this to track the females while remaining out of sight by keeping at a distance of 10 cm. Males, in other words, behave like primates; females behave more like goldfish. Praying mantids also track their prey, with their heads. Against textured backgrounds, the tracking is saccadic, but against plain backgrounds, it is smooth, presumably because the optokinetic signal is too weak to prevent head rotation (Rossel 1980).

Outside the arthropods, the only other major group of animals with mobile eyes are the cephalopod molluscs (*octopus*, cuttlefish and squid). They show the same kind of nystagmus as vertebrates when placed in a rotating striped drum (Hanlon and Messenger 1996), and in the cuttlefish *Sepia*, saccade and fixation movements occur during spontaneous swimming (Collewijn 1970). These compensate for yaw and roll. *Octopus* has seven eye muscles, but cuttlefish and squid have an additional six or seven. These extra muscles are involved in the convergent eye movements which provide binocular vision prior to prey capture, movements that are absent in *octopus* (Budelmann 2009).

There are a few invertebrates that break all Walls' rules by making slow scanning eye movements during which they take in information. Jumping spiders scan images with slow torsional movements and faster side-to-side movements whose functions are to determine identity: specifically, whether a newly detected object is a conspecific or potential prey. Mantis shrimps (Stomatopoda) use scanning movements to extract information about colour and polarisation. Heteropod sea snails scan the water beneath them to detect plankton to feed on. In all these cases, the retinas (or relevant parts of the retina) are one-dimensional strips a few receptors wide, and the scanning movements are sufficiently slow that they do not interfere significantly with resolution (Land and Nilsson 2012).

4 Conclusions

Walls (1962) argued that vertebrate eye movements originated in the need to avoid motion blur by maintaining a stationary image and that this was achieved via vestibulo-ocular and optokinetic fixation reflexes, which evolved in the earliest fishes. Saccades evolved initially as movements to recentre eye direction when an animal turned. This saccade and fixate strategy is found in animals with good eyesight in all major phyla. In man, and other foveate vertebrates, this pattern of eye movements became adapted for a second function: the targeting of particular objects by the fovea, to obtain the benefits of improved resolution.

In primates two other types of eye movement supplement this targeting role. Smooth pursuit allows a moving object to be kept in central vision, but this inevitably means that the background is allowed to blur, with VOR and OKN temporarily suspended. Primates, and some other animals with forward facing eyes, use vergence to direct both foveas to targets at different distances, incidentally allowing stereoscopic range finding.

Head movements augment eye movements in many vertebrates and in birds almost replace them. In insects, with immovable eyes, neck movements, and sometimes whole-body movements, perform saccades and stabilise fixations. Cephalopods have a range of eye movements remarkably similar to those of fish, including vergence movements in cuttlefish and squid when they are about to strike prey.

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Visuospatial Integration and Hand-Tool Interaction in Cognitive Archaeology



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Abstract Testing cognitive hypotheses in extinct species can be challenging, but it can be done through the integration of independent sources of information (e.g., anatomy, archaeology, neurobiology, psychology), and validated with quantitative and experimental approaches. The parietal cortex has undergone changes and specializations in humans, probably in regions involved in visuospatial integration. Visual imagery and hand-eye coordination are crucial for a species with a remarkable technological and symbolic capacity. Hand-tool relationships are not only a

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matter of spatial planning but involve deeper cognitive levels that concern body cognition, self-awareness, and the ability to integrate tools into body schemes, extending the body's functional and structural range. Therefore, a co-evolution between body and technology is to be expected not only in terms of anatomical correspondence but also in terms of cognitive integration. In prehistory, lithic tools are crucial in the interpretation of the cognitive abilities of extinct human species. The shape of tools and the grasping patterns associated with the corresponding haptic experience can supply some basic quantitative approaches to evaluate changes in the archaeological record. At the physiological level, electrodermal activity can be used as proxy to investigate the cognitive response during haptic experiences, revealing differences between tools and between subjects. These approaches can be also useful to evaluate whether and to what extent our complex cognitive resources are based on the capacity to export and delegate functions to external technological components.

Keywords Electrodermal activity · Grasping pattern · Human evolution · Neuroarchaeology · Parietal lobes · Tool shape · Visuospatial integration

1 Prehistory and Neuroscience

Cognitive inferences in prehistoric archaeology have often been provided on the grounds of general terms and processes, rather than specific cognitive theories. The main framework has been a gross and generalized assumption that relies on anatomical and cultural complexity as a proxy for behavioral and cognitive complexity. That is, complex brains are supposed to generate complex behaviors, and complex behaviors are supposed to be necessary to produce complex tools. In the last decade, however, there has been an increasing exchange between anthropologists, archaeologists, neurobiologists, and cognitive scientists, and these research areas have undergone a stimulating multidisciplinary development. Thanks to technical improvements (from digital anatomy to numerical modeling) and the increase in the archaeological record, prehistoric and cognitive sciences have stepped into a more intense and reciprocal process of integration. Some fields have been enhanced, and some others have been introduced as brand-new methodological perspectives. *Paleoneurology* deals with the anatomical study of the endocranial cavity in fossil species and has been improved by the introduction and development of biomedical imaging (Bruner 2017). *Neuroarchaeology* concerns the study of prehistory-related behaviors through physiological and neurobiological approaches, such as functional imaging (Stout and Hecht 2015). *Cognitive archaeology* integrates the archaeological evidence with theories in cognitive science, through neuropsychological perspectives (Coolidge et al. 2015).

Despite the noticeable advantage of mixing archaeological and cognitive knowledge, the limitations are also clear: prehistoric studies are based on indirect traces of structures or processes, and not on the actual targets of interest. In terms of fossil

anatomy, paleoanthropology generally works with the fragmented bones of few individuals. Instead of a brain, there is a mold of the endocranial cavity or *endocast*. An endocranial cast can provide information on brain size, some gross cortical proportions, brain geometry and spatial organization, sulcal patterns, and meningeal vascular morphology. All this information is extremely valuable, because it is the only direct evidence we have on the brain anatomy of extinct species. Nonetheless, an endocast is not a brain and should be interpreted with this limitation in mind.

In the case of neuroarchaeology and cognitive archaeology, a main drawback is due to the fact that cognitive processes are investigated and simulated according to the information we have on modern humans (*Homo sapiens*), and not on extinct species. This is of course an intrinsic limitation of these fields. Nonetheless, we often use other species as models when investigating our own biology and evolution (mice, macaques, or chimpanzees), and the differences among species of the same genus (*Homo*) are supposed to be plausibly smaller. The fact that we use cognitive information on modern humans to make cognitive inference on extinct humans must be taken into account, but it should not be taken as a reason to reject the field as a whole. The aim of disciplines that integrate prehistory and neuroscience is to provide consistent hypotheses according to the available information, which can be tested against parallel and independent evidence. Testing hypotheses may be more difficult in extinct species than in living organisms, but the methods and rules are, after all, exactly the same as in any other scientific context.

2 Working Memory and Visuospatial Integration

Early steps in cognitive archaeology were particularly focused on working memory, following the model proposed by Baddeley (see Baddeley 2000, 2001), attempting to trace its components back to archaeological evidence (Coolidge and Wynn 2005; Wynn and Coolidge 2016). Frederick Coolidge and Thomas Wynn, integrating archaeology and neuropsychology, investigated the appearance of behaviors associated with a central executive system, a visuospatial sketchpad, and a phonological loop, in order to evaluate whether our species, *Homo sapiens*, could have enhanced its working memory capacity through a process of selection and adaptation. They suggested, for example, that, according to the technological evidence, Neanderthals' long-term working memory was similar to modern humans, while their working memory capacity was less developed, possibly because of a smaller phonological store or reduced attention levels (Wynn and Coolidge 2004). This conclusion, based on archaeological information, can be used for making behavioral predictions than can be contrasted against the ecological, cultural, and social evidence we have on Neanderthals. Following a similar principle, they also investigated specific behaviors like those associated with managed foraging, as a proxy for cognitive capacities linked to working memory, response inhibition, or space-time integration (Wynn and Coolidge 2003).

The Baddeley model (Baddeley and Hitch 1974) is assumed to rely mainly on a frontoparietal cortical network, and, according to the principles of cognitive archaeology, its functional units can be tentatively tracked back in the cultural remnants of human behaviors, looking for specific aspects associated, for example, with tool use and production, food storage, navigation, art, or social and economic dynamics. The executive system works through inhibition of emotional and spontaneous behaviors, which is probably a crucial hallmark of modernity. The phonological store influences speech and cognitive capacity associated with recursion and hierarchical cognitive organization. The visuospatial sketchpad deals with an egocentric perspective based on imagery (visual) and relational (spatial) capacity.

This last component was relatively neglected in many working memory analyses, but nonetheless it could have been crucial in human evolution. In fact, if we consider the paleoneurological evidence, a major morphological change along the human lineage has been precisely described for the dorsal parietal cortex (Fig. 1), a brain region which is crucial to visuospatial functions (Bruner 2018). Neanderthals display wider superior parietal lobules when compared with more archaic human species, and modern humans show an even larger parietal lobe expansion, which causes a bulging of the parietal profile and their classic “rounded head” (Bruner et al. 2003, 2011; Bruner 2004). Ontogenetic changes suggest that only modern humans have a specific morphogenetic stage of “brain globularization,” expressed very early during ontogeny, which is lacking in Neanderthals or chimpanzees (Gunz et al. 2010).

It is interesting, therefore, that the two human species with more complex technological levels display a cortical expansion of areas dedicated to brain-body-environment management and integration, especially when considering that for the human genus “environment” also means “tools.” Spatially, the lateral dorsal enlargement of Neanderthals can be tentatively associated with the intraparietal sulcus and superior parietal lobules, while the longitudinal enlargement in modern humans matches the position of superior parietal lobules and precuneus (Bruner 2010; Bruner et al. 2014a; Pereira-Pedro and Bruner 2016). The intraparietal sulcus is more complex in humans than in other primates, and it is largely involved in eye-hand coordination and tool use (Grefkes and Fink 2005; Choi et al. 2006; Tunik et al. 2007; Martin et al. 2011; Verhagen et al. 2012; Zlatkina and Petrides 2014; Kastner et al. 2017). Human specializations of this region are supposed to be directly associated with the evolution of our unique technological skills (Peeters et al. 2009; Goldring and Krubitzer 2017). The precuneus is extremely variable among adult humans, and it is much larger in humans than in chimpanzees (Bruner et al. 2014b, 2017a). It is considered crucial for processes based on integration between somatic (body) and visual cognition, like spatial coordination, visual imagery, mental simulation, auto-noesis, and egocentric memory (Fletcher et al. 1995; Cavanna and Trimble 2006; Margulies et al. 2009; Zhang and Li 2012; Freton et al. 2014; Land 2014). The precuneus can be seen as a bridge between the external environment (vision), body cognition, and self-perception, with imagery and inner levels of consciousness. The correspondences

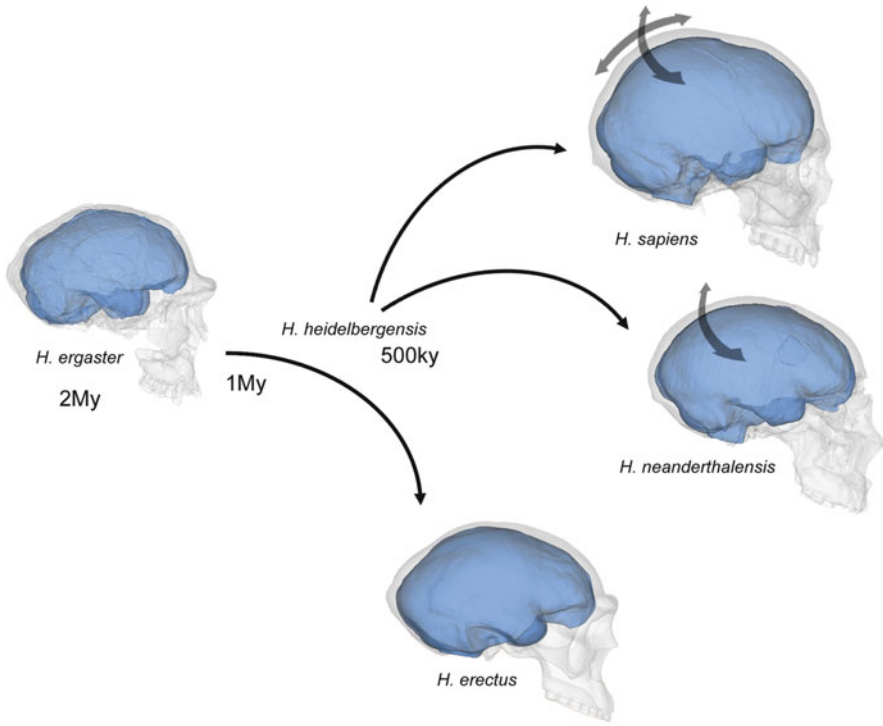


Fig. 1 The earliest fossils of the human genus (*Homo*) are dated to around 2 million years (My). In terms of endocranial morphology, the difference between these early African representatives and later *H. erectus* is apparently a matter of brain size, larger in the latter species. *H. sapiens* and *H. neanderthalensis* also evolved a larger brain size, but in these two cases, there was also evidence for changes in cortical proportions. Some of these changes are related to parietal cortex. Neanderthals display wider parietal lobes, and modern humans have wider and longer parietal lobes. Both lineages probably diverged after 500,000 years (ky) and derived from *H. heidelbergensis* which, as with *H. erectus*, had larger brain size than *H. ergaster* but no noticeable changes of the brain form

between humans and nonhuman areas are not completely clear, although some areas on the primate intraparietal sulcus may have outfolded in humans and the superior parietal lobule might be largely an outer extension of the precuneus (Scheperjans et al. 2008). These cortical areas are also very sensitive to environmental influences, including training and sensorial/somatic stimulation (Quallo et al. 2009; Iriki and Taoka 2012). Furthermore, they are all naturally crucial to specific conceptual and technical skills which range from imagination to tool use. Together, they have all the features of a very powerful visuospatial sketchpad.

3 Visuospatial Integration and Human Evolution

3.1 *Body and Space*

Most mammals possess homologous areas to the posterior parietal cortex, associated with functions that involve aspects of the body management, but this region is particularly developed in primates, and in particular in humans, due to manipulation skills and technological capacity (Goldring and Krubitzer 2017). The posterior parietal cortex is also crucial to processes aimed at filtering the sensorial information to coordinate attentional and intentional mechanisms (e.g., Posner et al. 1984; Mountcastle 1995; Rushworth et al. 2001; Yantis et al. 2002; Andersen and Buneo 2002; Bisley and Goldberg 2003; Corbetta et al. 2005; Wardak et al. 2004; Freedman and Assad 2006). Such filters are based on experience, as well as on somatic and visual feedbacks. Vision is used to coordinate body and environment, and the body is used as a metric unit of such an environment, in terms of space, time, and even social perspective (Land 2014; Hills et al. 2015; Maister et al. 2015; Peer et al. 2015). Our body perception is largely based on the hands, and the same areas involved in eye-hand coordination are also recruited in decision-making (Tunik et al. 2007). Namely, we can probably say that we often “think with our body,” particularly with our hands, planning and simulating actions by using our own body as reference and taking decisions according to simulated or expected body experiences, feedbacks, and capacities. In a behavioral and even neurobiological perspective, the somatosensorial experience is therefore intermingled with the motor experience, generating a blurred separation between “feeling” and “acting” (Ackerley and Kavounoudias 2015).

This framework between body and action becomes further entangled when the body interfaces with technological extensions, namely, during tool use (Bruner and Iriki 2016). Tools are intended as extension of the body schemes, through a functional distinction between *personal space* (the body), *peri-personal space* (within the range of the body), and *extra-personal space* (out of the range of the body) (Maravita et al. 2003; Maravita and Iriki 2004; Farnè et al. 2005; Cléry et al. 2015). The relationship between personal, peri-personal, and extra-personal spaces is particularly relevant when dealing with our evolutionary capacity to extend our body and cognitive functions into technology. The frontoparietal system, in fact, reacts differently to objects positioned in the three spaces, which map to different cortical areas as a function of distance from the body (see Cléry et al. 2015 for a detailed review). A crucial cognitive change takes place when an object is included into the peri-personal space, becoming a potential tool, reachable in terms of body contact and extension. The own body is the metric unit that defines the peri-personal range, and vision supplies the feedback to establish its frontiers, mainly centered on the position of the whole body, of the head, and of the hands. This peri-personal space is updated according to both dynamic changes (momentary and punctual variations) and plastic changes (neural changes after training), and tools have a special role in this sense, artificially altering the extension and capacity of the arms.

Even in simple physical terms, the contact between the body and the tool influences the muscular and sensorial perception of the body itself and, accordingly, all the cognitive mechanisms that use the body as a functional and structural reference (Turvey and Carello 2011). Therefore, visuospatial integration not only concerns gross spatial and mechanical adjustments, but it is also central to fine cognitive functions that deal with self-properties.

In sum, the posterior parietal cortex is involved in cognitive integration between the brain, body, and environment, between body and tools, and between vision and body, using the same resources to coordinate space and time, egocentric perspectives, imagery, and personal memories. This is particularly interesting in the light of the so-called *extended cognition theory*, which interprets cognition as a process generated by the interaction between the nervous system, body experience, and material culture (e.g., Malafouris 2010, 2013; Bruner et al. 2018a).

3.2 A Case Study in Cognitive Archaeology

Neanderthals represent an interesting case study in body cognition because, although they had a brain size comparable with modern humans, the archaeological and paleontological evidence point to distinct visuospatial behavior (see Bruner and Lozano 2014, 2015; Bruner et al. 2016). In particular, the cut marks on their incisors suggest that Neanderthals – and probably their ancestors – used their teeth and mouth to manipulate their technology much more than any extant or extinct modern human population. The mouth is second to the hands in terms of cortical representation of the somatic territories (the “cortical homunculus”), so it is expected that it can be used to provide an additional manipulative body element when hands do not suffice. However, its involvement in manipulation is indeed a risky choice and should be intended as a suboptimal alternative. The significant involvement of the mouth as a “third hand” in Neanderthals may hence suggest a lack of manipulative specialization, when technology reaches a given degree of complexity. These dental marks would not be sufficient to support such cognitive hypothesis, unless associated with many other independent sources of evidence. In Neanderthals the parietal cortex, crucial for visuospatial integration, was probably not enlarged as in modern humans (Bruner 2018). For this species there is no evidence of projectile tools, a technology which is specific of modern humans and associated with throwing ability and visuospatial capacity (Williams et al. 2014; Gärdenfors and Lombard 2018), and Neanderthal hunting techniques were probably based on physical confrontation with the prey (another risky choice, if you are able to catch a prey by shooting from a distance). Also, for Neanderthals there is no evidence of a noticeable iconographic or visual culture. Their few minor suspected graphic manifestations are extremely simple (Hoffmann et al. 2018) and definitely incomparable with both the early and late artistic expressions of *Homo sapiens*. Paradoxically, many people are surprised to see that Neanderthals could have been the authors of very naïve sketches, but in reality we should ask the opposite question: taking into account their large brain size

and high encephalization index, why did they not display more complex behaviors? If brain size really matters, with such a large brain (the same size as *Homo sapiens*), they would be expected to go well beyond a scratch or a colored shell. Although the Neanderthal archaeological record may be incomplete, the discrepancy with modern humans is, even only by grade, enormous, suggesting noticeable cognitive differences between the two groups (Wynn et al. 2016). Taken together, all this information (smaller parietal cortex, manipulation by teeth, no projectile technology, absent or negligible graphic culture) supports the hypothesis of a lack of visuospatial specialization and body cognition in Neanderthals when compared with modern humans. Of course, a less specialized cognitive ability is not necessarily a sentence to extinction, and we should not even discard the possibility that Neanderthals may have had other cognitive skills that we did not evolve.

Despite subtle uncertainties in chronology and definitions, it is worth noting that the morphological expansion of the parietal cortex in our species is probably a late acquisition of our lineage, and it matches the appearance of a definite behavioral modernity, including a noticeable visual and iconographic culture and complex technology. In fact, early modern humans shared similar lithic industries with Neanderthals and display only a partial development of the parietal surface (Bruner and Pearson 2013; Bruner et al. 2018b; Neubauer et al. 2018). However, they already had different hand proportions when compared with coeval Neanderthals, and a distinct use of the mouth when supporting manipulative procedures, more associated with the strength of the grip than with its precision (Niewoehner 2001; Fiorenza and Kullmer 2013).

It remains to be considered whether the neuroanatomical changes of the posterior parietal cortex are due to genetic evolution and selection or else to feedback between biology and culture, including training or epigenetic effects (Bruner and Iriki 2016; Krubitzer and Stolzenberg 2014). According to the traditional parcellation approach after Brodmann (see Zilles and Amunts 2010), it can be hypothesized that specific areas evolved, enlarged, or were reused for new emerging functions. By contrast, if brain organization is the result of gradients between sensorimotor regions (Huntenburg et al. 2017), the specialized posterior parietal cortex in primates – and in particular in humans – must be interpreted as an increase of connections and integration between the sensorimotor elements it bridges: body and vision.

4 Haptics and Body Cognition

Human evolution has been characterized by bio-cultural adaptive feedbacks between hand and tool morphology (Susman 1998; Marzke 1997; Almécija et al. 2015). Force distribution during tool use largely depends on the action performed, and it is likely that some behaviors may have had a major influence on hand shape, mostly

when dealing with the thumb and the distal phalanxes (Rolian et al. 2011; Williams-Hatala et al. 2018). Hand size is also relevant for tool use, and it is a major factor of variation also among modern adult humans (Key and Lycett 2011; Bruner et al. 2018c).

We can expect that this coevolution between the brain, body, and technology was not only a matter of biomechanics but involved specific cognitive functions associated with hand-tool integration. In general, most studies in this sense are interested in those cognitive abilities that concern planning, decision-making, and the executive functions of the brains. Nonetheless, additionally, we should also consider whether the hand-tool relationship may also require some cognitive process that enhances the integration of the tools into the body schemes.

Visuospatial functions are indeed necessary when planning tools or tool use (the visual imagery functions associated with the precuneus and the intraparietal sulcus). However, beyond these aspects, taking into consideration the importance of the neural management of the personal, peri-personal, and extra-personal spaces, it should be expected that the capacity to integrate tools as body extensions (e.g., in terms of neural plasticity) could be a crucial target of adaptive processes. Although modern humans (*Homo sapiens*) evolved a very specialized tool-based functional extension, the whole human genus (*Homo*) is characterized by a culture and behavior which make us *dependent* on technology (Plummer 2004). In the last 2.5 million years, our ecological, economic, and cultural niches have depended on tools, as essential elements of our behavioral abilities (Key et al. 2016). Such “prosthetic capacity” (Overmann 2015) can therefore not only be an important part of our cognitive system but also a specific ability influenced by natural selection. Interestingly, functional specialization within human brain areas has been shown to be less constrained by genetic factors compared with other living apes and so may be more plastic and sensitive to external influence (Gómez Robles et al. 2015). Such capacity to export cognitive functions to technological (extra-neural) extensions would depend on neural mechanisms, on body experience, and also on the properties of the tools themselves. It is hence mandatory, in cognitive archaeology, to investigate all these three elements, as well as their interactions.

This target is not easy, because of the many factors involved (individual cognitive and sensorial differences, multiple cognitive tasks involved, physical and functional tool parameters and variables, etc.). At experimental levels, simplistic paradigms can be easier to analyze, but scarcely informative. Moreover, many processes involved in behavior and cognition follow complex networks in which the final mechanism is not the simple sum of its parts, and there are emergent properties that can be observed only when analyzing the system as a whole. Actually, the network underlying cognitive extension is supposed to be complex itself, in the sense that, according to the extended cognition hypothesis, there are processes that are activated specifically by the interaction between the brain, body, and culture. Finally, there are major difficulties when trying to quantify specific behavioral resources emerging from body-tool integration because, at present, we still do not know what kind of ability is directly involved in such prosthetic capacity and how to measure it. All these limitations mean that this research area is still in a preliminary methodological

stage, in which distinct targets and techniques are investigated so as to evaluate their applications and potentialities. Quantitative methods are, of course, necessary, to step into a full experimental perspective. Three basic components behind body-tool interactions are tool shape, grasping patterns, and cognitive response to hand-tool integration. In the next sections, we show some applications in this sense.

5 Tools, Hands, and Attention: A Synthetic Analysis

5.1 Shape and Technology

Tool physical and geometrical properties influence the interaction with our body by virtue of both visual and haptic information. Beyond affordances associated with possible functional employment of the tool (purpose), the haptic experience is essential to generate an ergonomic spatial and physical integration between body and tool (Turvey and Carello 2011), which is ultimately projected into the newly emerging body schemes. The term “cyborg” has been popularized in a context of science fiction, but technically it refers to any functional integration between a body and a technological element, and humans are a special evolutionary case study of prosthetic extension (Clark 2004). Such “hybrid bodies,” in which external components come in contact with the body generating new emerging functions, can be traced back at least 2.5 million years to Africa, when we found the most ancient human technology, the Oldowan. Actually, there is preliminary evidence of older tools (see, e.g., Harmand et al. 2015), but Oldowan is the first technology for which we have a robust and consistent archaeological record (Semaw et al. 1997; Braun et al. 2008; Stout et al. 2010). It was essentially composed by flaked stones with a cutting edge, like the typical “choppers.” The raw materials were collected, prepared, and used locally, probably for a quick and momentary utilization. This technology was initially associated with *Homo habilis*, although at present this species is not regarded as a real and homogeneous taxonomic unit, and the hominid (or hominids) associated with this industry remains yet to be determined.

The earliest species undoubtedly assigned to the human genus (*H. ergaster* and *H. erectus*) are associated with stone tools which are much more elaborate and generally labeled as Acheulean technology (Lycett and von Cramon-Taubadel 2008; Hodgson 2015). Acheulean archaeological record begins after 1.7 million years, and the most typical tool in this case is the handaxe, a stone flaked for a larger part of its border, elongated and roughly symmetrical, probably used for multiple tasks. Some features of this industry can be due to stone geometrical constraints (Moore and Perston 2016), but nonetheless it is generally assumed that the complexity of handaxes, when compared with choppers, reveals a cognitive change, because of their design, preparation, and geometry (Wynn 2010; Gowlett 2013). Although Oldowan is more archaic and simpler, it was not substituted by Acheulean, and the two different technologies coexisted independently for at least 600,000 years (Clark and Schick 2000).