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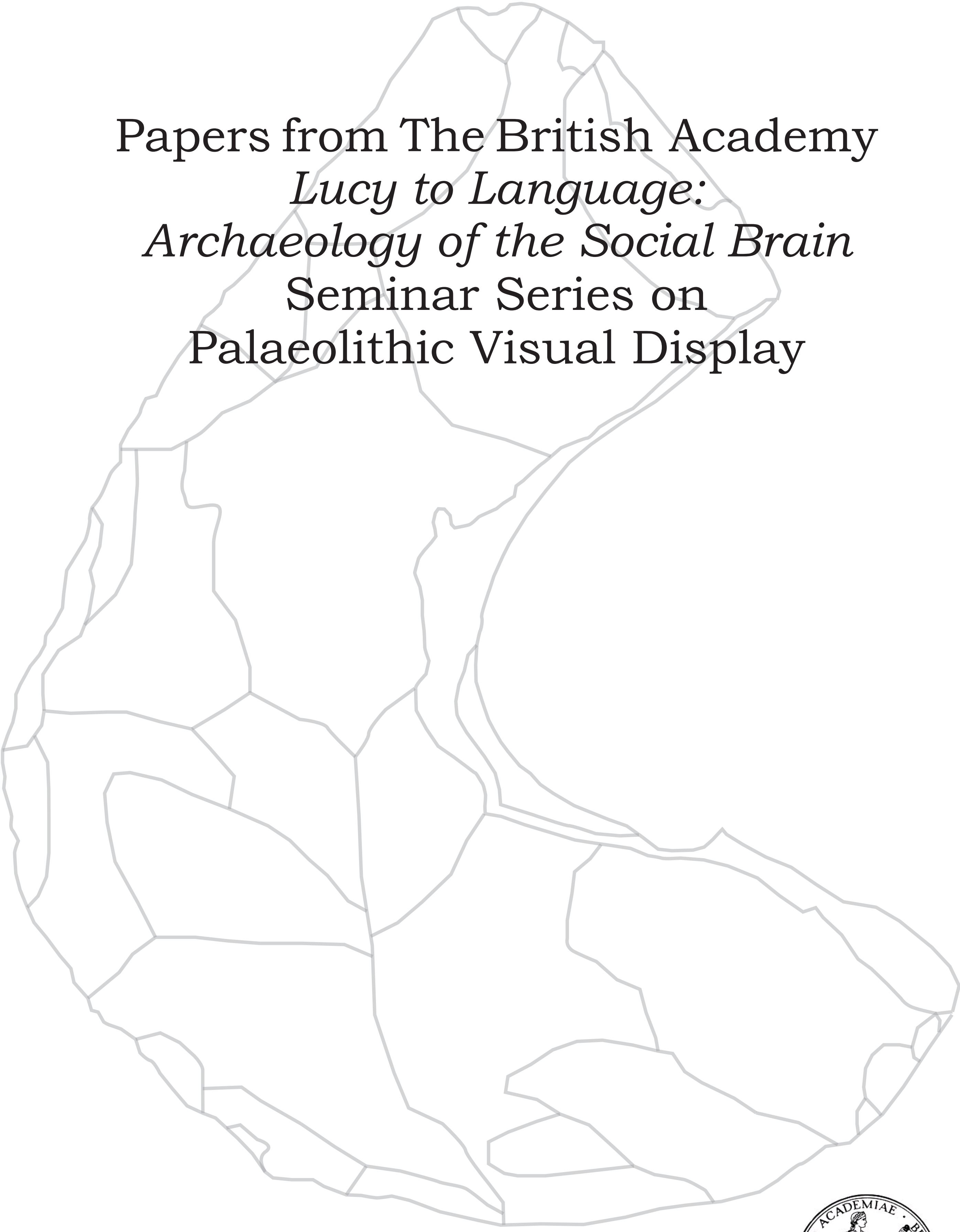

Papers from The British Academy *Lucy to Language: Archaeology of the Social Brain* Seminar Series on Palaeolithic Visual Display

edited by
James Cole and Karen Ruebens

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THE IMPORTANCE OF CONVEYING VISUAL INFORMATION IN ACHEULEAN SOCIETY. THE BACKGROUND TO THE VISUAL DISPLAY HYPOTHESIS

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Abstract

This paper is intended to provoke discussion. It is based on asking two simple questions, both of which are inter-related. The first is: what would it be like to live in an Acheulean social group? The second is: how would Acheulean flint knappers learn their craft in an Acheulean social group? The premise is as follows. In a hominin species which does not possess the linguistic capability of a modern human (in terms of the physical ability to produce speech as we understand it), or the cognitive capability to imbue speech with abstract meaning (i.e. the capacity for symbolic understanding that we can achieve), information exchange must be primarily visual. Information and knowledge designed to change the mental and behavioural state of another individual will have to be generated, disseminated, and understood through visual acts. Comparisons with the natural world suggest that display behaviour may be a key factor in this. This paper does not discuss what is being displayed and how. Instead it looks at the underlying mechanisms that could have contributed to focusing and enhancing individual perception of visual stimuli.

Introduction

A paper on this subject must, by nature, be speculative. From the outset I must admit that there is very little empirical support for what I suggest, and much of it cannot be tested on the basis of currently available evidence. What follows is a discussion on how the makers of the Acheulean may have organised their social relations. My purpose is to engender debate on an aspect of Pleistocene archaeology that does not get the attention it deserves. This lack of broader interest in the nature of Acheulean society (but see Mithen 1994 and Gamble 1999 for important exceptions) is, in part, explained by the strongly empirical character of Acheulean studies (e.g. Potts 1998; Potts *et al.* 1999; Sharon 2007; Sharon 2008; McNabb 2009). Additionally, there has always been a difficulty in passing beyond a descriptive archaeology primarily rooted in an ethological approach that privileges hominin adaptations to environment and landscape as its core dialogue.

I will begin by setting a basic premise.

> The Acheulean as a technological package was practiced by hominins who did not possess the same capacity for spoken language, and abstract thought, as modern humans. This more limited capability (by comparison) was both cognitive and physical (Walker and Leakey 1993; MacLarnon and Hewitt 2004). Consequently, the transfer of subject specific information, and any semantic content within that information, between individuals and their broader social groups, was primarily based on visual display. Any meaning beyond that referable to the overt and the 'here and now', could only be comprehended through the medium of observed physical action.
>
> This does not preclude the possibility that Acheulean hominins possessed a limited grammatical language, composed of specific sounds intended to convey particular meanings. But even in these cases visual display (and context) would still remain the most important conduit for information exchange. In fact, MacLarnon and Hewitt (*ibid*) suggest that the ability to produce any kind of speech may have been very difficult for *H. erectus*.

This approach does not preclude the input of other senses in acquiring information from the outside world (Gamble 2010), nor the power of emotion and emotional reaction to external stimuli as learning tools (Gamble *ibid*). It merely asserts that visual display by hominins is a more powerful medium of information exchange than any of the other senses. Visual action can convey more information, a higher degree of complexity, and greater subtlety than the other senses.

This represents the core of the visual display hypothesis (VDH). Acheulean knappers will have engaged in acts of purposeful display (Porr 2000; Porr 2005). These will be designed to enhance an individual's status in the eyes of others within the social group. Such acts of visual display were intended as platforms for individual preferment. Individuals competed with others for preferment and greater access to resources. Visual display was underwritten by competition and selection for the most successful 'show offs'. These acts are not always intended to increase access to mating opportunities (*sensu* Darwinian sexual selection), though this could obviously be an important part of this.

To this I will add four assumptions that develop the premise.

- Whereas many animals in the natural world broadcast visual and audible information to each other, any semantic content that passes beyond the level of transmitting information on current emotional states will at the very least require a sense of self and other. More complicated meaning content will require a theory of mind. In Baron-Cohen's terms (Baron-Cohen 1999), communication acts are intended to change the knowledge state of the listener, but you need to be aware at least to some extent that the listener has a mind that can be enlightened by the knowledge.

- Visual display will always limit the complexity and depth of information imparted between individuals and groups by comparison with spoken language.

- Arising from the previous point, the ability to engage with, and even manipulate others in the social group, will be restricted by the limited information carrying capacity of visual display. This will in turn set certain limits on the kind of society the makers of the Acheulean could construct.

- The physical context and location of acts of display will enhance the power of display (Porr 2005; McNabb 2007b). Particular locations, perhaps associated with significant events may have had emotive potential, and have allowed hominins to construct landscapes of significance (Gamble 1999; Matt Grove pers comm. 2010)

The concepts that will be explored further in this paper such as theory of mind, intentionality, and mind reading are explained in text box 1.

Text Box 1.

Theory of Mind (Dunbar 2004). All modern humans have a theory of mind. It is the understanding that others in your group have a mind not dissimilar to your own allowing you to predict their actions and their intentions based upon your assessment of their state of mind.

As used here there are three pre-requisites to a full theory of mind as found in modern humans.

- The agent must be aware that he/she has a mind of their own and have the capacity to reflect on its contents (to varying levels)
- The agent is aware that others have minds of their own and that they also have the capacity to reflect on the contents of their own minds
- The agent is aware that others may hold beliefs about phenomena that differ from the beliefs that the agent holds

Mind reading (Dunbar 2004). The basis of modern social relations. Based on the possession of a theory of mind, an agent predicts the belief states of others as well as anticipating and interpreting the actions others take based upon their belief states. The agent is able to act, or alter intended actions because of his or her opinions on the belief states of others in their group.

Orders of Intentionality (Dunbar 2004). This is an ordinal scale for measuring cognitive complexity.

Zero order intentionality. Organisms that have no awareness that they possess a mind, if indeed they do; bacteria or plants for example.

- 1st order intentionality. An organism is aware of its mind and its contents, if only dimly; it knows its hungry, it needs to sleep soon, it is anxious.
- 2nd order intentionality. Holding a belief state about some one else. You have to be aware of your own mind, be aware of another's mind, and be conscious you hold a belief state about someone else's belief state. This is the equivalent of a full theory of mind. Most everyday human relations operate at this level.
- 3rd order intentionality. At 3rd order the agent has to include a third belief state belonging to a third mind. But the agent is not simply second-guessing the third person's belief state. Rather, the agent will attempt to anticipate what the second person believes is the belief state of the third person. For example, James *thinks* that Dave *supposes* that Karen has an *opinion* on something..

With each new person added to the chain, the agent has to try and comprehend what each individual believes is the point of view of the next person in the chain, about the point of view of the next person in the chain, and so on. Modern humans can operate at up to four or five orders of intentionality.

- 4th order intentionality. James *thinks* that Dave *supposes* that Karen is of the *opinion,* that Iza *believes* something about Eleanor
- 5th order intentionality. James *thinks* that Dave *supposes* that Karen is of the *opinion,* that Iza *believes,* that Eleanor *thinks* her PhD supervisor is an idiot.

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What do I mean by the Acheulean here?

The Acheulean is an Old World phenomenon that begins in Africa c. 1.8 mya, and is widespread throughout north, east and south Africa by 1.4 – 1.0 mya. It is found in western Eurasia from 1.4 mya, and is widely present in western Europe after 0.65 mya (McNabb 2007b; but see Scott and Gibert (2009) for a possible earlier date of Acheulean entry into Europe). It continues until c. 0.3-0.25 mya when it is superseded by assemblages more heavily dependent on Levallois technology (McNabb 2007a). As a phenomenon, Acheulean stone tool assemblages are defined by the presence of the handaxe (or biface) and/or other large cutting tools (LCTs) such as cleavers, unifaces, or picks/trihedrals. In the absence of LCTs, an assemblage may still be identified as Acheulean by the presence of particular stone working techniques intended to produce large flake-blanks which are further knapped into LCTs. Among these techniques are the Victoria West (McNabb 2001; Sharon and Beaumont 2006) , Kombewa, Talbalbal/Tachengit techniques (Sharon 2007), and a variety of methods designed to reduce boulder cores and so-called giant cores to provide large flake-blanks for modification into LCTs. These techniques are mostly found in areas other than western Europe largely because in Europe the higher incidence of naturally occurring fine grained siliceous lithologies like flint and chert, render the manufacture of large flake-blanks unnecessary. In Europe LCTs are usually (but by no means exclusively) made by *façonnage* (White and Pettitt 1995). In Africa, south western Asia, and India LCTs are frequently (but again not always) a product of both *façonnage* and *debitage*; the flake-blank is *debitage*, but then it is treated as a core/nodule and shaped into an LCT – *façonnage*.

Other than LCTs and the technology for the production of their blanks, the Acheulean is accompanied by a suite of cores, core-tools, flakes, and flake tools (Leakey 1971; Isaac 1977; Leakey and Roe 1994; Isaac and Isaac 1997; McNabb 2009). Not surprisingly the Acheulean encompasses a considerable degree of assemblage variability over time and space, with local circumstances, resource affordances, and presumably local traditions of learned practice influencing the specific character of individual assemblages. There is also a widely held belief amongst scholars of the Acheulean that it becomes more sophisticated over time with handaxes in particular showing an evolution toward more refined and more symmetrical examples (Hodgson 2009). It is believed this reflects the evolutionary development of the hominins who make the handaxes (see below). However no substantial body of data exists that underpins this belief, whereby a *number* of geographically distinct local sequences all show clear LCT evolution within a long stratigraphic profile that is well dated. For example, Olduvai Gorge contains a long sequence of Acheulean distributed across four major sedimentary units and representing nearly 1.8 myr. The excavator suggested that there was development in the Acheulean over time (Leakey 1971; Leakey and Roe 1994). Qualitative changes in the Acheulean assemblage here are tracked in Figure 1 (McNabb 2005), but whether these represent true patterns of development, or just differences in assemblage composition because of a variety of factors remains to be determined. The better made handaxes, higher in the Olduvai sequence, often reflect increasing use of finer grained lavas such as phonolite.

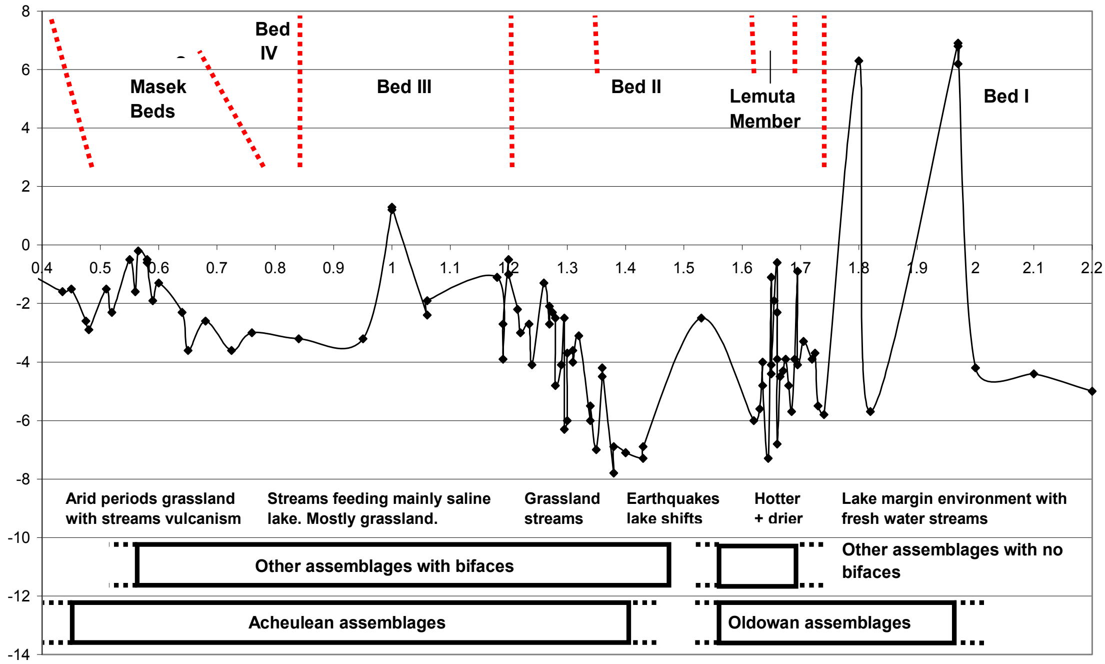

Figure 1: This shows that the stability of the tool types over time in Olduvai was set against dramatic change in local and regional topography and climate, with all the changes in habitat such conditions would entail. The archaeological signal is not much affected by local shifts in habitat. Horizontal scale is time in millions of years and vertical scale is carbon 13 values used as a proxy for shifts between C3 and C4 photosynthetic pathways. Details of environmental reconstruction in McNabb 2005. Descriptions of the archaeology differ slightly from figure 1a. The Oldowan refers to those assemblages described as such by Leakey (1971). Developed Oldowan A and other assemblages lacking bifaces but not given a cultural label are in the 'other assemblages with no bifaces' group. The Acheulean is as described by Leakey & Roe (1994). Developed Oldowan B and C and all those assemblages with bifaces that were not given a cultural label are grouped together under 'other assemblages with bifaces'.

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Should the VDH apply to all Acheulean social groups across the length and breadth of the Acheulean world, and the whole of its time span? A safe option would be no, especially since the Acheulean is the product of at least three distinct hominin species (see below); a safe bet would be to restrict it to the earlier time span only within Africa. However, given that the Acheulean as a body of material culture, does not (in my opinion) appear to follow a clear cut developmental evolution, I will suggest that the VDH does apply to all of the Acheulean where ever and whenever it is found within the period 1.8 to 0.30 mya; I will also assume that inter-assemblage variability is primarily a reflection of differing local social traditions and variability in lithic resources across time and place.

Which hominins are responsible for the Acheulean?

The Acheulean appears at c.1.8 mya, at roughly the same time as *Homo ergaster* makes its earliest appearance in the fossil record (Harris *et al.* 2007). It is commonly assumed that the two are related, and that this early African form of *Homo erectus* is responsible for the Acheulean. By 1.0 mya in Africa *H. ergaster* is more commonly referred to as *H. erectus*, and the species may persist for some time after this date; Daka/Bouri (Asfaw *et al.* 2002), and Buia (Ghinassi *et al.* 2009), dated at about 1.0 mya, are amongst the youngest examples of this group of hominins yet discovered in Africa.

The Middle Pleistocene hominin record of Africa is sparse and complicated. *Homo rhodesiensis*, is at the moment an umbrella label for a number of different fossils which are suggested to be the lineal descendants of *H. erectus* in Africa. Fossils from sites such as Bodo (c. 600 kya, with Acheulean - Klein 1999), Elandsfontein (c. 1.0 - 0.6 mya probably associated with Acheulean, Wadley and McNabb 2009), Florisbad (c. 260 kya and associated with either late ESA or early MSA lithics - Kuman and Clarke 1986), and Kabwe (c. 300 – 600 kya no artefacts associated Klein 1999), all demonstrate a large degree of morphological variability, and it is possible that more than one species is contained within the group. Most are assumed to be handaxe makers. The Cave of Hearths mandible, securely dated to the middle Middle Pleistocene, is certainly associated with an Acheulean assemblage (Mason 1988; McNabb and Sinclair 2009).

In Europe handaxe makers are associated with *Homo heidelbergensis* (McNabb 2007b) often taken informally to be a European equivalent of the African *H. rhodesiensis*. It should be noted that not all *H. heidelbergensis* were handaxe makers however. Assemblages such as the British Clactonian or the non-handaxe assemblages from Vértesszöllös for example are assumed to have also been made by members of this fossil species.

The label *H. heidelbergensis* encompasses a considerable degree of morphological variability. It is often assumed that there is a difference between earlier (pre-MIS 12) and later members of the species. Again, there may be more than one species encompassed within the single species label. The origins of *H. heidelbergensis* are unclear. It is possible that it represents a descendent of *H. antecessor*, currently believed to be a purely Eurasian species. Alternatively it may represent one or more waves of African *H. rhodesiensis*-like migrants carrying the handaxe technology with them, adapting under strong selective pressure to the challenges of the European Middle Pleistocene environment.

Should the VDH apply to all of the three hominin species (*H. erectus/ergaster; H. rhodesiensis; H. heidelbergensis*) currently suggested to make the Acheulean? The safe bet would again be no, restricting it to African *H. ergaster/erectus* up to 1.0 mya. However, as noted above, the Acheulean appears to represent a form of variable-sameness everywhere it is found, with that variability being explained by a variety of (interacting?) local circumstances. All three hominin species clearly used the Acheulean material culture adaptation in much the same way *at least in terms of its manufacture and appearance* (patterns of discard distribution are likely to have reflected very different local practices). So for the moment, I will suggest that the VDH will apply to all three handaxe making hominins as well.

At what point in human evolution does a sense of self and other emerge?

A sense of self and other will have been an important prerequisite for information exchange in hominin society, without which the VDH could not operate. It is the minimum level of awareness that would be necessary in order to communicate information designed to change the knowledge state of a listener. It is also an important first step in developing theory of mind. Most social animals will possess a sense of self and other to some extent, but it is not possible to measure the continuum between those who are simply aware of the presence of others, through to the point at which an animal begins to recognise the other as possessing a mind similar to its own which will also hold belief states.

The standard Social Brain Hypothesis interpretation, as reflected in figure 2, would suggest that by the time of *Homo ergaster/erectus* intentionality level 3 had been achieved, and by *H. heidelbergensis* (often characterised as archaic *Homo sapiens* in the SB diagrams) level 4 was present. Both of these imply a full theory of mind and, I would suggest, further imply that Acheulean society was based on some (significant?) level of mind reading, particularly at level 4.

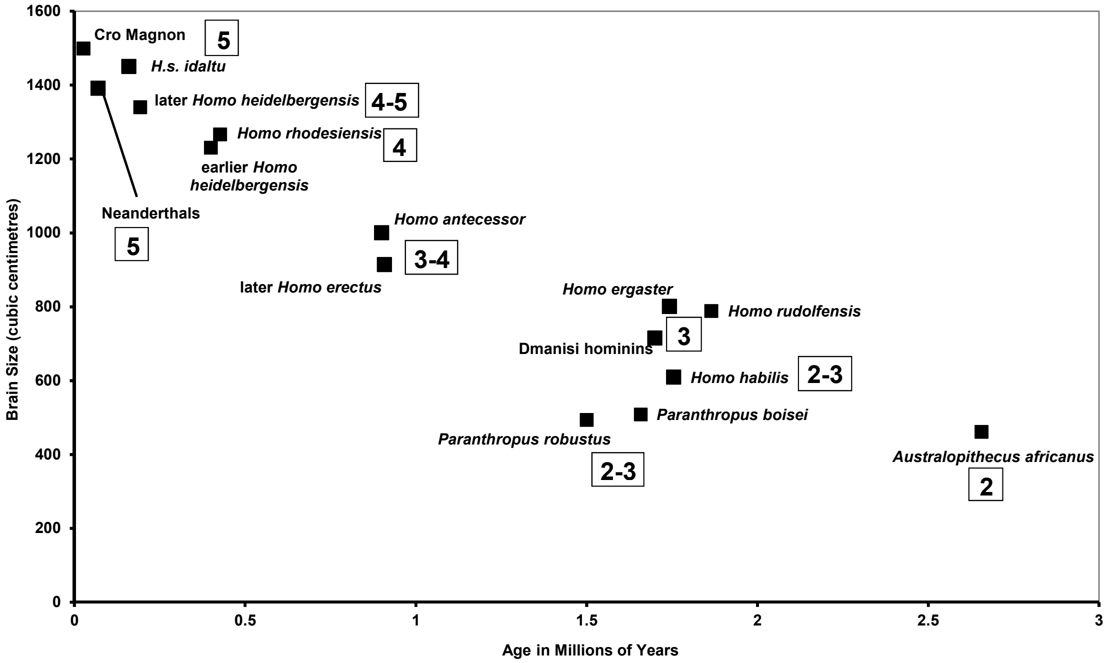

Figure 2. Redrawing of the Social Brain Project's standard diagram measuring orders of intentionality against hominin species and time. Data courtesy of Matt Grove. Approximate orders of intentionality are represented by large numerals in boxes.

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In order to explore these assertions I would like to pose the following inter-related questions.

- What is there in the archaeological record that could support the presence of a theory of mind? Can archaeology ground truth this proposition?
- Could Acheulean society be constructed solely on a sense of self and other, and not involve mind reading?

I will begin with the second question and start by comparing levels of cognitive ability, measured from an archaeological perspective, between Acheulean knappers, and their Oldowan predecessors.

Figure 3 depicts the *chaîne opératoire* for an idealised Oldowan knapping event. Here the *chaîne opératoire*, like a psychologist's use of orders of intentionality, is presented as a proxy for cognitive complexity. The more stages/decisions confronting the knapper the more cognitively demanding the activity. Two scenarios are envisaged, one were the hominins make do with raw materials locally available, and the other were they have to travel to obtain suitable lithic resources for knapping. In the former case there are two levels of decision making (two choices) prior to the decision to abandon the tool or transport it elsewhere for further use. In the second scenario were a trip to the raw material source is involved, four levels of decision making are involved before the decision to abandon the tool or carry it elsewhere is made. Each level is a decision which may or may not involve a choice and a consequence that the hominin must appreciate (for example the decision not to use a local rock type, for whatever reason, will entail a journey and a transport event). Parts of this Oldowan *chaîne opératoire* might be applicable to chimpanzees (though no specific chimpanzee to hominin cognitive comparison is implied). Favourite anvils or hammers may involve journeys to or from resources, possibly cached. Trips to assess distributed food resources are common.

I think few would doubt that chimpanzees possess a sense of self and other, as they are clearly aware of their conspecifics and react to them. Their social relations are built on this awareness. It must be inherent within any society that has a strict social hierarchy where the individual understands its own place in the pecking order. Examples could be socially cooperative predators such as lions, hyena, African wild dogs (and possibly a socially cooperative bipedal predator like *Homo ergaster* and *H. heidelbergensis*). By extension, the complexity inherent in the Oldowan *chaîne opératoire* would suggest that these knappers also had a sense of self and other.

There is indirect evidence that supports this inference. There is no genetic basis to knapping. You have to learn it, and learn it within a social context. A sense of self and other has to be a basic requirement for this kind of learning task. Moreover, the Oldowan shows a mastery of alternate flaking (Leakey 1971; Toth 1985; Kuman 1996; Kimura 1999; Braun *et al.* 2005), something that Kanzi, a highly adept Bonobo chimpanzee has been shown how to do, but has never achieved (Toth *et al.* 1993). This suggests the cognitive demands for producing Oldowan material culture, as knapped at Olduvai or Sterkfontein nearly 2.0 mya, is a level beyond that of modern chimpanzees at present. Again, alternate flaking and its significance for a successful knapping episode is something a knapper has to learn and *intuitively appreciate* through practice in order to successfully apply it.

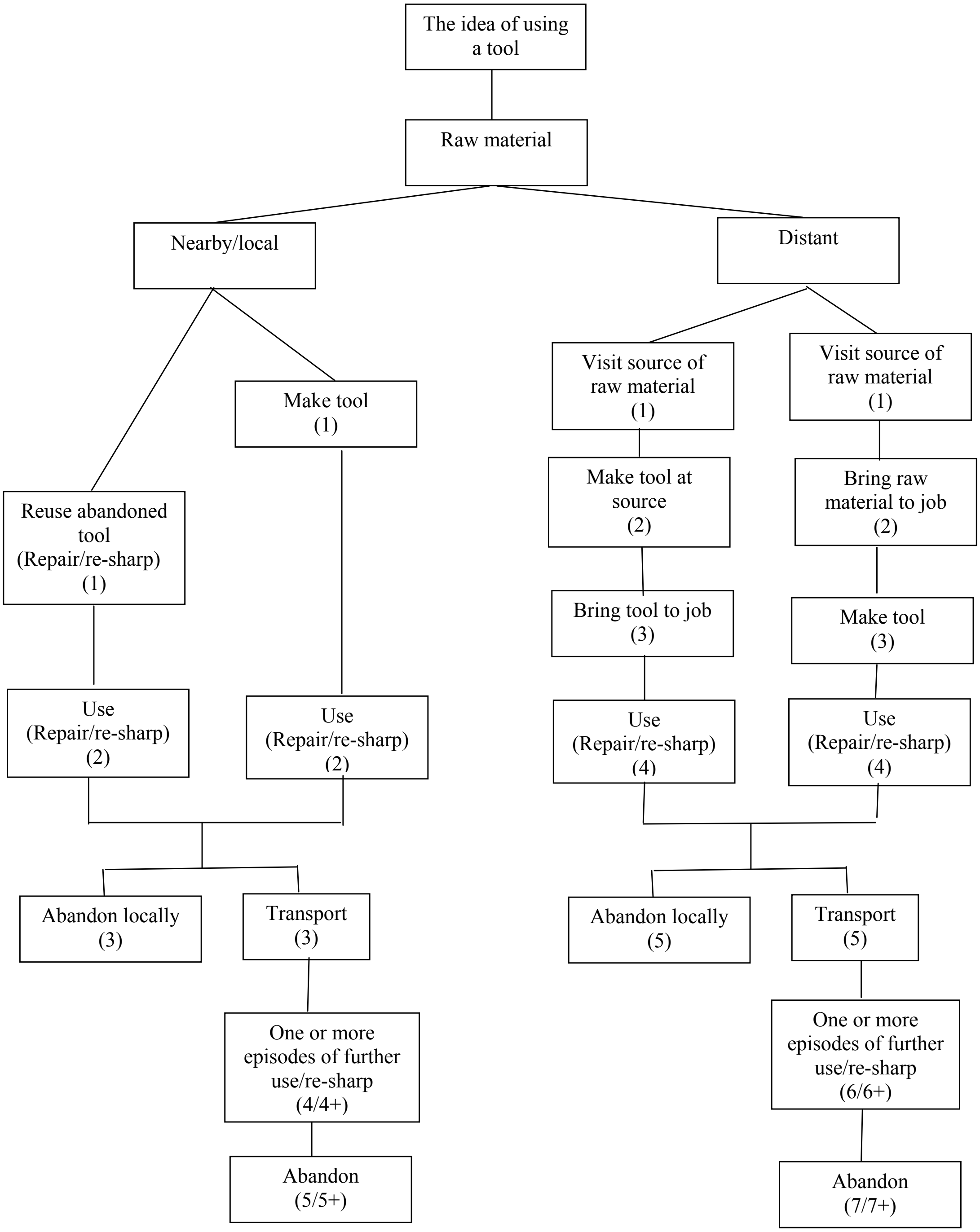

Figure 3. The chaîne opératoire for an idealised Oldowan knapping event. Figures in parenthesis reflect the level of decision making incorporated in the actions carried out up to that point.

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In my opinion a sense of self and other would be absolutely essential for this. It is something you learn from watching others, and appreciate by doing yourself. Iriki and Osamu (2008) suggest that tools themselves bespeak a basic ability to objectify the external world, objectifying both tools and the people who use them, and that this capacity to objectify must also logically include the perception of self. They note, in passing, that the transferability of tools between individuals supports the notion that other people and things will be objectified by the self. To learn how to make and use a tool by watching another individual at work implies the ability to comprehend another individual's discreet existence, in order to conceptually separate them from their tool before attempting to make and use your own example of that tool.

Indeed, Grove and Coward (2008) describe a neural architecture (bimodal neurons) designed to adapt the perception of the body as self, in order to include a tool as an extension of self during an episode of tool use. It allows for the 'incorporation' of an external object into the body schema to make the use of the tool more effective. Unfortunately we do not know which of *H. ergaster's* precursors are responsible for the Oldowan; *H. habilis*, *H. rudolfensis*, or even one or more of the Australopithecines (or a combination of these).

Accepting that a sense of self and other is suggested by the very fact of producing Oldowan material culture, it must also by extension be present in the Acheulean. The chaîne opératoire for the Acheulean is presented in figure 4, further developing the same hypothetical example. What distinguishes the Acheulean sequence from the Oldowan is the inclusion of extra stages, irrespective of whether the LCT is made from local or distant rocks. These stages are the preparation of a boulder or outcrop and the detachment of a large flake from this to serve as a blank on which the LTC is made. There are between two and four levels of decision making for the locally sourced raw materials, prior to abandonment or further transport. There are six stages of decision making if a visit to a distant raw material source is undertaken. The greater complexity inherent in the Acheulean scenario is clear. Qualitatively, as well as quantitatively there are differences between the Oldowan and the Acheulean. For the latter, a suitable boulder or outcrop must be factored into the decision to make a tool, selected, worked and prepared, then flaked for a successful blank before the knapping of the LCT even begins. This flake-blank preparation and production step for a LCT lifts the Acheulean chaîne opératoire out of the zone potentially appropriate to chimpanzee troupes. To my knowledge, no such intermediate stage has ever been identified in chimpanzee tool manufacture to date, or in the Oldowan.

The above highlights a second and complementary issue concerning complexity that is present in the Acheulean but absent in the Oldowan. This is the question of finished tool forms. When the Oldowan first achieved prominence as a result of the excavations of the Leakey's at Olduvai Gorge (Leakey 1971; Leakey and Roe 1994), it did so at a time when there was an unquestioned typological assumption by archaeologists that the morphology of a tool was the exact form intended by the knapper. Ancient hominins reproduced a fixed repertoire of tool types more or less to a specific mental template (Bordes 1961; Kleindienst 1962). But the rise of experimental studies (Jones 1979; Jones 1981; Toth 1985) and shifts in theoretical approaches (Trigger 1989), began to question this. In particular the knapping experiments of Nick Toth *(ibid)* established the possibility that the standardised Oldowan core morphologies (chopping tools, discoids etc.) were actually the waste product of intentional flake production and not core tools

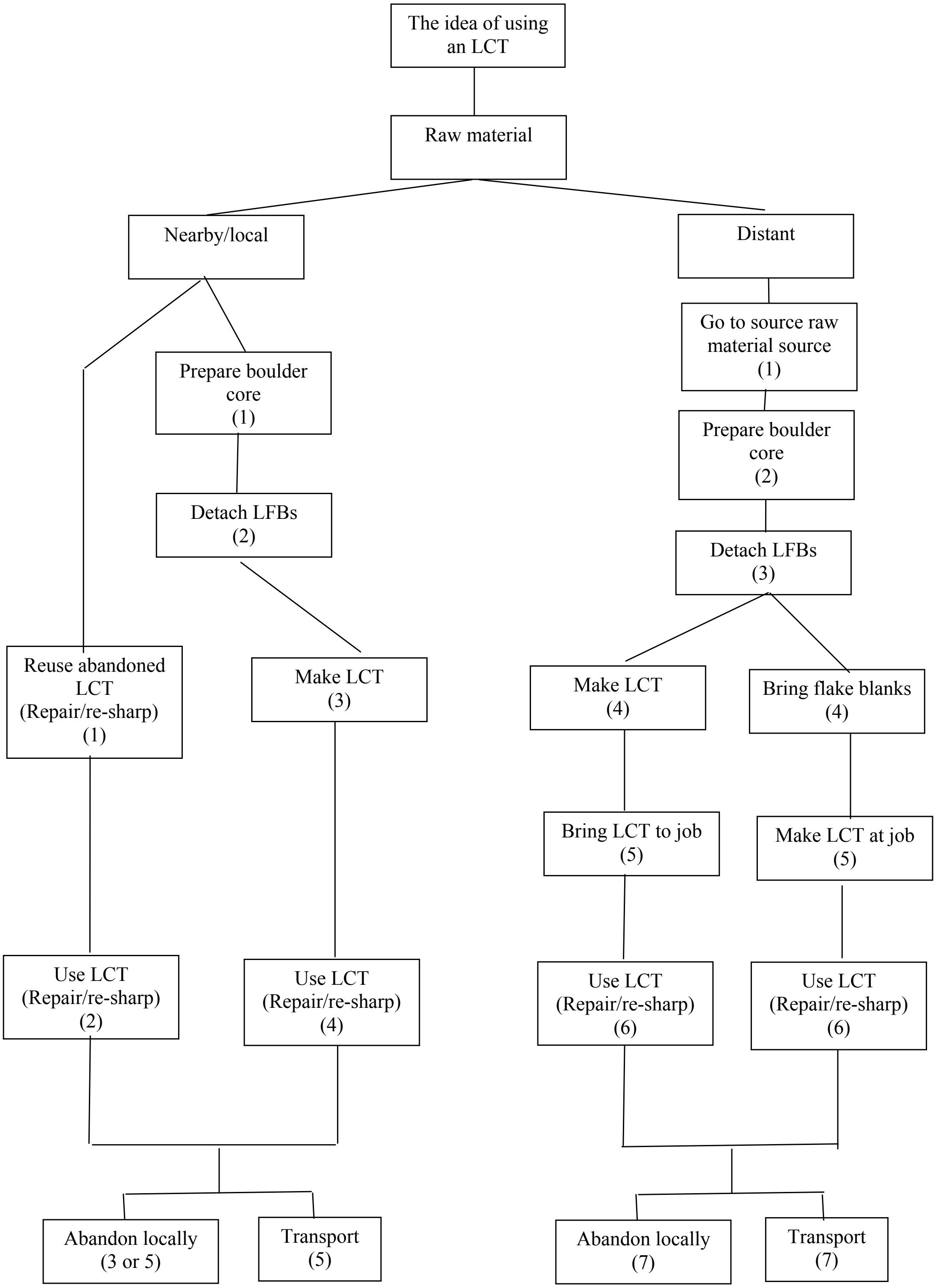

FIGURE 4. THE CHAÎNE OPÉRATOIRE FOR AN IDEALISED ACHEULEAN KNAPPING EVENT. FIGURES IN PARENTHESIS REFLECT THE LEVEL OF DECISION MAKING INCORPORATED IN THE ACTIONS CARRIED OUT UP TO THAT POINT

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(although they could be used as core-tools in some circumstances). An extensive knapping programme in which I was involved at Sterkfontein (McNabb *et al.* in prep) has amply confirmed and expanded the conclusions of Toth. The final shape of the core simply reflects the *choice* of the knapper to stop flaking at that point, for what ever reason. A few more blows and the core's shape would be entirely different. Consequently, core shape naturally drifts through a number of different permutations as knapping proceeds (personal observation). It is not that Toth and subsequent experimenters have proved that the Oldowan was a flake-based assemblage, rather these experiments show that it cannot be *automatically assumed* that core forms were deliberate. In my opinion the default interpretation ought to be that they were not. The knapping experiments of Toth and others imply that those who believe core tools were deliberately made will have to prove it, not the other way around. It certainly cannot be established on technological and manufacturing grounds.

In terms of the questions facing us in this paper then, I would suggest the above data supports the following interpretation. The makers of the Oldowan did not conceive of core morphology in terms of discreet shapes. In fact the concept of discreet tool types was not present in the Oldowan at all. Knapping was for flakes (Toth *ibid),* or just sharp edges in some cases (Kuman and Clarke 2000; Kuman *et al.* 2005). Some of these were retouched into a variety of smaller tools (themselves with no preconceived outline form). What was present in the minds of the Oldowan knappers was the *concept* of a sharp or retouched edge and the type of blank (flake, knapping fragment) which could support such an edge, as well as the process (alternate flaking of cobble) by which these could be made. Put another way, Oldowan knappers did not possess specific mental representations of the forms of the tools they needed to make, rather they held more generalised representations (concepts) in their minds of the kinds of edges that would get the job done.

None of the above, in my opinion, conflicts with an animal that has a sense of self and other. Nor would the making of such material culture necessarily require a full theory of mind and social relations built upon mind reading. Oldowan material culture could be produced by a creature with developed skills of mimicry, imitative learning, memory, and the ability to apply knowledge and adapt it to different circumstances (ie. an Oldowan knapper skilfully negotiating the problems inherent in different cobble shapes and rock types; or perhaps hunting the same species of animal in very different environments). The ability to mind read is not essential to any of this in my opinion.

But what of the Acheulean with its more complicated chaîne opératoire and LCTs? By comparison I would suggest that the Acheulean knappers were able to hold a mental representation – in this case a deliberately *shaped* tool. The proof of this is the LCT itself – a tool not just flaked, but deliberately thinned and deliberately shaped. They had the ability to hold a specific mental representation in their minds-eye. It was a reflection of the greater cognitive potential for engaging with complexity inherent within *Homo ergaster* as revealed in the Acheulean *chaîne opératoire* itself. Indeed, the idea of a flake-blank, the product of *debitage*, to be thinned and shaped and therefore conceptually *façonnage*, demonstrates the ability to hold one mental representation embedded within another. In other words, they were able to conceive of a distinctive stage in an LCT's manufacturing process, with its own end-product (flake-blank), yet not loose site of the fact that this was just a stage in the making of something else, the LCT itself. This implies cognitive levels beyond those displayed by Oldowan knappers. In my opinion this is entirely compatible with a hominin with a clear cut sense of self and other.

But readers will readily appreciate that having a well-developed sense of self and other is not the same as having a full theory of mind. Being aware of the other does not automatically imply a conscious awareness of the actual content of other's mind. Whereas I would suggest that the archaeological data for the Oldowan and Acheulean does suggest an ability to perceive and interact with the other, it does not necessarily imply a full theory of mind as described in text box 1, or by extension the kind of society that depends on mind reading as is the case with modern humans (see below).

The answer to the second question posed above is therefore yes.

At what point in human evolution does a sense of self and other give way to a theory of mind?

I will now turn to the first question posed above.

That modern humans have a fully developed theory of mind suggests that it has an evolutionary heritage. If this is the case then theory of mind has emerged since the split with the common ancestor of hominins and chimpanzees, since its presence in our closest evolutionary cousins is hotly debated (Gallese and Goldman 1998; Gallese 2005), if it is there at all. As explained in the text box, theory of mind is the equivalent of intentionality level 2. Dunbar (2004) has suggested that modern humans regularly operate at an intentionality of 5, at which level social relations are intimately entwined with mind reading.

> "Mind-reading is the activity of representing specific mental states of others, for example, their perceptions, goals, beliefs, expectations, and the like. It is now agreed that all normal humans develop the capacity to represent mental states in others, a system of representation often called folk psychology…."
>
> (Gallese and Goldman 1998, 495)

The Social Brain Hypothesis (Dunbar 1998; Dunbar 2003; Dunbar 2004) links group size to the evolution of the brain, implying that as the size of hominin groups grew over time, brain expansion was driven by the need to cope with ever more complicated social relations. Modern humans regularly engage with group sizes of 150 other individuals (Gamble 1999; Dunbar 2004). Extrapolating from these data, and that of modern extant primates with known group sizes, the Social Brain Hypothesis predicts levels of intentionality for various stages of human evolution. This was shown in figure 2. Australopithecines and Paranthropines achieve a basic theory of mind with level 2 intentionality, and an average group size predicted at c. 60 individuals. *Homo ergaster/erectus* achieves level 3 with a group size of c. 95-100, and *Homo rhodesiensis/heidelbergensis* achieves intentionality levels of between 3.5 and 4, based on groups of 120-130 or more (Dunbar 2003; 2004).

But these levels of hominin cognitive sophistication are predictions, based upon other predictions, namely estimated human, hominin, and primate group size, and brain size. Both of these can be difficult to predict. Moreover, figure 2 depicts mean values based on what are very small samples with large standard deviations. How genuinely these samples will reflect their parent population is not known. We must turn to the archaeological record and enquire if there is anything in the material culture of hominins that can be used to ground-truth these predictions.

That modern humans operate at or near intentionality level 5, with all of the communicative potential that language and the ability to manipulate abstraction implies is self-evident from looking at our own lives in our own social worlds. The implication that ancient populations of modern humans, the Cro-Magnon people, possessed the same capabilities is suggested by Palaeolithic art, which for many archaeologists is a clear signal that symbolic and abstract potential was present with the arrival of modern humans in Europe. The earliest modern humans in Europe date between c. 35 and c. 43 kya BP in radiocarbon years, an underestimation of the true calibrated age by 2 – 4 kyr (Mellars 2004). The material culture of these earliest European Cro-Magnon is the Aurignacian which first appears in eastern Europe at about 43 kya calibrated BP (Davies 2007). Some of the earliest art in Europe, cave paintings at Chauvet Cave, is dated to 32 kya (see Conard below for references on debate surrounding the dating). For me, the clearest evidence of abstract thought in the Palaeolithic art record is the ivory figurine of a lion headed man from Hohlenstein-Stadel, also Aurignacian (see Bahn and Vertut 1997 for a dramatic image of this object). It may well be part of a regional tradition of such figurine carving in the mountains of the Swabian Jura (Conard 2003). In that it reflects no known creature from the real world, and an unnatural fusion of humans and felines, it is a powerful demonstration of the ability to comprehend the other, and otherness. (In fact it shows an ability to conceive of the fusion of self with otherness). No objects similar to these exist elsewhere to my knowledge. So a very acute sense of the other was present in modern humans at least as much as 35 kya.

Outside of Europe the record for the abstract abilities of modern humans is less clear. No cave paintings are known from these earlier modern human phases. The famous inscribed ochre from Blombos (Jacobs *et al.* 2006; Henshilwood *et al.* 2009), and shell beads from the same layer are dated to 72 – 74 kya, and are assumed to be a product of modern humans. Even older inscribed ochre, dating to c. 100 kya, is now reported from the site (Henshilwood *et al. ibid*). The genetic record for modern humans suggests they emerge between 200 and 100 kya (determinations varying between c 190 kya (Oppenheimer 2009), c. 171 kya (Ingman *et al.* 2000), >130 kya (Forster 2004) for mitochondrial data). The skeletal record parallels this with the earliest examples of anatomically modern humans being from Omo Kibish at 195 kya (McDougall *et al.* 2008), and Herto at 160 kya (Clark *et al.* 2003). No art accompanies these finds.

In summary, the evidence for modern humans in Europe from almost the beginning of the western European Upper Palaeolithic does imply the presence of a theory of mind, and intentionality levels that correspond with the ability to comprehend symbolic behaviour and manipulate abstraction. Blombos extends this to a slightly earlier point in Africa, but beyond this data is currently lacking.

What about earlier hominins? The Social Brain predicts Neanderthals will have intentionality levels of 5 or just below. This would imply capacities equivalent to Cro-Magnon. The subject of Neanderthal cognitive development has been a long and sometimes bitter debate, one that is not necessary to restate here. Neanderthals did not produce cave art, or carve figurines as far as is known. They may however have possessed, or developed through enculturation with moderns, a sense of self (personal identity?) or aesthetic as suggested by the necklace and pendants from Arcy sur Cure (Hublin *et al.* 1996), although the Neanderthal status of these pieces is not without detractors (references in Hublin *et al. ibid*). The perforated and pigment stained shells from Cueva de los Aviones and Cueva Antón (Zilhão *et al.* 2010), dated to c. 50 kya, and therefore Neanderthal by implication, may also imply personal adornment through body decoration. At the very least this suggests a sense of self and other and, more likely, a theory of mind since personal adornment requires a sense of aesthetic that must have a shared basis (at least to some extent). But this is largely speculative, Crucially, just because a species is predicted to have a certain potential does not mean it will automatically realize it – an important point to note when interpreting figure 2.

I do not accept the Australopithecine face from Makapansgat (Bahn and Vertut 1997) or the Tan Tan (Bednarik 2003) and Berekhat Ram (Pelcin 1994) Acheulean figures as genuine art. Neither does the material culture record help us any. As noted above, the much quoted belief that handaxes become more refined and symmetrical over time has no substantial body of data to support it. The data for pre-modern hominins does not contain any robust evidence for hominin engagement with abstraction or symbolic activity, and therefore does not help us to pin-point when the emergence of theory of mind took place.

So the answer to the first question posed is a negative one. There is nothing prior to the appearance of *Homo sapiens* that will allow us to infer a theory of mind - at least the full theory of mind described in text box 1.

If the archaeological record cannot help us to identify when theory of mind began to emerge, what of other disciplines, can they help?

The neurological basis to theory of mind.

There has been considerable work in the last 15-20 years on the neurological basis of cognition which impacts upon theory of mind studies. The subject is too vast to review here, but excellent introductions are presented (Iacoboni 2005; Iacoboni and Mazziotta 2007; Grove and Coward 2008).

Louise Barrett and colleagues (Barrett *et al.* 2003; Barrett and Henzi 2005; Barrett *et al.* 2007) have suggested that primate society is actually underpinned more by behaviour reading rather than mind reading. In behaviour reading primates (research primarily based on monkeys) read physical clues from the behaviours of others which they intuitively understand. These clues come from bodily reaction to other individuals, similar reactions of others to objects, and the reactions of others to the agents' own actions. Comprehension is distributed across all of the actions that a group will perform since individuals, objects, and context can not be parsed. The understanding of individual behaviours here is rooted in an emotional empathy generated while observing contextualised action. It is a society of the here and now, not far removed from that suggested by Gamble (1999) in promoting a face-to-face hominin society set in a routinized landscape of habit. Any form of visual action would need to be interpreted literally at face value, and, I would add, a sense of self and other would be required. The key here is that the interpretation of meaning is solely based on reading visual clues in the physical world, not mind reading. Moreover, there is a neurological basis for behaviour reading that links the actions of others in the external world with the observer via the generation of an empathic sympathetic response to what is being observed. This is the mirror neuron system – MNS.

First discovered in macaque monkeys, the MNS is now recognised in humans as well (Gallese *et al.* 1996; Gallese *et al.* 2004; Gallese 2006). Mirror neurons represent neural architecture which creates an empathic reaction when an agent observes an external action, especially if associated with an object. When the MNS is firing it generates in the observer an unconscious sympathetic understanding of the action and its intention or context. The observer becomes consciously aware, via an empathic reaction, of a sympathetic relationship with what (and who) is being observed.

> "Even more intriguingly, there is evidence from monkeys and humans that both goal-directed intentions toward an object…[references omitted]…and communicative facial actions…[references omitted]…are encoded into perceptual representations in the same way. Thus, our mental representations of the world, the objects and individuals within it, are fundamentally linked to the actions that bodies perform in the world. This, then, provides us with a sound neurological mechanism by which concepts are physically grounded in bodily action." (Barrett and Henzi 2005, 1870; references quoted by the authors omitted by me.)

So the MNS represents a neurological basis for focusing the attention on external action and being able to contextualise it. It could easily underpin the behaviour reading of hominins as Barrett and colleagues imply it does for primates, and without requiring a full theory of mind. The MNS is especially attuned to the manipulation of objects, and given the fact that neuronal pathways can adapt to changing circumstances, there is evidence to suggest that engaging with and manipulating objects can strengthen the existing neural pathways specifically attuned to objects, or create new ones (Ferrari *et al.* 2005; Catmur *et al.* 2007; Iacoboni and Mazziotta 2007; Grove and Coward 2008). Macaque monkeys, not natural tool users, became habituated to tool use in captivity and developed the MNS architecture that responds to observed tool related acts. *The ability to contextualise external signals from others and their relationship to objects would be a critical element in a behaviour reading society*. By enchaining sequences of actions, all related to a single goal, the MNS is able to interpret the broader meaning of those actions (Gallese 2007). Emotional states can be read easily, and concepts can be understood because the actions associated with them elicit sympathetic responses in the observer, and these provide the potential for understanding other's actions. That the Oldowan as posited here is compatible with a behaviour reading society will not be a surprise at this point.

But some of the more enthusiastic MN researchers have argued that the MNS underpins the development of theory of mind. At the very least, they suggest that the presence of the MNS in monkeys (and presumably apes) implies that the primate version is similar to the evolutionary precursor of that in hominins and humans. This is rooted in simulation theory, a term psychologists use to describe how minds learn about other minds, and then act on that knowledge.

"The notion of simulation is employed in many different domains, often with different, not necessarily overlapping meanings. Simulation is a functional process that possesses a certain representational content, typically focusing on possible states of its target object" (Gallese 2005, 41).

Descriptions differ between researchers, but the essence of the idea appears to me to be the same as that for theory of mind. Simulation theory (only one of a number of competing theories about the mind, but the only one to be discussed here) was developed independently of MN research. But Gallese and colleagues convincingly show how the MNS maps onto and complements this hypothesis (Gallese and Goldman 1998; Gallese 2005; Gallese 2006).

But simulating an action is not necessarily the same as truly understanding that action. This requires an additional element be added to the equation.

> "The argument that seems to suggest the presence, in non-human primates, of elementary
>
> forms of mind-reading abilities comes from the discovery of deceptive behaviour…Deception is particularly relevant here, since deceptive behaviour calls for the existence of second-order intentionality, and therefore for the capability to attribute mental states to conspecifics." (Gallese and Goldman 1998, 499).

Gallese and Goldman (*ibid*) admit the evidence for deception in non-human primates is limited and hotly disputed (see also Barrett and Henzi 2005 for this, and references therein). However it is the presence of deceptive behaviour, a proxy for genuine comprehension in mind reading, and present within the primate repertoire, that implies a similarity and possible evolutionary precursor to the hominin/human theory of mind.

Gallese (2007; see also Barrett and Henzi 2005) develops an idea he calls embodied simulation theory. All actions are understood by reading the body and via the MNS are understood through sympathetic bodily responses to what is observed. Therefore all action, including its context, is only really comprehended through the body. Emotions expressed by others are read and then experienced by self as the MNS creates a bodily awareness (simulation) of the same emotion observed.

> "By means of embodied simulation, we do not just "see" an action, an emotion, or a sensation. Side by side with the sensory description of the observed social stimuli, internal representations of the body states associated with these actions, emotions, and sensations are evoked in the observer, "as if" he/she would be doing a similar action or experiencing a similar emotion or sensation. (Gallese 2006, 20)

For example, viewing facial expressions of disgust in someone can trigger a sympathetic response in the observer.

> "When we see the facial expression of someone else, and this perception leads us to experience a particular affective state, the other's emotion is constituted, experienced and therefore directly understood by means of an embodied simulation producing a shared body state. It is the activation of a neural mechanism shared by the observer and the observed to enable direct experiential understanding. (Gallese 2006, 19)

Gallese and his colleagues suggest that this emotional mirroring is what lies at the root of interpreting the content of other minds. The key is emotion. If I have understood correctly, the MNS allows the observer to (consciously?) empathise with the emotional state of the observed. The sympathetic bodily understanding elicited within the observer *is therefore the same as mind reading*.

But I perceive a problem here. The observer is actually interpreting an emotional state, but this is not the same as mind reading were by an agent consciously interprets the desires and aspirations within another mind, something that modern humans do intuitively. Unfortunately then the neurological basis for behaviour reading does not help us in assessing whether mind reading contributed to Acheulean society, or when theory of mind first occurs in human evolution.

The implication of Gallese's work is that theory of mind must have deep evolutionary roots since it is present in monkeys and apes (arguably?). But as noted earlier, having the potential for something is one thing, realising it is an entirely different matter. In my opinion Gallese's embodied simulation, and Barrett's behaviour reading are separate sides of what is essentially the same coin – behaviour reading. But there is a world of difference between emotionally comprehended bodily action, and an actual rationalised interpretation of the contents of another's mind. These are very different things. Although embodied simulation, driven by the MNS, may lie at the root of the later development of theory of mind, I do not think that it can be the same as mind reading in the sense that it is used in text box 1.

Conclusions.

At the outset of this paper I made it clear I was speculating about how Acheulean knappers constructed their social relations. My aim has been to engender debate, nothing more. I have assumed that building a society in the Lower and Middle Pleistocene was predicated on visual display because the hominins responsible for the Acheulean did not possess the capacity for fully developed language and abstract comprehension.

I have tried to establish that the Oldowan is compatible with a primate-like behaviour reading social pattern, one predicated on a specific neural framework that accentuates the importance of visual action and display. A clear sense of self and other is implied by the very fact of Oldowan tools, the skills for which were learnt in a social environment. Stone tools imply an ability to objectify the world and what is in it. This includes other hominins. So a sense of self and other facilitates social interaction on the basis of behaviour reading whose efficacy is engendered by embodied emotional simulation. This would be particularly effective if the empathic response of the MNS was to familiar and repetitive actions (*sensu* Gamble 1999), and in the case of the Oldowan enacted in familiar locations. The empathic reactions of hominins would be particularly responsive to familiar gestures and procedures. There would be a common intuitive understanding of what a tool was and which edges would be suitable for getting the job done, but, I argued, no fixed concept of how a tool should look.

This will represent the default hominin condition after, say, 2.0 mya. But is the Acheulean similar, or is there more to it? Is this a mind reading society? Is the ability to hold a conceptual representation of a tool (the LCT) a viable proxy for the presence of theory of mind? I suggest that the answer is no. At the very least what the LCT does represent is a more developed ability to objectify the surrounding world and the others of your kind within it. Or in other words, the Acheulean shows increased cognitive complexity and a much more developed sense of self and other, but it still does not show theory of mind.

In text box 1, a full theory of mind, as present in modern humans, involves three things; an understanding that the agent has a mind and is able to reflect on its contents; an understanding that others have a similar mind and are equally capable of self-reflection; an understanding that others' minds can hold belief states that are different to that of the agent. These three represent intentionality level 2 and the basis of social relationships based on mind reading.

It will be recalled that a number of social predators, who engage in co-operative hunting enjoy rich and complicated social lives. African wild dogs, lions, hyaenas are all cases in point. No claims for theory of mind are made for these animals. Chimpanzees, who may approach theory of mind, are equally adept at socially co-operative hunting and show all the hierarchical agent positioning of the other less cognitively developed social hunters. They too have rich cultural lives. So a full theory of mind is not a prerequisite for hierarchical co-operative sociality. I suggest behaviour reading, particularly in a more cognitively developed hominin like *H. erectus* or *H. heidelbergensis*, could accommodate quite complicated social networking while still remaining in the here and now for which visual display would remain the key mechanism of information exchange.

It will be evident form the above that I have concentrated in this paper on only one aspect of the VDH, namely the basis for empowering the belief that visual display will be the major medium by which meaning and information content were transmitted. The MNS is a significant plank in this hypothesis. I have deliberately avoided the subject of what information was being transmitted. I have also avoided discussing imitation learning, which will be a key component of the VDH. This too is recognised to be heavily dependent upon the MNS (Iacoboni 2005). Sexual selection, based on specific visual display, may also be underpinned by the MNS, and is in my opinion another important component of the VDH. The importance of a sense of time in relation to a sense of self and other is equally significant, what Barrett and Henzi (2005) call the ability to represent the self and other in differing socio-temporal locations.

Finally, a number of commentators and reviewers have made very cogent observations on this paper at various stages in its development and there are issues raised I think it important to confront, One repeated comment is that if there is no proof for any of the above why bother to ask these questions in the first place? I have some sympathy with this view. That the makers of the Acheulean material culture repertoire were social animals and must have constructed their social relations in some way seems self-evident. We study the culture of other species, why not those that made the Acheulean? In this sense I think the topic is a legitimate area for study. We investigate many things we don’t yet understand. It may well be that other students of the Acheulean have more appropriate data sets, or can suggest approaches that are more fruitful. In that case the purpose of the VDH is satisfied, dialogue has begun. Another comment has been there is no hypothesis to test and no predictions are made? Again I have sympathy with this. In truth, the term visual display hypothesis has been retained because it has a nice ring to it.

A particularly cogent comment has been that by comparing the Acheulean with the cognitive levels of modern humans, the Acheulean will always seem by comparison inferior and never achieve its own voice. I agree, but it should be noted that the difference is nonetheless real. We should not forget that the brains of Lower and Middle Pleistocene hominins were smaller than modern humans and may have been organised somewhat differently. This implies there will have been genuine differences between ourselves and earlier hominins. The comparison with modern humans serves to highlight those differences. I am not arguing that ancient hominins did more or less what we do, but didn't do it as well. I am arguing there are real differences at work, and the comparison with moderns highlights the scale of the potential differences.

Lastly, one reviewer noted the construction of the argument was of the 'house of cards' variety. Disprove one part of the argument, and the other cards all fall apart. I fully accept that criticism. If students of the Acheulian are able to provide alternative interpretations with better supporting data, then the VDH has served its purpose.

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THE IDENTITY MODEL: A THEORY TO ACCESS VISUAL DISPLAY AND HOMININ COGNITION WITHIN THE PALAEOLITHIC

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Abstract

The question of the development of hominin social communication is a subject that is of continual interest to researchers of human development, behaviour and cognition. Language development has in particular been related to studies in cognitive capacity and the ability for mind reading, often termed a theory of mind (ToM). There has only really been one successful attempt to correlate a cognitive scale of complexity that incorporates a ToM, in the form of intentionality orders, to the archaeological record and hominin phylogeny, and that is the Social Brain Hypothesis (Aiello and Dunbar 1993; Dunbar 1996; 1998a; 2003; 2004). However, a method is still lacking that allows a correlation of the orders of intentionality (and by inference a ToM and language development) to the archaeological signatures that represent the physical expression of hominin behaviour. This paper is primarily concerned with introducing a new theoretical framework – termed the identity model – which suggests a heuristic correlation between a scale of cognitive acuity, hominin behaviour and the archaeology. The aim of this paper is to refresh debates corresponding to hominin behaviour by illustrating a different and innovative approach in relating the Palaeolithic record to cognitive development, and not to make definitive statements.

Introduction

Accessing the cognitive potential of our hominin ancestors has been a long standing dilemma within Palaeolithic studies (Mithen 1996; Carruthers and Chamberlain 2000; Lewis-Williams 2002; Dunbar 2004; Gamble 2007 to name but a few examples). What I propose in this paper is a new theoretical perspective, the identity model. The identity model is a theoretical construct that assesses the cognitive potential of ancient hominins through concepts of identity linked to the body and material culture apparent within the Palaeolithic record by examining their role in social communication. I also present new definitions for social communication and the body which break away from the Cartesian attitudes that have dominated studies in archaeology for so long. I emphasise at this point that this paper is a theoretical perspective intended to encourage lively discussion and debate rather than make categorical statements on hominin cognitive abilities, social constructions or behavioural characteristics.

The background for the identity model focuses on the Social Brain Hypothesis (SBH) (Aiello and Dunbar 1993; Dunbar 1996; 1998a; 2003; 2004), a biological predictive model relating to *Homo sapiens* brain encephalisation where increasing group size and the subsequent byzantine social pressures required to maintain group cohesion provided the selection criteria for increasing brain size. The SBH was the first arena where orders of intentionality and ToM (Dunbar 1998a) were applied to the development of hominin social communication and the evolution of language. The identity model offers an insight into how the increasing cognitive abilities of hominins (articulated as orders of intentionality) may be expressed within the archaeological record through systems of social communication such as visual display (see McNabb this volume) and the construction of individual and group identity. However, before expanding on the identity model, it is necessary to provide some background information on the orders of intentionality, ToM, the body and constructs of identity.

Background information: orders of intentionality and Theory of Mind

In order for social interactions (of any degree of complexity – gestural to grammatical) to work as a successful social bonding system, the sender must be able to anticipate how a receiver will interpret the sent message, and *vice versa*. In other words, the sender must be able to access the mental state of the receiver. Dunbar highlights that in order to achieve a true understanding of speech and language, a ToM is required

(Dunbar 2004). A ToM may be defined as the ability to comprehend the mental state of another's mind but also to recognise that the mental state of another's mind may differ from the mental state of one's own mind.

ToM in humans (and primates) has been tested by using first - and second-order false belief tasks - tasks that relate to the understanding that different people have different thoughts regarding the same situation (Baron-Cohen 2001) - where subjects are tested in their inference of one or more embedded mental states. I will briefly describe this using an example of Xi the hunter. First-order tests refer to the mental state of one individual: what Xi *thinks*; second-order tests infer two individual mental states: Xi *thinks* that O'wa *believes*. First and second-order false belief states are linked to first and second-orders of intentionality - 'intentionality' being a term that refers to the mental states held when one is aware of the contents of one's own mind through beliefs, desires and intentions (Premack and Woodruff 1978; Dunbar 2004: 45). The crucial point about orders of intentionality as proxy measures of cognitive ability is that a great deal of complexity may be inferred even if only a small number of different belief / mental states are linked (Premack and Woodruff 1978). For example, Xi *thinks* that O'wa *believes* that Shasa *knows*. The number of differing belief states (italicised) indicate the order of intentionality. Modern humans operate at a comfortable level of five with an upper extent of six (Dunbar 2004). Orders of intentionality and a ToM have been directly correlated with ToM corresponding to a second order of intentionality. In this paper I shall view a ToM as a critical factor of the human condition, essential to the cognitive separation in primate versus human evolution (expanded below), whilst orders of intentionality are used as an ordinal scale of cognitive complexity in relation to the behavioural and material archaeological record of the hominin clade.

As has been established, ToM and orders of intentionality allow the individual to mentally interpret the intentions behind a deliberate action. Without a ToM, agents are limited to reading the superficial behaviour which leaves the individual or group open to misinterpretation and deception (Dunbar 1998b). It should be clear that without a ToM, language as we know it today would not exist. It is possible that there would be forms of verbal communication, but these would likely be limited to factual statements conveying pragmatic information, with no works of fiction, abstract ideas, poetry or embellished oration (Dunbar 1998b). It is certain that fully-developed grammatical language did not emerge through the hominin psyche at the same time as a ToM was attained. Rather, I would suggest that a more holistic gestural language, based around the body as a canvas for social communication through visual display, developed into a combination of meaningful utteral and gestural communications as developmental precursors to fully grammatical language.

The body is vitally important in modern human communications today, with people often taking conscious and subconscious cues as to the emotional state of the individual by looking at facial expressions and body posture (Meeren *et al* 2005). Primates in turn gauge the goals and intentions of others by reading their body posture or facial orientation (Tomasello and Call 2008). The approach adopted in this paper is to explore how the body has been an active agent in the development of hominin communication throughout our evolutionary development.

What do I mean by social communication?

Before detailing how the body can be used as a vehicle for social communication, it is important to define social communication. The word 'communication' describes a range of behaviours of varying degrees of cognitive intent and complexity. Indeed, systems of communication are found at all levels within the animal kingdom – for example, the honey bee shaking signal (Nieh 1998) - where communication can be defined as involving the "targeted exchange of information between a sender and a receiver, using a mutually agreed code" (Zanker 2007: R806). Communication defined in this way can encompass any form of communicative behaviour by any animal, such as a macaque alarm call or a modern human conversation. These two forms of communicative behaviour do not require the same cognitive abilities, so a tighter definition of 'communication' is needed. One way to differentiate between the egocentric, dyadic and context specific communications of animals, specifically primates (Flack and de Waal 2007), and the complex abstract communications of humans, is to define communication in relation to ToM.

Baron-Cohen (1999) describes eight behaviours that are not possible without a developed ToM, including 'intentional communication'. Intentional communication was here defined as "communicative acts that are produced in order to change the knowledge state of the listener" (Baron-Cohen 1999: 262). It focused on the specific idea that a ToM is required for intentional communication, because, in order to change the knowledge state of a listener, you need to conceive that the listener has a knowledge state (or mind) that can be changed (Baron-Cohen 1999). Arguably, the predator-specific alarm calls of bonnet macaques (Coss *et al* 2007) or the variable gestural repertoire of bonobos (Pollick and de Waal 2007) are examples of primate 'intentional communication' designed to change knowledge state. However, these primates do not have a ToM because the success of these communications are entirely dependent on the context of the signaller and receiver. Once a ToM has been achieved, social communications can move beyond the dyadic dynamics into the triadic, where individuals may communicate about something beyond the visual or auditory context of the signallers and receivers. ToM induces a shift in the mental representation of the world, from a perspective grounded in the egocentric, context-specific present, to the other-centric, context-independent past, present and future.

A ToM allows the communication of information about a third party figure whether present or not, and allows perception and comprehension of the triad of time (something happened in the *past*, something happens in the *present* and something that will happen in the *future*). The predator-specific alarm calls of macaques are context- and time-specific: the predator is visible in the present, so the alarm call is sounded (Coss *et al* 2007), and the grooming gestures of bonobos, although not context-specific in action (Pollick and de Waal 2007), are context-specific in intention (of the signaller) and, crucially, interpretation (by the receiver). Modern humans, however, do have the ability to communicate triadically; we can communicate about an individual or object without the dyadic restraint of context or time. Therefore, I propose a redefinition of Baron-Cohen's (1999) 'intentional communication' to clarify the role that a ToM bestows on social communication:

Theory of Mind communication – a communicative act produced by a signaller in order to change the knowledge state of the receiver *without necessary recourse to the presently-inhabited context*.

By redefining intentional communication in this way it is possible to highlight the differences between animal and human communications. Therefore, when I refer to social communication in reference to hominins, I refer to the ToM communication with all of the possibilities it entails as defined above. In reference to primates, I refer to the simpler context-specific, dyadic communications currently seen within non-human communication (body language through the body's inhabited context).

What do I mean by the body?

Having touched on the importance of the body in modern human and primate communications, it would be beneficial to define exactly what I mean by the body. Attempting to define 'the body' is a difficult task because the term itself can have a number of diverse meanings depending on individual theoretical preferences. Critically, social sciences have tended to view the body as a biological canvas which attains significance through cultural factors (Lock 1993). In this light, some scholars follow Grosz's definition of the body as a:

"concrete, material, animate organization of flesh, organs, nerves, skeletal structure and substances, which are given a unity and cohesiveness through psychical and social inscription of the body's surface" (Grosz 1995: 104 cited in Joyce 2005: 141).

This definition is centred on the biological aspects of the body while acknowledging that social factors may play a part in interpreting how the body is read from the 'surface'. Grosz seems to imply that it is the external social world that defines the body. However, the body is much more than the biological components that allow it to function in a social world, and the body is not dependent on the external social world in order to exist or to be a cohesive whole. Alternatively, Lock iterates that "bodily practices mediate a personal realisation of social values" (Lock 1993: 137), where the individual defines and constructs the body (adopting or rejecting external social rules), before the peripheral social world imposes its own definition. Indeed, it is the individual and the living body that lends, "substance to the social distinctions and differences that underpin social relations, symbolic systems, forms labour and quotidian intimacies" (Moore 2000: 317).

Therefore, I would suggest that the body should be viewed as a vehicle that enables a corporeal grounding for the life form we call 'human', a creature that exists in both the physical and conceptual realms, with the body not only playing an essential role in defining what it means to be human (Sofaer 2006) but also in bridging the gap between the physical and metaphoric worlds that we construct around ourselves. The body is both a container and an instrument (Gamble 2007), which allows us to relate to the essence of what it is to be human through a medium (the body) of which we have an inherent understanding. Sofaer states that the body:

"is not just an instrument that…carries out…the orders of an insulated and 'disembodied' mind in which meaning and intentions reside" (Sofaer 2006: 42),

Here Sofaer correctly describes that the body itself is not a single unit, but rather is made up of a multiple number of components both physiological and conceptual. Therefore, a definition of 'the body' must remove the Cartesian dualistic view of the body and the mind as two separate and independent entities. Instead the definition should take into account all aspects of the physical and conceptual worlds that the body inhabits. Subsequently, I regard the body as:

The body - a holistic vehicle containing the biological components that constitute its physical structure (skeleton, nerves, organs, muscle etc) integrated with and dependent upon, a conceptual cognizant state (the mind) that both constructs and is constructed by the world (social and physical) in which it inhabits.

As such, the body is both a receptacle and an agent capable of creating a physical *and* abstract environment which it occupies. Using such a definition allows us to begin to understand how the body's role in hominin social communications becomes increasingly complex as cognitive ability, driven by ever more byzantine social communications, correspondingly intensifies. The body is also crucial in developing a comprehension of self and other, by creating a physical difference between the two. However, there must also be a conceptual awareness of self and other which I believe is primarily informed through constructs of identity, which I shall expand upon below.

Identity: a vehicle to self awareness

Archaeology as a discipline has unconsciously and consciously been dealing with issues of identity since the beginning of the discipline. Through the creation of typologies (such as Bordes 1961; 1972) and archaeological 'cultures' (such as Childe 1929), archaeology has created, defined and imposed chronological cultural boundaries on material culture and human life-ways (Shepherd 2003), constructing and imposing identities on aspects of the human past through the simple process of labelling and classifying. Questions of identity in archaeology allow a discourse with other academic fields such as psychology, philosophy, geography, biology and with the wider public audience in general (Meskell 2002). Psychology is one particular area where studies of identity have come closest to placing identity into a testable system of empirical research (Stryker and Burke 2000).

Examinations of identity vary enormously (see Banaji and Prentice 1994; Stryker and Burke 2000; Devos and Banaji 2003; Chen, Boucher and Tapias 2006 for basic reviews and bibliographies); however, there is a broad consensus that individuals define themselves in relation to their associations with individual 'others' and larger collectives (Greenwald and Breckler 1985; Breckler and Greenwald 1986 cited in Brewer and Gardner 1996: 83). This view of identity essentially dictates that the self is created and defined from the actions and reactions of the 'other' in relation to the self in three ways: the individual self, the relational self and the collective self. The assumption is here that the three identities of the self co-exist within the same individual yet may be separately defined (Sedikides and Brewer 2000). The individual self depends on comparing the self to an ‘other’ on an individual basis, elevating or ensuring the self’s differentiation from the surrounding ‘other’ (Markus 1977; Brewer and Gardner 1996; Sedikides 1993; Sedikides and Brewer 2000). The relational self is primarily concerned with personal attachments with the purpose of enhancing the ‘significant other’ (Brewer and Gardner 1996; Sedikides and Brewer 2000). The collective self focuses on formal relationships with others that have a common association to a group. The collective self’s incentive is the enhancement of the so called ‘in-group’ (the group that the self belongs to) versus the ‘out-group’ (any other group or collection of individuals that are external to the ‘in-group’) (Brewer and Gardner 1996; Sedikides and Brewer 2000).

From the three classes of the self it seems that self and identity are not static concepts, but fluid notions that shift according to the social interactions of the individual in relation to the single or mass ‘other’. The external social world does indeed play an important role in how individuals access and construct identity; however, an individual’s identity is not *entirely* constructed or informed by these interactions. The individual always has a choice to either accept or reject the identity that the ‘other’ ascribes to them. Indeed, individuals as active agents within their environment can not only accept or reject the identities that the external ‘others’ assign to them, but they also have the power to change and adapt the imposed identities of the ‘others’ to fit their own perception of their own identity. This can be related to the idea of ‘symbolic interactionism’ (Cooley 1902; Thomas 1923; Mead 1934; Schlenker 1985), where “people are not just passive reactors to situations, programmed by society with fixed action patterns” (Schlenker 1985: 17). The individual is an active agent in the construction of the social world and should not be forgotten when discussing the construction of the individual’s identity and self within the world.

Furthermore, the psychological classes of self described above only seem to consider the ‘mental self’, failing to acknowledge the physical embodiment of the individual, relational and collective selves. As with definitions of the body, the self must be seen as a construction of the body *and the mind*. Being the fabric upon which the understanding of the ‘self’ and ‘other’ is written, the body relates to the construction of identity by acting as the porous interface through which the individual, relational or collective self interacts with the abstract and physical worlds that surround it. The body separates the ‘other’ from the individual self: it is the book where the reactions of the ‘significant other’ are read (and constitute the building blocks of the relational self); and the bodies of the in-group form the physical boundary that separates the out-group of the collective self. Indeed, identity acts as the mechanism by which the ‘self’ becomes a realised fusion of body and mind. The realisation of identity becomes the vehicle for conscious self awareness. Conscious self awareness in turn opens the road to a ToM and to higher orders of intentionality.

The Identity Model

The identity model put forward here allows archaeologists to measure the cognitive potential of hominin species based on an understanding of the body through the material and behavioural archaeological record as opposed to predicted brain or group size. It assumes that there are a minimum of seven categories of identity, each requiring a certain degree of cognitive complexity measured through the orders of intentionality. The seven categories of identity:

Take into account both individual and group action in their construction.

Fit comfortably within the three psychological classes of self described above.

Relate to evolutionary theory through a correlation to orders of intentionality laid out in the SBH.

Directly acknowledges the importance of the body not only in identity construction, but also in identity perpetuation.

I must stress here that the identity model offers a theoretical position in which the body and material culture may play a part in social communications, both lingual but predominantly non-lingual (as the majority of hominin communications would have been – and still are – non-lingual and centred around visual display).

The categories of identity are summarised in figure 1and will be defined below.

Internal identity – is the *comprehension* of the body and mind as the single entity of the self. Self being an internally sentient organism with a conscious realisation of this state of mind. The internalisation of such a mental state means that an individual's internal identity is only truly known to them and therefore cannot be viewed or accessed by the other.

Internal identity is both the prerequisite and the vehicle to ToM. The realisation that the body and the mind constitute the 'self' is not an inherent comprehension; individuals must *reach* a conscious understanding that this is the case before progressing along the cognitive scale. I suggest here that the realisation of an internal identity is the vehicle to attaining a ToM and is therefore a vital step between first and second-order intentionality. The way we view another separate Ego is entirely informed through internal identity. The internal identity is in turn informed through the exposures of the 'self' (body and mind) to the experienced world. Every individual's exposure to the experienced world will be different thereby informing different internal identities for each individual. It is this difference that creates the discreet entities encapsulated within each individual. Following this reasoning, although extant primates and other mammalian have first-order intentionality, unlike modern humans they do not have a realised / conscious sense of self or a realised internal identity; therefore they are not able to reflect on the contents of their own minds. I believe this offers one possible description for why non-human primates have yet to break the ToM barrier.

Subsequent categories of identity can only exist once the ToM barrier has been breached and second order intentionality (at minimum) is secured. The reason for this is that all the additional types of identity relate to the individual's conception of the 'self' and the 'other'.

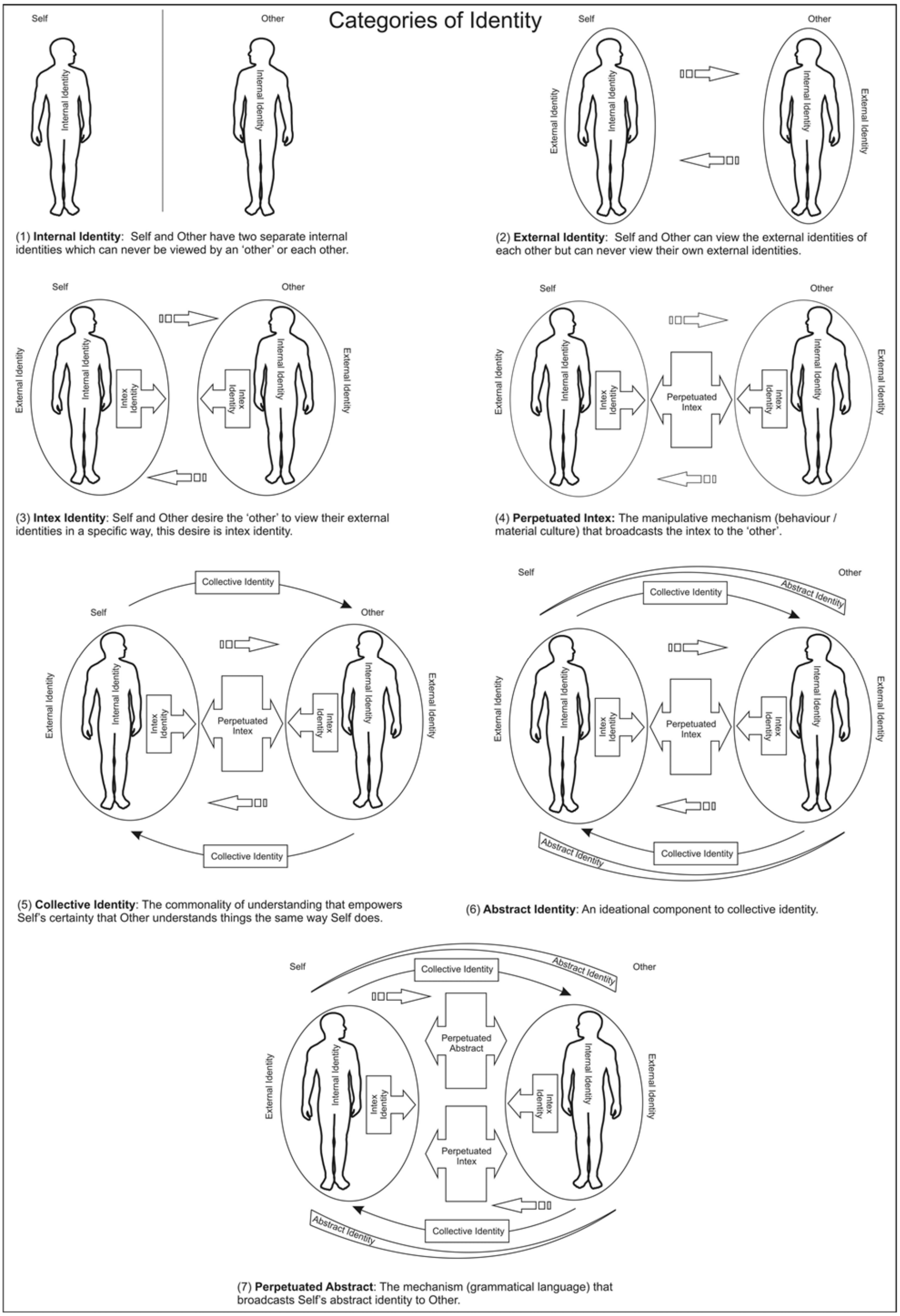
External identity – is the external view of the other by the self (and *vice versa*). The external identity is the identity created by the self for the other as a scaffold when accessing other's mental state.

External identity is the acknowledgement by self that the other has a mind similar to self's and may hold views that are similar or different to self. As self is able to reflect on their own minds' contents, then self is aware that other can do the same. Therefore, the self constructs an identity for other (external identity) as a mechanism to allow the self to access the intentions of the other. In order to be able to access the mind of the other, a ToM must be achieved.

Intex identity – is the internal to external view of the self (**intex** = **int**ernal to **ex**ternal). This category of identity differs from external identity in that intex identity is how the self would *like* others to view it, whereas external identity simply acknowledges others' will have views of the self (and *vice versa*).

The intex and internal identities are not necessarily mutually exclusive; an individual could wish to project an intex that is very different to their actual internal identity, depending on the social situations of individual. However, desire alone will not manipulate the view of the external identity – action is required. Therefore an external mechanism must be in place to broadcast the desire of the intex identity to an external observer. This mechanism is encapsulated within the fourth category of identity:

Perpetuated intex – is the mechanism by which intex is propagated or broadcast through behaviour and material culture to the other. Perpetuated intex deals with the use of the body and / or material culture to *manipulate* the projection of the intex to the other in such a way that this increases the chances that the other will accept the intex that the self wishes to project.



(1) **Internal Identity**: Self and Other have two separate internal identities which can never be viewed by an 'other' or each other.

(2) **External Identity**: Self and Other can view the external identities of each other but can never view their own external identities.

(3) **Intex Identity**: Self and Other desire the 'other' to view their external identities in a specific way, this desire is intex identity.

(4) **Perpetuated Intex:** The manipulative mechanism (behaviour / material culture) that broadcasts the intex to the 'other'.

(5) **Collective Identity**: The commonality of understanding that empowers Self's certainty that Other understands things the same way Self does.

(6) **Abstract Identity**: An ideational component to collective identity.

(7) **Perpetuated Abstract**: The mechanism (grammatical language) that broadcasts Self's abstract identity to Other.

FIGURE 1. THE SEVEN CATEGORIES OF IDENTITY WITHIN THE IDENTITY MODEL.

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Perpetuated intex deals with the deliberate manipulation of how the Other views the external identity of the Self in relation to the intex identity (i.e. Xi wears a necklace of lions teeth to prove to O'wa that he is a courageous hunter of some prowess, yet he actually plundered the teeth from a carcass of an elderly lion previously despatched by hyena). Both intex and perpetuated intex fall within a minimum of third to fourth-order intentionality bracket where the self is able to take into consideration that three or four states of mind are involved within the identity propagation.

The use of the body is vital for the propagation of the intex because it is the body that manipulates the perpetuated intex in its projection to the 'other' through visual display in a non-lingual society. In many ways, the body forms the link between intex identity and external identity, the body being one of the vehicles for projection of intex. The manipulation of the body in perpetuated intex is achieved through visual display with a potential incorporation of material culture into the display. Through the creation process, the perpetuated intex of the creator becomes embodied within material culture and will remain so through the material culture's history. With perpetuated intex, material culture begins to take on an additional, culturally-significant meaning.

The use of the body and material culture in the context of third- to fourth-order intentionality relates to physical body manipulations such as gesture or visual displays, in which material culture is involved in a non-utilitarian but culturally significant role (such as the supposed role of symmetry in handaxes – Saragusti *et al* 1998). The body becomes the context and the engine for the effectiveness of perpetuated intex. In order for the manipulation of the perpetuated intex to carry meaning across to other from the self, the self must be sure that the other will correctly interpret the intended meaning within the perpetuated intex. Culture is the framework that ensures standardised meaning is present in perpetuated intex.

In order for culture to impose a standardised meaning within a social structure, there must be a framework of common understanding. This framework of understanding is the fifth category of identity described here:

Collective identity – is the commonality of understanding (culture) that empowers the self's belief that everyone understands things the way self does. Collective identity therefore creates and propagates culture and in turn culture creates and propagates collective identity.

Collective identity is informed by the internal, external, intex and perpetuated intex identities of all of the individuals involved in the identity propagation, and by the internal and external identities of the receivers (figure 1). Because of this, culture / collective identity can either be accepted or rejected by individuals who subscribe, or not, to the collective identity put forward by the one or many. Similarly, due to the uniqueness of each internal identity/intex and perpetuated intex and their relationship to collective identity, culture / collective identity has the potential to change as each individual propagates the culture / collective identity in relation to their own internal identities: essentially a form of 'cultural drift'. Collective identity involves groups as well as individuals within identity propagation; collective identity is therefore situated within a minimum of third- to fourth-order intentionality. The commonality of understanding allows the material culture production involved in perpetuated intex to be broadcast to and understood by a range of audience scales – individuals and groups - and as such informs the construction and propagation of the collective identity.

In order for collective identity / culture to develop beyond a commonality of understanding, constrained by behaviour governed by visual display and an embodied material culture, an ideological scaffold must be in place. This scaffold is the sixth category of identity:

Abstract identity – is an ideational component to the commonality of understanding within collective identity. Abstract identity is a conceptual framework that, once attained, creates and propagates collective identity, and in turn, collective identity propagates and creates abstract identity.

Abstract identity is concerned entirely with a conceptual component of collective identity / culture. As such, abstract identity is informed by collective identity (and all the identities involved therein), and therefore may be accepted or rejected by individuals or groups depending on whether the receivers subscribe or not to the collective and abstract identities offered by the propagators. Collective identity is an integral component of the abstract identity, and once an abstract identity has been achieved, abstract identity becomes a key constituent of collective identity.

Abstract identity cannot endure as a purely ideological construction; it must be represented in the physical world – perpetuated by individuals acting through a collective framework. Therefore, a mechanism must be in place to broadcast the abstract identity to (an) external observer(s). This is the seventh category of identity:

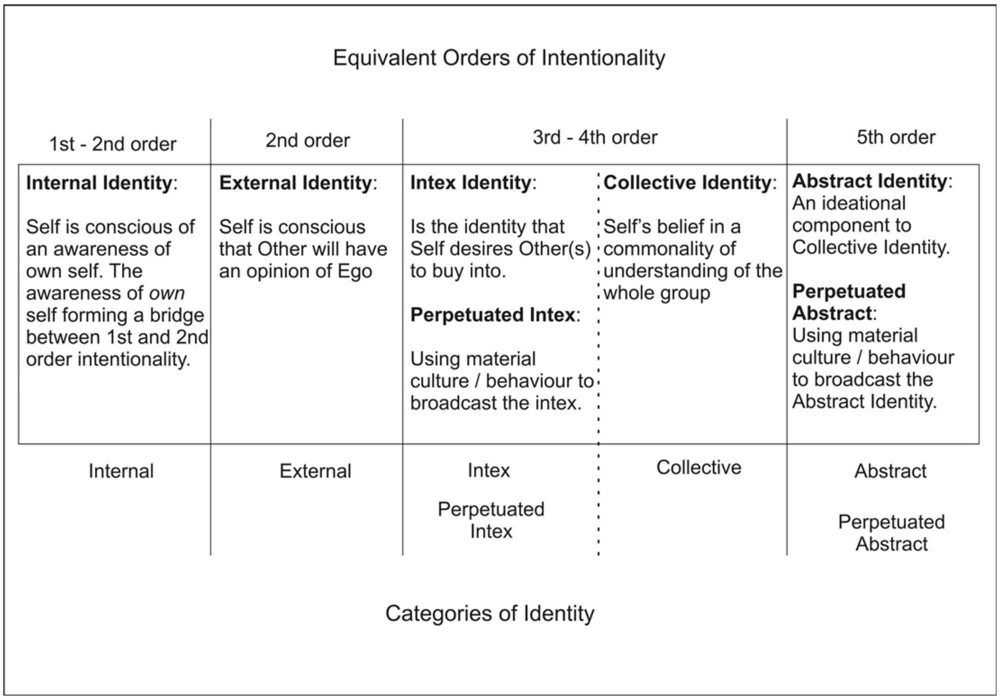
Perpetuated abstract - is the mechanism by which the abstract identity is propagated/broadcast through behaviour and material culture to the other. Perpetuated abstract is concerned with the dissemination of the conceptual through a physical medium (the body); such examples of this abstract perpetuation are grammatical language and related by-products such as art and ornamentation.

Abstract identity and perpetuated abstract deal with the deliberate creation and dissemination of an ideology and are therefore only possible once fifth-order intentionality has been achieved. Fifth-order intentionality is the minimum requirement where fully abstract concepts, such as religion, can be formulated in a cogent manner. Furthermore, perpetuated abstract can only be expressed and disseminated through fully-grammatical language. The archaeological evidence for grammatical language relate to abstract constructions for instance art, figurines and ornamentation (for example, Conard 2003; d'Errico *et al* 2005). It is signatures such as these that constitute the perpetuated abstract. Once grammatical language markers enter the archaeological record, fifth-order intentionality must have been reached by the hominin creating the marker. Additionally, once abstract identity and perpetuated abstract enter the identity construct, they begin to have a direct effect on the previous categories of identity. For example, in the case of ornamentation, the body incorporates material culture into itself, changing the boundaries of the body, and subsequently, ornamentation is used to broadcast/display a specific message to an 'other'. Therefore, perpetuated abstract becomes involved with, and complements, the mechanisms and manipulations of perpetuated intex.

Relating the Identity Model to the orders of intentionality

In terms of relating the categories of identity to orders of intentionality, the approach illustrated below may be taken for each of the seven categories of identity. The latter may be related to the orders of intentionality, where each mental state present within a category of identity corresponds to an order of intentionality. For example, the number of mental states present within intex identity may run like this: Xi desires O'wa to believe that Xi considers himself to be a good hunter - there are three mental states represented within this example: Xi's desire, O'wa's thought, and Xi's consideration. There are at the same time three orders of intentionality within this intex example - Xi *desires* O'wa to *think* that Xi *considers* himself a good hunter and so on. Table 1 shows how each category of identity may be correlated to a corresponding order of intentionality, whilst Table 2 uses an example to illustrate how the categories of identity operate within the orders of intentionality.

By correlating the categories of identity to the equivalent orders of intentionality not only has the Identity Model been connected to a scale of cognitive complexity, but the Identity Model may also inform on how the orders of intentionality may be useful as a measure of hominin cognitive ability. Figure 2 shows how the orders of intentionality are currently related to the evolutionary context through the Social Brain Hypothesis where there is an implicit step like progression through time between one order of intentionality and another. What is missing from the Social Brain's application of the orders of intentionality to the hominin record (Dunbar 2004) is the mechanism that allows a progression from one order of intentionality to another. For example, how do you progress from a first order of intentionality to a second? However, if we examine the orders of intentionality through the Identity Model in relation to group size and time, I propose that the mechanism of progression is linked to concepts of identity construction of the self, and the single or collective other (figure 3). I do not propose that the cognitive steps proposed in figure 3 represent



Equivalent Orders of Intentionality

1st - 2nd order	2nd order	3rd - 4th order		5th order
Internal Identity: Self is conscious of an awareness of own self. The awareness of *own* self forming a bridge between 1st and 2nd order intentionality.	**External Identity**: Self is conscious that Other will have an opinion of Ego	**Intex Identity**: Is the identity that Self desires Other(s) to buy into. **Perpetuated Intex**: Using material culture / behaviour to broadcast the intex.	**Collective Identity**: Self's belief in a commonality of understanding of the whole group	**Abstract Identity**: An ideational component to Collective Identity. **Perpetuated Abstract**: Using material culture / behaviour to broadcast the Abstract Identity.
Internal	External	Intex Perpetuated Intex	Collective	Abstract Perpetuated Abstract

Categories of Identity

Table 1. Correlating orders of intentionality to the categories of identity found within the identity model: illustrating the cognitive steps required for each category of identity in relation to the orders of intentionality.

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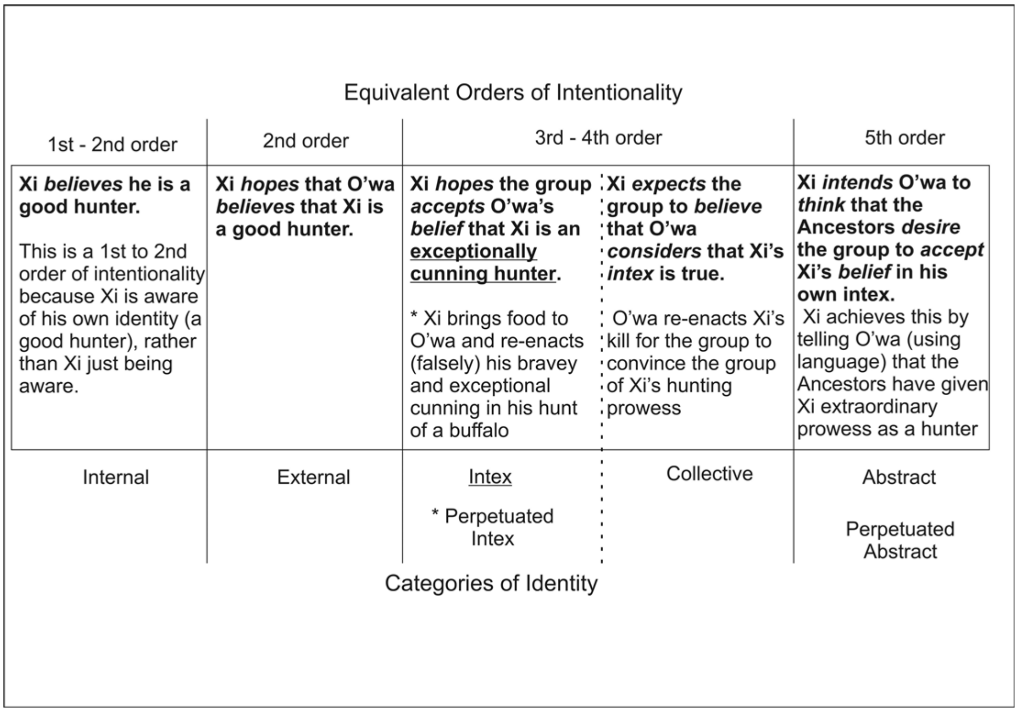

Equivalent Orders of Intentionality

1st - 2nd order	2nd order	3rd - 4th order		5th order
Xi *believes* he is a good hunter. This is a 1st to 2nd order of intentionality because Xi is aware of his own identity (a good hunter), rather than Xi just being aware.	**Xi *hopes* that O'wa *believes* that Xi is a good hunter.**	**Xi *hopes* the group *accepts* O'wa's *belief* that Xi is an exceptionally cunning hunter.** * Xi brings food to O'wa and re-enacts (falsely) his bravey and exceptional cunning in his hunt of a buffalo	**Xi *expects* the group to *believe* that O'wa *considers* that Xi's *intex* is true.** O'wa re-enacts Xi's kill for the group to convince the group of Xi's hunting prowess	**Xi *intends* O'wa to *think* that the Ancestors *desire* the group to *accept* Xi's *belief* in his own intex.** Xi achieves this by telling O'wa (using language) that the Ancestors have given Xi extraordinary prowess as a hunter
Internal	External	Intex * Perpetuated Intex	Collective	Abstract Perpetuated Abstract

Categories of Identity

Table 2. An example illustrating how the categories of identity work within the orders of intentionality.

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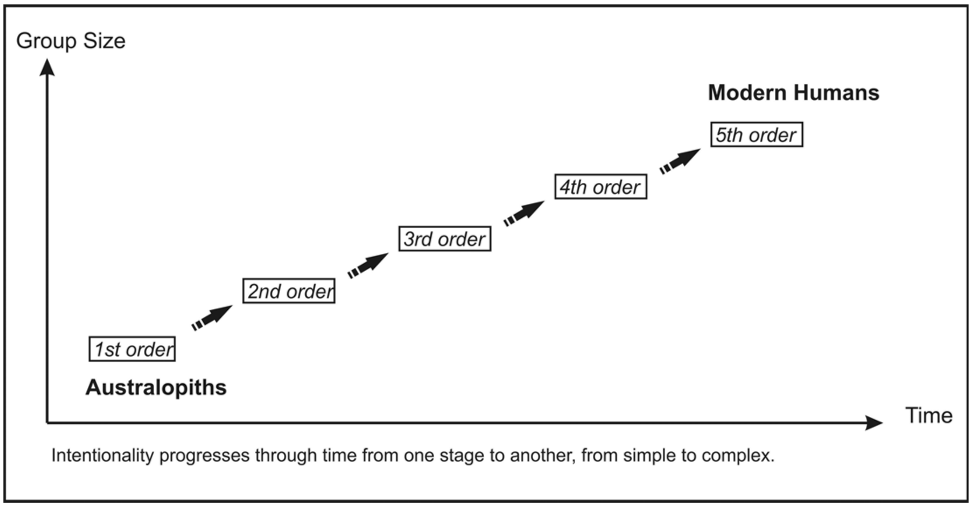

Figure 2. A simplified view of the way the Social Brain Hypothesis lays out the orders of intentionality in a linear fashion through time.

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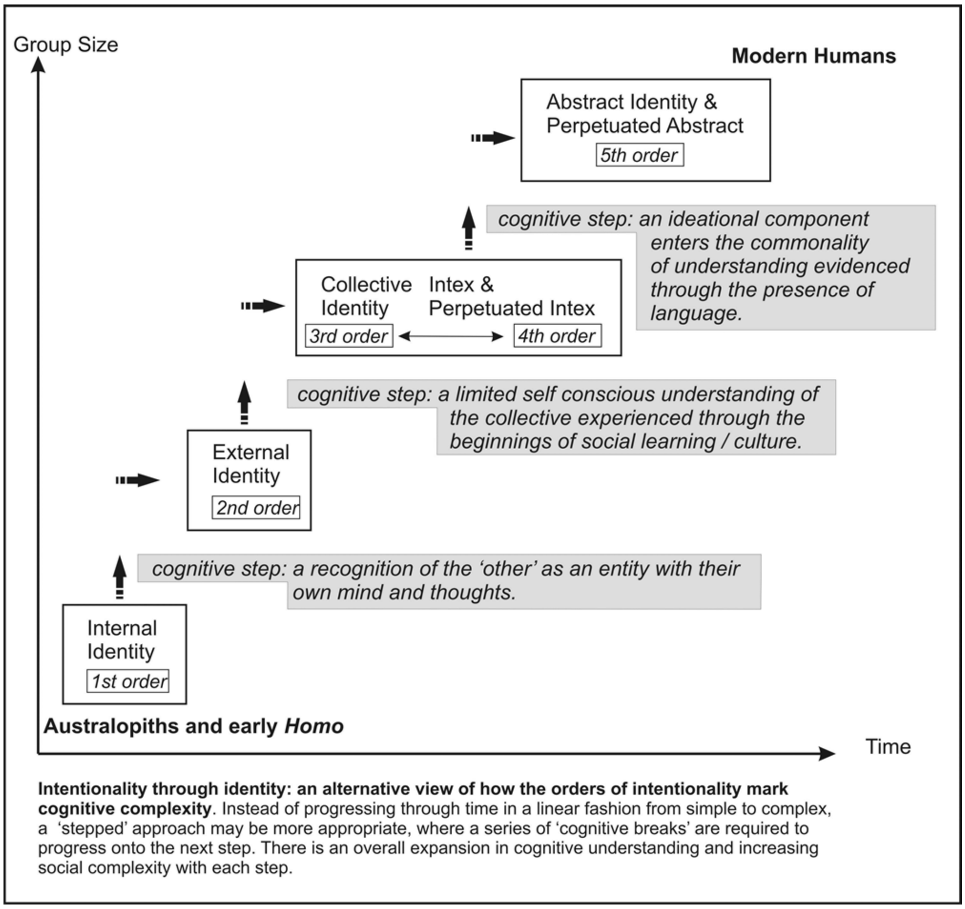

Figure 3. A simplified view of the way the identity model lays out the orders of intentionality in a stepped fashion through time.

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the definitive cognitive mechanisms relating to increasing orders of intentionality. Rather I would suggest that viewing the progression of increasing cognitive complexity over time through the filter of the Identity Model allows a discursive heuristic when considering how increasing levels of social complexity, group size and the constructions of individual and group identities correspond to an increase in the order of intentionality. This is not to advocate a series of 'cognitive revolutions' within the evolution of the hominin, rather the recognition of identity in 'self' and 'others,' must march in lockstep with increasing social complexity. Furthermore, due to the body's inherent position within the understanding and propagation of identity in lingual and non-lingual societies (particularly exemplified within the perpetuated intex and perpetuated abstract categories of identity), the use of the body and material culture as vehicles for social communication should therefore also become more byzantine and multi-layered as social complexity increases. The next section investigates how the identity model relates to the archaeological record.

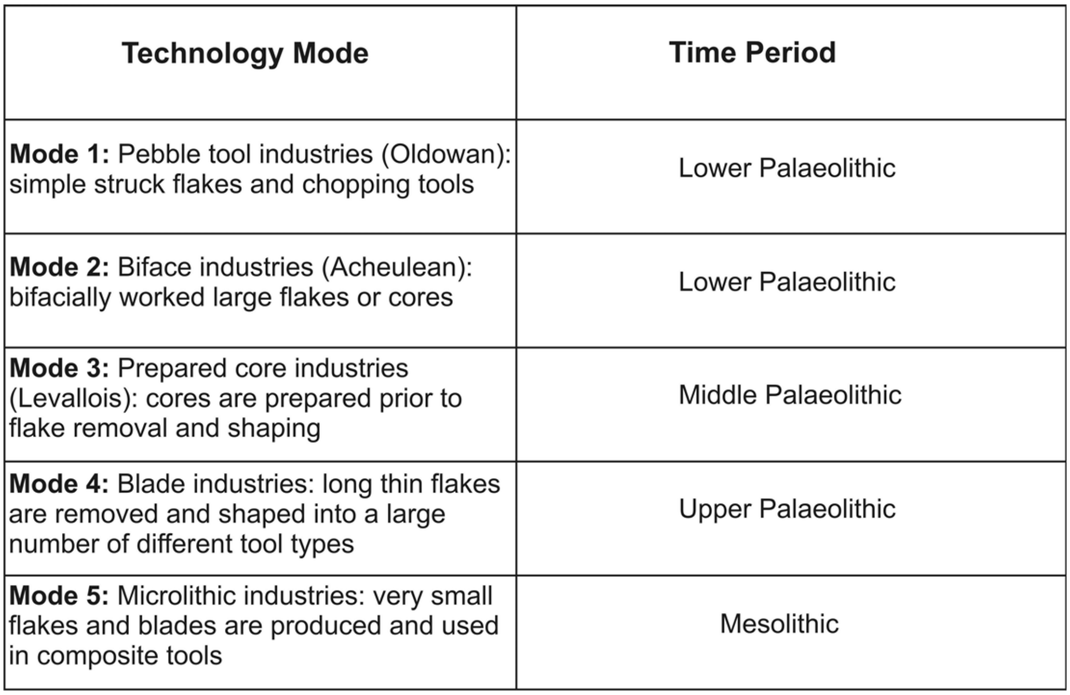
A theoretical / heuristic relation of the Identity Model to the archaeological record

In order to relate the identity model to the archaeological record, one must view intelligence as an embedded state within the dynamic interactions of social cognition occupied by many individuals. This is what Anderson (2003) terms embodied cognition. Furthermore, through embodied cognition, cognition manipulates environmental interactions through the interface of the body, creating structures that advance and reduce cognitive tasks to a point where anthropogenically-modified props, "count as proper parts of (an) extended cognitive processes" (Wheeler and Clark 2008: 3566). Essentially, archaeological artefacts become a physical expression of the cognitive potential of the producer. One of the great difficulties of examining archaeological data from a cognitive perspective is establishing the link between the inferred behaviour underpinning the artefacts, and the underlying cognitive mechanism. However, if we examine the same archaeological record through embodied cognition, the holistic definition of the body given above, and the identity model, then I believe that a stronger methodology for examining the behavioural attitudes of our hominin ancestors may be formed.

Through such a methodology it may be seen that any form of material culture that has been produced must be linked to the body of the creator and the level of cognition inherent within that body. Material culture therefore becomes an extension of the body and the level of cognition held by the architect. One of the short comings of the SBH is that it lays out a cognitive map based on predicted group and brain size with no attempt to acknowledge the role of the body in cognition and little to no direct grounding in the archaeological record. I propose that through the theory of embodied cognition, the identity model may relate different potentials for different parts of the Palaeolithic record to the SBH whilst offering insights into the behavioural and social significance of the body and its role in material culture production and cognitive development.

When discussing the anthropogenically modified stone artefacts of the Palaeolithic record, there exists a plethora of terminology from different geographical regions, describing a number of diverse lithic technologies spanning more than two million years. In addition, the different approaches to examining the technological diversity seen within lithic artefacts tend to emphasise different aspects, ranging from flake production, typological form, metrical variation, core reduction and microwear analysis (Foley and Lahr 2003). Within the context of this paper, I believe that a scheme of terminology that reflects broad changes across a global (as opposed to a regional) scale is required. An appropriate *heuristic* device to which many researchers may immediately relate and that allows such a broad classification system is Clark's (1969) technological modes (table 3). Although there are valid issues with Clark's modes and their application by archaeologists to the Palaeolithic record (as shown by Bar-Yosef and Belfer-Cohen 2001 and Villa 2001), the technological modes should be viewed in this context as a framework for examining changes in lithic taxonomy, typology and technology that allow a broad comparative look at hominin behaviour (Gamble 2001), rather than the rigid homotaxial sequence seen by many researchers.

The technological modes developed by Clark describe the basic manufacturing procedures and broad tool outputs for each classification. There are obviously continuities between the technological modes and time



Technology Mode	Time Period
Mode 1: Pebble tool industries (Oldowan): simple struck flakes and chopping tools	Lower Palaeolithic
Mode 2: Biface industries (Acheulean): bifacially worked large flakes or cores	Lower Palaeolithic
Mode 3: Prepared core industries (Levallois): cores are prepared prior to flake removal and shaping	Middle Palaeolithic
Mode 4: Blade industries: long thin flakes are removed and shaped into a large number of different tool types	Upper Palaeolithic
Mode 5: Microlithic industries: very small flakes and blades are produced and used in composite tools	Mesolithic

Table 3. Describing the technological modes and their approximate corresponding time periods. Table modified after Clark 1969: 31 and Foley and Lahr 2003: 114-115, Box 1.

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divisions that table 3 does not illustrate; however, what Clark's modes do demonstrate is that, through time, methods of lithic artefact production become broadly more complex, leading to greater control in knapping techniques and raw material utilisation (Foley and Lahr 2003). Furthermore, these technological modes allow for an examination of lithic artefacts on a cladistic basis, stressing the cladistically-derived elements within assemblages under examination, thereby negating any analytical difficulties presented when lower mode industries persist once higher mode industries have been developed (Foley and Lahr 2003).

Table 4 below details how the archaeological record may inform on hominin behaviour, the use of the body in social communication and how they relate to the identity model. Clark's (1969) modes are used here purely as a heuristic device to describe the broad framework for the technological description of Palaeolithic artefacts and how these may be related to the complex notions of the identity model. The associations of the predictions given in table 4 are currently under rigorous investigation (Cole in prep) and the results of which shall be forthcoming.

The stress of this methodology is on the *developed / derived* artefact, and what that can tell researchers about hominin behaviour, use of the body, identity perpetuation and cognition. Furthermore, in relation to table 4, it is assumed that if a minimum of one of the derived elements from each material culture category is securely provenanced within an assemblage, for example if a predominantly prepared core technology assemblage (category 3) contains an element of ornamentation (category 4-5) then it may be cautiously inferred that the creating hominins have attained a degree of identity perpetuation seen within the higher category of material culture.

Category of material culture (modified after Clark 1969: 31)	Description	Behavioural implications	Role of the body in social communication	Category of identity
1	• Deliberate lithic tool production to create specific edges for use. • No standard form imposition, tool shape governed by raw material size, shape and mechanical properties. • Consists of pebble tool industries dominated by small flake removals (<10cm) and chopping tools (Oldowan). • Bone or wood tools that have limited evidence for anthropogenic modification.	• Hominins have a realised sense of self which compliments the egocentric goal directed behaviour reflected in the strategies of tool production. • Evidence for some forward planning in raw material procurement. • Social communications governed by egocentric, dyadic, gestural and attention directed auditory signals with a greater repertoire than extant primates. • The beginnings of simple imitative learning may be evidenced here.	• Similar to that of extant primates. • The body is limited to egocentric, context specific and dyadic non-theory of mind social communications. • The body is used in sexual selection through visual display with an increased propensity for female choice in mate selection within a predominantly polygynous mating strategy. • Visual display plays an important role in social communication on an intra and inter-group level.	• Internal
2	• Deliberate imposition of shape and form to lithic tools evidenced through the presence of symmetry and a high degree of standardisation. • Lithic tools predominantly based on large flakes (>10cm) or bifacially reduced cores. • Consists mostly of bifacially knapped handaxes and cleavers (Acheulean). • Regional variation in shape and form primarily affected by raw material.	• Hominins have a ToM which marks the beginnings of abstract thought reflected in the imposition of deliberate shape and form on lithic artefacts. • Evidence for goal directed behaviour associated with greater planning capabilities and complex imitative learning. • Social communication centered around visual display and gesture.	• With the attainment of a ToM, the body becomes a focal point for socially significant triadic visual display and gesture accompanied by limited vocalisation. • Complex imitative learning focuses on the body where individuals acquire the ability to recognise familiar actions performed by an 'other' and are able to repeat or perform novel actions constructed from a familiar repertoire. Visual display and social signalling are direct and context specific. • The body plays a reduced role in direct sexual selection evidenced through a reduction in sexual dimorphism. Reflecting a higher degree of female choice and an increasing importance in material culture?	• Internal • External
	* Toward the end of Mode 2 (later Acheulean), an element of prepared core technology may enter the archaeological record, although there is still a strong emphasis on large flake production and bifacially reduced cores.	* If assemblages have a definite bias toward 'true' symmetry or contain artefacts of 'extraordinary design' (e.g. giant handaxes) then it may be that such artefacts have an implication beyond the purely functional and may hold some limited social significance.	* The body may begin to play a more pronounced role in identity perpetuation broadcast on a context independent and individual by individual basis.	• Internal • External • Intex • Perpetuated Intex

TABLE 4. ILLUSTRATING THE METHODOLOGY THROUGH WHICH THE IDENTITY MODEL MAY BE RELATED TO THE PALAEOLITHIC RECORD. TOM = THEORY OF MIND. ARTEFACT DESCRIPTIONS AND BEHAVIOURAL IMPLICATIONS DERIVED FROM CLARK 1969 AND AMBROSE 2001.

Category of material culture (modified after Clark 1969: 31)	Description	Behavioural implications	Role of the body in social communication	Category of identity
3	• A shift from producing lithic tools from cores and flakes, to preparing cores to extract flakes of a particular form. • Prepared core technologies (e.g. Levallois) focuses on producing standardised flakes with the potential for later modification (e.g. into points or handaxes). • This type of lithic production also indicates the presence of composite tools. • Regional variation possibly driven by cultural influences rather than raw material, although raw material may still govern shape and size of artefact to a certain degree.	• Hominins have a commonality of understanding (cultural affinities) and a clear sense of shape and form that begin to play a role beyond the purely functional. • The capability to produce composite tools displays an ability for abstract thought on a functional level, which further manifests itself in the beginnings of cultural influences seen within the archaeological record. • Artefacts maintain a predominantly functional significance but may carry limited social meaning in regards to the creator (on an individual and group scale). • Social communication is centered around complex gesture and utterance incorporated within visual display.	• The body has a central role in social communication becoming a transmitter and receiver of social information centered around visual display and manual gesture accompanied by vocal utterance. • The body also plays an important role in identity perpetuation, the social boundaries of the body begin to be extended through material culture on a limited individual and group basis. Visual display and social signalling may begin to be indirect and context independent. • However, material culture remains predominantly functional within this category. • Sexual dimorphism reaches levels similar to modern humans indicating a greatly reduced role of the body in direct sexual selection possibly indicating active female choice in mate selection with an emphasis on skilled visual display and material culture as selection drivers.	• Internal • External • Intex • Perpetuated Intex • Collective
4 - 5	• Continued emphasis on flake production with a predetermined shape and form. • Flake blanks within this category are primarily concerned with composite tool production with limited secondary shaping. • This category includes an expanded repertoire of complex bone tools (such as harpoon heads). • In addition, material culture with a purely non-utilitarian design enter the record in the form of ornamentation (beads), art and figurines (humanoid and anthropomorphic). • Clear evidence for regional variation in material culture production on a cultural basis.	• Hominins have a commonality of understanding, a clear sense of shape and form, and the capacity for fully symbolic and functional abstract thought evidenced through the presence of non-utilitarian and composite material culture and behaviours (such as burial). • Social communication is centered around visual display, gesture and grammatical language. • Artefacts carry social meaning in relation to the creator and user (individual and group) and are now fully complicit in identity propagation.	• The body maintains a prominent role in social communication as a transmitter and receiver of social information centered around visual display (enhanced through bodily ornamentation), manual gesture and grammatical language. • The body's boundaries are now fully extended through material culture (through ornamentation, figurines, art and tool production) on an individual and group basis with material culture adopting a functional and symbolic role. Visual display and social signalling now completely indirect and context independent. • The body plays a full role in identity perpetuation through visual, vocal display and material culture. • The body may play a more important role in sexual selection aided through ornamentation, although skilled visual display in material culture production may	• Internal • External • Intex • Perpetuated Intex • Collective • Abstract • Perpetuated Abstract

TABLE 4 CONTINUED. ILLUSTRATING THE METHODOLOGY THROUGH WHICH THE IDENTITY MODEL MAY BE RELATED TO THE PALAEOLITHIC RECORD. TOM = THEORY OF MIND. ARTEFACT DESCRIPTIONS AND BEHAVIOURAL IMPLICATIONS DERIVED FROM CLARK 1969 AND AMBROSE 2001.

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Conclusion

The aim of this paper is to encourage discussion and debate by proposing a new and original idea relating hominin cognition to the archaeological record through constructs of identity. By offering up a more holistic definition of the body, I hope to encourage researchers to think beyond Cartesian dualism and engage with a perspective of the body that brings together the physical boundaries of the body with the conceptual autonomy of the mind. Furthermore, by defining social communication in relation to a ToM, I hope to have illustrated the difference between the social interactions of extant primates, of ourselves, and of our ancestral hominins. Through the identity model I propose a new hypothesis on how identity constructs inform social interactions and cognitive development through the hominin record. Through the relation of the identity model to the archaeological record in table 4, I illustrated a link between hominin material culture and cognitive development within the context of social communication (such as visual display and language). This in turn may allow the cognitive predictions of the SBH to be tested against the archaeological record (Cole in prep).

It is reasonable to assume that the majority of hominin social communications were dominated by mechanisms of visual display (see McNabb this volume), primarily centred on the body. However, once a third order of intentionality was gained, the identity model suggests that material culture would be incorporated into visual display and would cease to play a purely utilitarian function within the social context. The identity model further suggests that the emergence of grammatical language is directly linked to the ability to construct complex ideologies and the need to communicate these complex abstract ideals, which, I propose, can only be achieved through the use of grammatical language. Table 4 describes a method through which the identity model may be related to the Palaeolithic record. This is currently being explored and tested with encouraging results in supporting the premises put forward here (Cole in prep.).

Future research will further test the usefulness of the identity model to other researchers exploring issues of hominin cognition and behaviour. However, at the least, I hope the methods put forward here will encourage a lively discussion and debate from which a new direction in Palaeolithic research may form.

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HOMININ TOOL PRODUCTION, NEURAL INTEGRATION AND THE SOCIAL BRAIN

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Abstract

The conservatism and standardisation of Oldowan and Acheulean tools have been the focus of much debate, especially as to how such conformity over a prolonged period might be informative regarding the cognitive profile of the hominins responsible for producing such artefacts. Thanks to the advent of brain scanning techniques, recent insights into the structure of both the nonhuman and human brain have, however, provided a means of understanding how the various neural tracts involved are associated with tool production and use. Such techniques have also promoted an understanding of how tool use might be related to other kinds of behaviour that can help clarify when socially mediated factors began to impact on the making and using of tools. This paper will, therefore, demonstrate how an understanding of the neurostructure of the modern human brain, when compared to nonhuman primates, can help clarify issues concerning the appearance of important cognitive markers in hominin evolution. In this regard, it will be shown that the structure of the human brain, although sharing certain features with nonhuman primates, also contains important differences that arose as a result of engaging in toolmaking—differences that later became even more pronounced thanks to the capacity to increasingly share information through social interaction.

Introduction

In this paper the following questions regarding Oldowan and Acheulean toolmaking will be addressed, 1) why was there such a lack of change in tool shape over an extended period in both cases, 2) what led to the change from the Oldowan and Acheulean, and from the late Acheulean to the composite tools of the Middle Palaeolithic. In order to address these issues, it is has been argued that a multidimensional approach is required involving a variety of diverse factors, ranging from social considerations to cognitive abilities and actual toolmaking practices etc., (see for example, Petraglia et al. 2005; Lycett 2008; McPherron 2000; Nowell 2002; Gowlett 1993; Sharon 2008, 2009; Machin et al. 2007; Porr 2005). One of the main outstanding issues arising from such considerations has been to determine the timing of when any one explanation might have been relevant.

Despite the number of factors that could have led to considerable variation in tool morphology, the shape of Acheulean and Oldowan seems to have remained relatively static throughout the respective periods (Lycett and Gowlett, 2008; Sharon et al. 2010; Stout et al. 2010); except, perhaps, up to when more sophisticated Acheulean tools began to appear around 500,000 BP that saw an increasing concern for shape e.g., twisted and congruent symmetries (See, for example, Wynn 2002, 2004; Wenban-Smith 2004; Read and van der Leeuw 2008;Mallol 1999; Barsky and de Lumley 2010). Moreover, the niche populated by hominins would have been subject to change thanks to the arrival of stone tools that would have impacted on the social environment (Grove and Coward 2008); not least because such tools not only required a significant investment in time and effort but also served as a means by which this environment would have been modified to the advantage of those producing such tools (akin to the Baldwin Effect which shows how intentional changes made to a niche by a species can lead to a modification of the evolutionary contingencies to the advantage of that species, see for example, Deacon 1997, p. 322). Thanks to this engagement, one would have expected the associated reciprocal dynamic to have promoted a faster rate of change with regard to the materials exploited but this does not seem to have been the case during both the Oldowan and earlier Acheulean.

Although Oldowan tools consist of a generic tool type where the emphasis seems to have been on the cutting edge (Read and ven der Leeuw 2008; de Lumley 2006) with little concern for shape per se, the range of Acheulean tools is essentially restricted to handaxes and cleavers—although there are also a variety of less common cores such a spheroids and flake tools—of which the standard shape is unable to be entirely accounted for by functional or cultural factors (Sharon et al. 2010; Sharon 2007). The soft hammers recovered from Boxgrove (Pope and Roberts 2005), and the antler-like tools from Bilzingsleben (Mania and Mania 2005), as well as the Schöningen wooden "spears" (Thieme 2005) also call for an explanation. Having said this, Ambrose (2001, 2010) makes the important point that Oldowan and Acheulean tools, as well as the Schöningen spears, can be categorized as reduction technologies that essentially consist of single component hand-held tools rather than multi-component technologies, which suggests some underlying neurocognitive factor[s] may be able to account for the dynamics associated with the making of such tools.

It is therefore hypothesised, that the transformation from the "pre-Oldowan" serendipitous use of tools (as indicated by tool use in modern chimps [Toth and Schick 2009]) to the Oldowan, and from the Oldowan to Acheulean and thereafter may have occurred in tandem with some predisposing neurocognitive events that both constrained and mediated change. It is only possible, however, to assess the minimal cognitive competence required to produce an artefact due to the fact that we are not privy to the behavioural complexity that may have been involved (Wynn 2002). In addition, once Acheulean tools had begun to appear in the archaeological record c.>1.6 million years ago (Ambrose 2001; Toth and Schick 2009), it seems that the concern for shape and other more sophisticated aspects to do with such tools appeared sporadically over widely dispersed geographical areas. It thereby appears that there may have been two main neurocognitive events that occurred relating to different tool morphologies, the first which led to the transition from the Oldowan to the Acheulean and a second that occurred around 500,000 BP that led to the appearance of more complex symmetries that eventually led to an increasing employment of a greater range of tools (Read and van der Leeuw 2008).

Cognitive explanations have been put forward as a way of accounting for both the conservatism and change in tools, with several factors being cited, usually in relation to spatial thinking (Parker and Gibson 1979; Gibson 2007; Wynn 2002). In this paper, I will attempt to demonstrate that, although these approaches have been instructive, nearly all fall short of accounting for the major changes that occurred in tool production, as Porr (2005) has demonstrated. Importantly, what seems to have been lacking in such discussions is a bringing together of the insights from neuroarchaeology, cognitive science, and recent progress in brain function, which this paper will attempt to address by showing how tool typology and production was initially constrained by certain neural events which led to the observed conservatism.

The fact that Acheulean tools may have been fabricated by different hominins on several continents at various times also does not disqualify the fact that toolmaking may have been contingent on certain neurocognitive events, as such an ability would have depended on a minimal cognitive competence shared by different hominins for producing a particular tool (see also below). The approach taken here is therefore based on the notion that the first instance when a certain tool type appeared in the archaeological record provides a marker for the existence of a particular cognitive ability. One cautionary note needs to be added here, namely that throughout the Oldowan and Acheulean a measure of variation continued to prevail on a local level ("continuous variability") and rudimentary and more sophisticated tool types often coexisted. The reader therefore needs to remain alert to the fact it is not being implied here that there is an obvious and clear cut trend towards more standardized tool types as the archaeological record is complex and morphological similarities can often obfuscate underlying differences in production, resource acquisition etc. Despite these reservations, it seems increasingly accepted by archaeologists that there was a general preoccupation with shape in later tools that gave rise to increasing standardisation (e.g., Stout 2011; Gamble et al 2011).

The main argument to be presented in this paper proposes that certain underlying neural structures became increasingly interconnected as a result of making and using tools and that this mainly involved the linking together of the consciously derived ventral neural pathway with the implicit (procedural) visuo-spatial/motor neural pathway that was further enhanced by a socially-mediated mirror neuron network. Recent evidence from neuroscience and cognitive research, which compares the visual and visuo-spatial/motor neural pathways of nonhuman primates and humans, especially in relation to tool use, will be presented to support this argument in association with evidence from the archaeological record. After addressing issues concerning the reliability of comparing nonhuman primates with homo sapiens, the first section will describe the implicit [embodied] visuo-spatial/motor tracts involved in producing Oldowan and early Acheulean tools, whereas the second will show how such embodied networks relate to more conceptually driven neural structures that gave rise to the complex tools of the late Acheulean and after. The insights gained from the first two sections will then be assimilated to show how they have important consequences for understanding the archaeological record.

Comparing nonhuman primates, humans and *Australopithecus*

A useful way of investigating how stone tools may be related to the brain from the perspective of evolution is to compare the modern human cortex with that of other nonhuman primates in relation to behavioural correlates and then attempt to "fill in the gaps." Although a modern nonhuman ape cannot provide an exact proxy for the behaviour of *Australopithecus* due to the fact that modern apes will also have been subject to evolution, by examining fossil cranial casts, as well as the behavioural indicators of modern apes and recent findings on functioning neural networks, it might be possible to gain important insights as to how these factors relate to early tools. Differences between the modern human brain and nonhuman primates may, accordingly, help to specify the neural structures significant to identifying important behavioural developments that post-date the divergence from a common ancestor (see for example Falk et al. 2009). It needs to be borne in mind, however, that *Pan troglodytes* and *Pan paniscus* display different behavioural profiles (de Waal 1995) regarding tool use and arboreal comportment (Tomasello and Call 1997; Doran and Hunt 1994), which suggests the cognitive demeanour of *Australopithecus* may have been different to both these species—especially as the last common ancestor is estimated to date back six to ten million years (Sayers and Lovejoy 2008; White et al. 2009). This divergence is further highlighted by the fact that *Ardipithicus ramidus* indicates that the last common ancestor of hominins was probably very different from Pan or Pongo (Suwa et al. 2009). The structure and organisation of the primate brain nevertheless seems to have been conserved in hominins in that it is based on a "primitive" format (see Stout and Chaminade 2007) shared by present day monkeys (Passingham, 2009; Koyoma et al. 2004; Sereno and

Tootel 2005). Modern nonhuman primates may therefore exhibit variations on a theme with respect to a common underlying neurostructure and, therefore, still represent the best approximation for understanding both *Australopithecines* and later hominins (Passingham 2009; Foley and Gamble 2009). In sum, although the various tools that appeared in the archaeological record may have been produced by different species, the fact that they were produced in the first instance indicates that the underlying neurostructures may have been similar. Earlier tools, however, were probably more dependent on biological imperatives relating to survival associated with the acquisition of a high protein diet that mediated brain expansion than was the case for later tools (Read and van der Leeuw 2008).

Implicit/embodied Visuo-Spatial Processing: vision for action

Although nonhuman primates need good integration of visual and motor coordinates for navigating the tree canopy, the skills to produce tools require abilities involving enhancement and assimilation of both procedural and visual capacities that needed to function at a coordinated level (Ambrose 2001). Unlike humans, chimps tend to manipulate objects from the shoulder/elbow with minimum involvement of the wrist. Thus, a tool acting as a prolongation or augmentation of the hand does not lead to complex transformations in directional coordinates (Goldenberg and Iriki 2007) that is typical of tool use in nonhuman primates. In order, therefore, to produce Oldowan tools, changes needed to take place with regard to the anatomy of the arm, wrist, as well as the hand/fingers that occurred in tandem with changes to brain structures for the purpose of exerting greater control. The question arises as to the nature of the changes that took place in the cortex that allowed Oldowan tools to be produced.

Wynn (2002), in a seminal work investigating Oldowan and Acheulean tools from the perspective of cognition, made reference to the importance of neural pathways sub-serving visuo-spatial, motor, and visual recognition, but did not examine the implications arising partially due to a lack of research data at the time. It has since been established that the "where/how" dorsal pathway—primarily concerned with on-line hand/eye co-ordination for visuo-spatial skills—is "blind" in that this pathway processes information but does not require overt awareness (Ungerleider and Mishkin 1982; Goodale et al. 1991; Milner and Goodale 1995, 2006) [a simplified summary of the neural networks to be discussed is available in note[1]]. In contrast, the "what" ventral pathway, which mediates consciously disposed visual recognition, may play down or even ignore visuo-spatial factors because these are largely irrelevant to a recognition system that strives to achieve object constancy (Turnbull et al. 1997a, Turnbull et al. 1997b). As the visuo-spatial pathway ("where/how" system), which interfaces with visuo-motor coordinates, is intimately associated with the making of tools, it is therefore more concerned with online visuo-spatial guidance than with the overt identity of objects and initially projects to the superior parietal lobe (SPL) and intraparietal sulcus (IPS) from early areas (Milner and Goodale 2006; Grafton 2010). The way these pathways function and interact have important implications for understanding toolmaking and will now be explored in greater detail.

Procession of shape in the Early Visual Cortex and Intraparietal Sulcus

Although information from early visual cortex is directed towards the superior parietal area (along the dorsal-dorsal pathway) and IPS (along the ventro-dorsal pathway) in both humans and monkeys, the difference seems to reside in the way shape is processed [see Figure 1 for specific areas cited in the text]. This is corroborated by the fact that, in macaque IPS, sensitivity to shape seems more concerned with

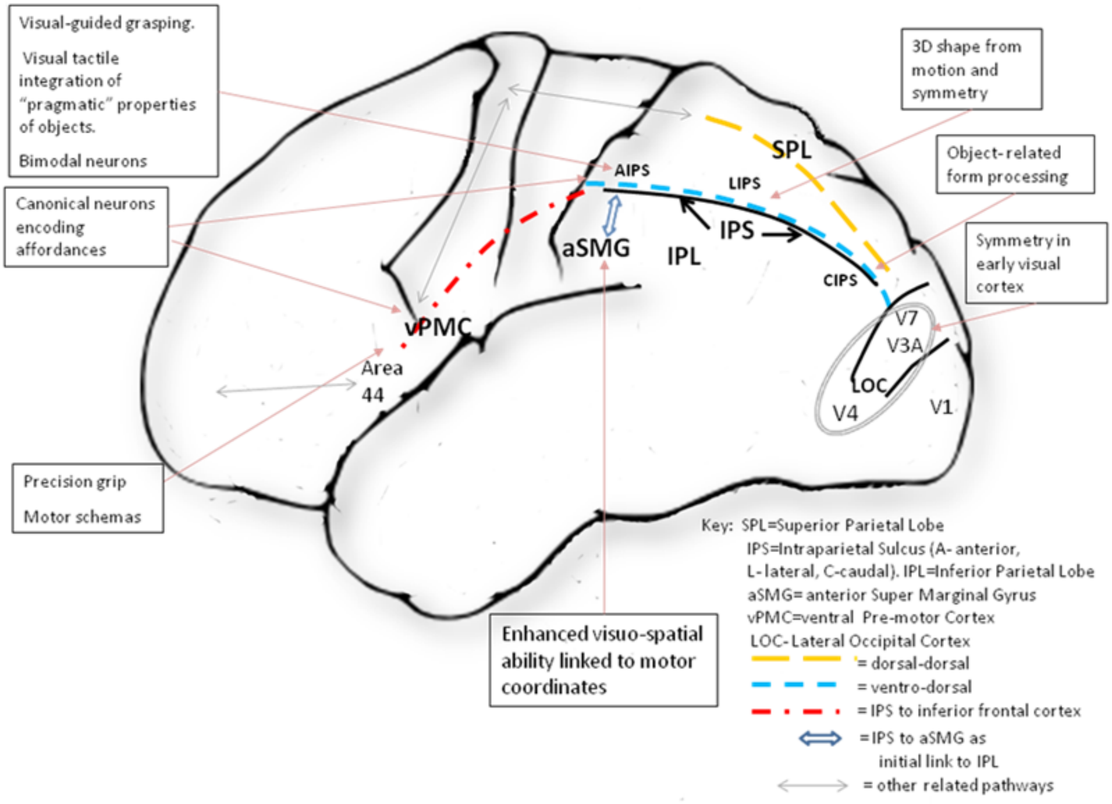

Figure 1. The primitive "what/how" enhanced dorsal reach grasp circuit in the human brain as indicated by the various coloured dashed lines

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two-dimensional co-ordinates than the equivalent area in humans that is more attuned to three-dimensional parameters (Denys et al. 2004; Orban et al. 1999, 2004, 2006). This finding is reflected in the fact that the processing of shape in this region is more cue invariant in humans i.e., there is a greater capacity to cope with variability in shape profile (Denys et al. 2004). Nakamura et al. (2001), in studying the Japanese monkey (*Macaca fuscata*), provide confirmation of the importance of this pathway for the processing of shape whereby the lateral intraparietal sulcus (LIPS), which responds visually to 3D objects, receives projections from V3A (a "gatekeeper" to IPS which is located in the mid layers of visual cortex) from where axons are sent to the anterior intraparietal region [AIPS] (responsive to hand movements for grasping 3D objects associated with a precision grip) that subsequently interface with motor and premotor areas (Devare et al. 2010). Similarly, Vanduffel et al. (2002) compared the patterns of activation produced by 2D and 3D displays in both monkeys and humans, where it was confirmed that the perception of 3D shape from motion produced widespread activation along the IPS in humans—a response that seemed to be completely absent in monkeys (Todd 2004; Orban et al. 2006),[2] although some 3D information may be preserved in monkeys especially in the anterior area of IPS i.e., AIP and LIP (Grafton 2010). In this regard, Durand et al. (2007) have suggested that the more anterior areas of IPS (i.e., AIP and LIP) may help discriminate 3D objects from background.

This has important implications for tool use for, as Sasaki et al. (2005) have noted, the response of V3A and later extrastriate areas to symmetrically shaped stimuli is much stronger in humans than simians. They also found that stimuli perceived as more symmetrical evoked greater activity than less symmetrical forms in V3A and adjoining areas (V4, V7 and LOC or lateral occipital complex). As symmetry responses were absent from areas earlier than V3A (though a marginal response to symmetry was found in V3), this indicates that such responses are restricted to extrastriate areas (regions beyond V1 or primary visual cortex) with large receptive fields that may serve to integrate information deriving from extensive parts of the visual array (Beck, Pinsk and Kastner 2005). Fundamentally, it was confirmed that symmetry related responses in macaque V3A, V4 and posterior inferior temporal area are generally weaker in monkeys compared to humans (Sasaki et al. 2005). Sasaki et al. (2005) also found that the extrastriate area (regions beyond V1) is responsive to a range of symmetrical stimuli varying in size suggesting a generalised response to this kind of form. Moreover, it has been established that symmetry can be processed at a preconscious level (Wagemans, 1997; Gurd et al. 2002; Hodgson 2009) that seems to be mediated by projections from the early visual cortex through to IPS.

Visual information relating to visuo-spatial, 3D shape from motion, symmetry, and other basic aspects of form processing therefore appear to be recruited by the dorsal "where/how" pathway from early visual cortex for the purpose of proactively engaging with objects. This seems particularly to occur along IPS as part of the implicit/embodied ventro-dorsal system that is much more developed in humans compared to nonhuman primates. These observations suggest that the human capacity to encode symmetry and 3D shape from motion is more complex than in nonhuman primates and is related to the need to both detect important environmental stimuli and process visual information with greater acumen for the purpose of making and manipulating tools especially during the Oldowan.

Bimodal and Canonical Neurons

The differences between nonhuman primates and humans with regard to IPS have been further confirmed in a study involving bimodal neurons. Such neurons, which mediate both the somatosensory and visual stimuli of hand movements, have been found in the anterior IPS of Japanese monkeys (*Macaca fuscata*) that had previously been trained to use a tool but which did not exist in naive monkeys; in fact, most of the neurons in the latter group were found to be unimodal (Hihara et al. 2006). Thus, when trained to use tools to obtain objects, monkeys show an increased activation in IPS where somatosensory and visual information is integrated in the form of bimodal neurons relating to the ability to integrate tools into an overall body schema that enables the extension of reaching space (Ishibashi et al. 2000; Hihara et al. 2006; Iriki et al. 1996; Maravita and Iriki 2004). Interestingly, it took two weeks of demanding tool-use training before bimodal neurons appeared and became active in monkeys. As such neurons do not exist in untrained monkeys, the associated ability may be beyond the capabilities of wild populations. Hihara et al's (2006) study suggests that, in artificial (laboratory) conditions, monkeys are able to improve their visuo-spatial dexterity for using tools that is reflected in changes to how the IPS is structured in terms of neural connections. Furthermore, IPS, as well as containing sensory neurons for specific shapes and orientations, seems to be related to visually guided grasping and also contains motor neurons that are activated during specific hand movements (Burgess, Jeffrey and O'Keefe 1999).

Canonical neurons have also been found in area F5 (located in the ventral premotor cortex) as well as the anterior IPS of the macaque brain (Grèzes et al. 2003). These fire at the sight of a graspable object and not when an object is actually reached for and held. Such neurons seem therefore to encode the pragmatic qualities afforded by an object in relation to the potential grip (Grèzes et al. 2003). Such findings confirm that this part of the cortex functions via implicit/embodied processes as part of the dorsal pathway (see Figure 1).

The above insights suggest that the tool skills potentially available to Pan when trained in artificial conditions regarding modifications to IPS and adjoining areas may represent the initial neural changes that occurred to the cortical connections of early hominins when they began to make and use tools that reflect pre-Oldowan abilities (Toth and Schick 2009; Kibunjia 1994, but see Stout et al 2010) i.e., basic throwing and a rudimentary but not very accurate percussion technique for producing crude stone tools (Toth et al. 1993; Schick et al. 1999) that is reflected in movement deriving mainly from the shoulder and elbow rather than wrist and fingers (Ambrose 2010). In order to produce Oldowan tools, however, changes needed to take place in IPS that appear to have involved integration of visual information for encoding both 3D shape from motion and object constancy that interfaced with somatosensory and motor contingencies by recourse to bimodal and canonical neurons. This stream, however, continued to be mediated by implicit (embodied) processes e.g., the making of tools depended on interaction with the actual materials concerned that served to structure the procedure (Malfouris 2010) as part of the aforementioned primitive stream.

The differences between nonhuman primates and humans therefore suggest an enhanced visuo-spatial-motor pathway in humans, particularly for processing 3D form, which projects from V3A through IPS to the ventral premotor area. In this regard, IPS, as part of the posterior parietal area, seems to have undergone expansion in humans (Roland, 1993; Bruner 2010; Orban et al. 2004; Zilles and Palomero-Gallagher 2001; Husein and Nachev 2007), and based on morphological variation of the brain, Bruner (2010) states that there is a strong possibility that important evolutionary changes occurred in IPS.

Evidence from Neuroimaging Studies of Early Toolmaking

The importance of the integration of visuo-spatial and motor pathways for understanding the cognitive factors relating to tools is reinforced by recent studies by Stout and associates. Appositely, such studies (Stout and Chaminade 2007; Stout et al. 2000; 2008) have demonstrated through brain scans how, in *novice* stone tool knappers producing Oldowan-like tools, the occipital regions of the brain become activated along with the superior parietal area and parts of the IPS (the dorsal-dorsal and ventro-dorsal streams). This was interpreted as reflecting the early processing required for visuo-motor skills associated with proximal solutions for completing a task. In *experienced* knappers, however, as well as the inferior parietal area, added activation was found in the visual association areas of the occipital cortex, such as the lateral occipital cortex (LOC) that reflect the affordances deriving from shaping cores (Stout et al. 2008). This was further corroborated by Stout et al. (2006) in a PET brain scan that found, as well as premotor cortex, the above cited areas of the brain were preferentially activated when a modern knapper made a symmetrical Acheulean hand-axe. Interestingly, when an expert produced an Achueleann tool, although the same areas were activated as in the earlier study on Oldowan tools (Stout et al. 2000), this occurred to a lesser degree with more forward areas involving the inferior parietal also becoming involved (Stout 2008). The prefrontal cortex, however, was not activated suggesting that the demands necessary for producing Oldowan and Acheulean tools do not require extensive planning. These observations indicate how, as task demands become increasingly challenging and knappers gain expertise, more forward areas of the brain are recruited including the inferior parietal and IPS. This suggests an assimilation of diverse capacities concerning the above mentioned neural pathways is necessary as part of what has been termed a "primitive" system (as described above) relating to an enhanced ventro-dorsal stream (which includes IPS and ventral premotor cortex) where increasing amounts of visual information from the early visual cortex is recruited for the purpose of tool production (see Figure 1).

Stout and associates investigations therefore suggest that the making of Oldowan tools by expert rather than novice knappers requires a greater interaction of pathways, involving enhanced visuo-spatial and motor coordinates, that seem to come together in the supramarginal gyrus (SMG) in inferior parietal cortex (Stout et al. 2008) as indicated in Figure 1. Importantly, this interaction would have been even more necessary for the production of the increasingly complex symmetries of late Acheulean bifaces in that such symmetries required a greater involvement of the inferior parietal area. In order to produce the later more refined Acheulean bifaces, however, further integration of visual information arising from the occipital area, (which projects to the ventro-dorsal → ventral premotor pathway) would have eventually led to interconnections between AIP and SMG. This scenario has recently received support from a study showing how, not only is IPS involved in simply tool use in humans, but also aSMG (anterior supramarginal gyrus)—a cortical area that does not seem to exist in non-human primates (Peteers et al. 2009). It is therefore no coincidence that Stout and associates found that SMG became more active when expert knappers were engaged in making tools.

The Pathway for Explicit Awareness: the ventral "what" stream

The Inferior Parietal and Temporal Cortex

The ventral pathway appears to converge on the IPL (inferior parietal lobe) via the inferior and middle temporal cortex (see Figure 2 for the areas cited in the text) which is involved in the integration of planning/action with object recognition as well as conceptual aspects relating to using tools (Glover, 2002; Glover 2004; Jeannerod et al. 1995; Milner and Goodale 2006; Ramayya et al. 2010). Moreover, Milner and Goodale (2006) suggest that this area is where the explicit awareness of objects ("what") is integrated with the implicit pathway relating to visuo-spatial and motor information ("where/how"), which has also been implicated in knowing how to use tools according to function (Ramayya et al. 2010; Randeratha et al. 2009). Interestingly, some aspects of IPL in humans are thought to be unique with no clear correlate existing in nonhuman primates (Singh-Curry and Husain, 2009; Roland 1980).[3] Similarly, Glover (2004) has proposed that enlargement of the phylogenetically newer human IPL may be involved in planning strategies for action. Importantly, Milner and Goodale (2006) propose that what demarcates human IPL is the interlinking of ventral functions for overt recognition with implicit online motor functions of the embodied "primitive" dorsal stream (see also Rizzolatti and Matelli 2003; Husein and Nachev 2007; Singh-Curry and Husain 2009). As suggested by Peeters et al. (2009), this realignment seems to have occurred through derived neurostructures in IPS that evolved in response to the demands associated with making and using tools.

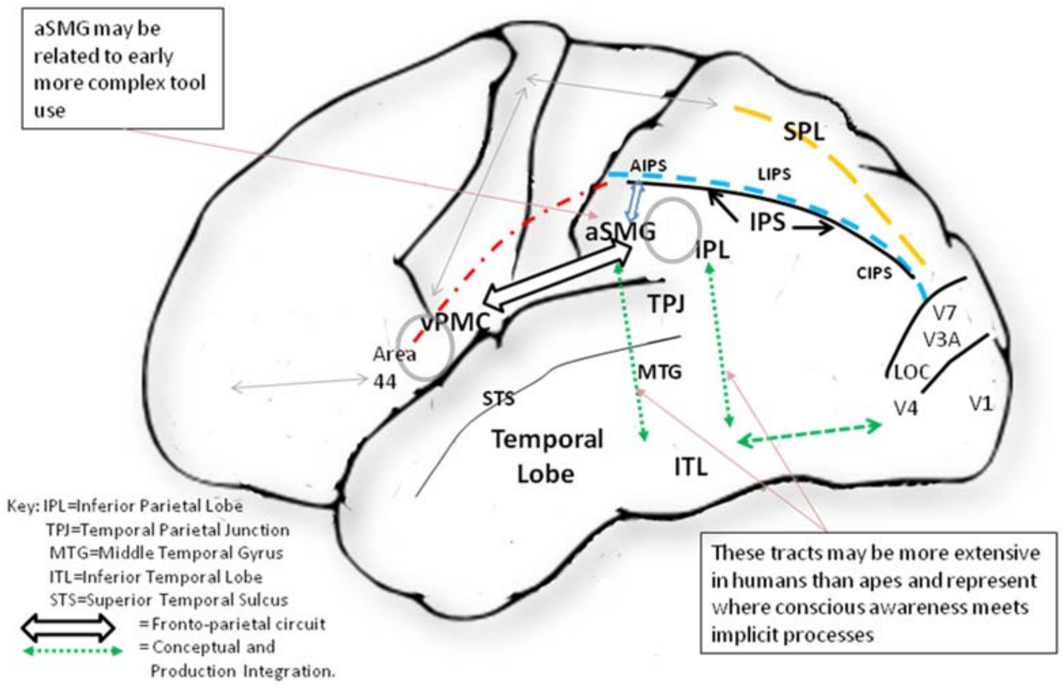

Figure 2. The ventral conscious "what" pathway (green arrow lines) that is also associated with conceptual aspects regarding ability to use more composite and a greater range of tools for different tasks. The two ellipses show the location of mirror neuron centres. Conventions the same as Figure 1 except where indicated.

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In order to produce the more refined symmetrical Acheulean tools, of which the 300,000 year old Isimila handaxe from Tanzanian or the 400,000 year old Furze Platt object provide typical examples (Wynn 2002), it would have therefore been essential for the consciously derived "what" system to undergo integration with the blind "where/how" pathway in order to realise the appropriate level of expertise (Hodgson 2005, 2006, 2007, 2009). Yet it is not just the fact that the ventral and dorsal pathways seem to have undergone greater integration in humans, but also the fact that this integration occurred at a more sophisticated level of processing than in nonhuman primates involving important perceptual and visuo-spatial capacities necessary for making tools; a task that requires the manipulation and detailed scrutiny of objects, as well as the three-dimensional rotation in visual memory of the tool to be shaped. Pertinently, Turnbull et al. (2002) proposed IPL may supply some explicit recognition of form to the visuo-spatial system, especially in non-optimal conditions and when mental rotation is required. This is supported by the fact that, as well as IPL and IPS, the temporal lobe, which mediates visual recognition and memory, has also undergone enlargement in hominins (Rilling and Seligman 2002; Singh-Curry and Husain 2009). The expansion of the temporal lobes in humans seems, however, to have predated changes to IPL (Joseph 1996; Rilling and Seligman 2002; Falk et al. 2009), which may be linked to the need for greater awareness to significant perceptual cues required for decoding human facial expressions for social purposes (Rilling and Seligman 2002). The architecture for explicit but "passive" form recognition seems, therefore, to have evolved before this ability became available for tool production. This is important in relation to Wynn's (2002) point that shape constancy was already in place before stone tools were fabricated in that symmetry required an awareness of self-similarity (awareness that an object remains the same despite variation) that later was able to be acted on through enhanced visuo-spatial and visuo-motor abilities for the production of symmetrical tools. The enlargement and reorganization of the parietal lobe suggests that this area was therefore favourably disposed to exploit a previous "passive" inclination for symmetry of which the making of regularly shaped tools would have been one outcome. The initial stages regarding the assimilation of the above mentioned dorsal and ventral pathways may thus constitute the crucial difference separating the brain architecture of *Australopithecus*/*Homo habilis* from that of *Homo erectus*. These pathways may well have been in the making with the appearance of *Homo erectus* and reinforced in *Homo heidelbergensis* as a result of a reciprocal dynamic with toolmaking that led to increased survival rates for their makers that was reinforced by the Baldwin/ Ratchet Effect. The ability to produce early to late Acheulean tools may therefore have been contingent on the primitive ventro-dorsal IPS to inferior frontal pathway, which initially formed links with the ventral stream in the temporal cortex by way of aSMG as Peeters et al. (2009) suggest, that subsequently interfaced with the fronto-parietal system (see Figure 2).

Support for this scenario is to be found in recent studies of conceptual deficits associated with tool use of those suffering apraxia (Randeratha et al. 2009) where the ability to access tool-use-knowledge and to integrate this into a movement plan has been disrupted. The interlinking of the ventral and dorsal pathways with the fronto-parietal system may, therefore, have eventually led to the ability to produce composite tools during the Middle Palaeolithic that also involved a greater dependence on IPL and a tendency towards recruitment of the anterior frontal lobes (Ambrose 2010; Dubreuil 2010).

Research into nonhuman primates thus suggests the existence of a parieto-frontal system that underpins prehensile abilities and neuroimaging studies indicate that this system may be preserved in humans. Research also shows that the simple tool use that is within the range of nonhuman primates may depend on modification to such sensorimotor networks based on ongoing experience. The sophisticated tool use typical of humans, however, is also dependent on semantic input from the left cerebral hemisphere. So, although basic sensorimotor functions that mediate production abilities are shared by all primates, including humans, there seems to be a separation as a result of the conceptual representations that are unique to the latter (Frey 2007) that is reflected in the way the ventral stream interconnects with the dorsal stream.

The Mirror System

Mirror neurons in nonhuman primates fire at the sight of another monkey completing an action, such as grasping an object, but not at the sight of the object alone or when viewing a mimed grasping action in the absence of a targeted object. Such neurons have been found in area F5 in nonhuman cortex (Gallese et al. 1996; di Pellegrino et al. 1992; Iacoboni 2005; Rizzolati 2005), and it has also been established that superior temporal sulcus (STS) and F5 (ventral premotor in humans) seem to be linked to the posterior parietal area, namely PF (SMG in humans) located in the inferior parietal lobe. Area PF also contains mirror neurons similar to those found in area F5 (Rizzolatti et al. 2001; Rizzolatti and Matelli, 2003), that together form an integrated fronto-parietal circuit (Seltzer and Pandya 1994) for mediating actions (see Figure 2). Crucially, and in contrast to nonhuman primates, mirror neurons in humans fire when a person views an observed individual miming or pantomiming a tool action (Ferrari et al. 2005). This finding is corroborated by studies of primates that possess only a rudimentary ability to make and use basic kinds of tools—as observed in the wild and in controlled conditions—where protracted learning through observation is necessary before such a basic ability can be acquired (de Waal 1999: Whiten et al. 1999; Tomasello and Call 1997; van Schaik et al. 1999). Correspondingly, Ferrari et al. (2005) also found that the response of mirror neurons in monkey F5 arose only after a relatively long training procedure. This suggests that, in nonhuman primates, stimulus enhancement or emulation (where the observed results are "copied" in an approximate way) underpins the ability to respond to others using tools i.e., through successive approximation based on unspecified cues through being in the immediate vicinity where an activity occurs. In humans, mirroring also activates the ventral premotor and inferior frontal cortex, which includes area 44 (Buccino et al. 2001; Nishitani and Hari 2000; Rizzolatti and Matelli 2003). This seems to underpin the ability to engage in informed imitation i.e., the ability to understand the intention of another agent and/or the goal of the action concerned, and to re-enact that action to achieve an intended objective (Jeannerod 2006, p. 121), which is a much more complex capacity than stimulus enhancement or emulation (Rizzolatti 2005). In hominins, this may also be directly related to the capacity for mimesis that Donald (2007) regards as culminating around the time of *Homo heidelbergensis* that probably involved social communication without language. Thus, humans not only require a less prolonged and rigorous training procedure to assimilate the affordance and motor programmes for using tools (Rizzolatti and Sinigaglia 2006) but can also take advantage of pantomiming to learn such behaviour as mediated by the ventral premotor area and inferior frontal cortex (Bucconi et al. 2001; Grèzes et al. 1998). Figure 3 indicates the specific areas in human left hemisphere that are involved in pantomiming. The left inferior parietal area, as part of the mirror circuit of the above cited fronto-parietal system (which is additionally involved in the integration of planning/conceptual/pure visual information with visuo-motor abilities), when damaged in humans, gives rise to ideamotor/ideational apraxia i.e., an inability to pantomime tools-use actions regarding conceptual abilities (Sunderland and Shinner 2007; Króliczak1 and Frey 2009) . Crucially, damage to this region does not seem to give rise to such syndromes in nonhuman primates (Husein and Nachev 2007; Milner and Goodale 2006).[2]

As the ventral premotor cortex has strong reciprocal links with IPL to which the ventro-dorsal pathway (i.e., the where/how stream) converges by way of fronto-parietal connections (Gallese 2000), this has obvious implications in terms of the increased abilities afforded to humans thanks to a fuller interlinking of the various contingencies identified with a greater level of control. As a result of the more complete level of integration of these various pathways, the action affordances arising allowed objects to be manipulated and acted upon with greater effectiveness, as is demonstrated by the distributed neural networks in humans for the planning and execution of actions when using tools (Johnson-Frey et al. 2005). Figure 4 shows how the connecting neural tracts in humans compared to nonhuman primates are more extensive. This is further supported by the fact that, in order to be able to use tools involving shape and more structured use beyond which chimpanzees are capable, skills are required that recruit the fronto-parietal circuit, as outlined. The inferior parietal area may therefore represent a crucial point where the "what" and "where/how" as well as the mirror system intersect to enable the production and use of more complex tools as part of a left lateralised system that sub-serves conceptual abilities (Frey 2007, 2008; Ramayya et al. 2010). The interaction of these factors seems to have become particularly prominent during the late Acheulean, which eventually led to the ability to intentionally direct the course of innovation in ways that increasingly benefitted those involved (see, for example, Read and van der Leeuw 2008). The later, rather than earlier (Shipton et al. 2009; Shipton 2010), Acheulean may therefore have served as a crucial point at which the influence of social factors relating to true imitation came to the fore and provided the conditions whereby

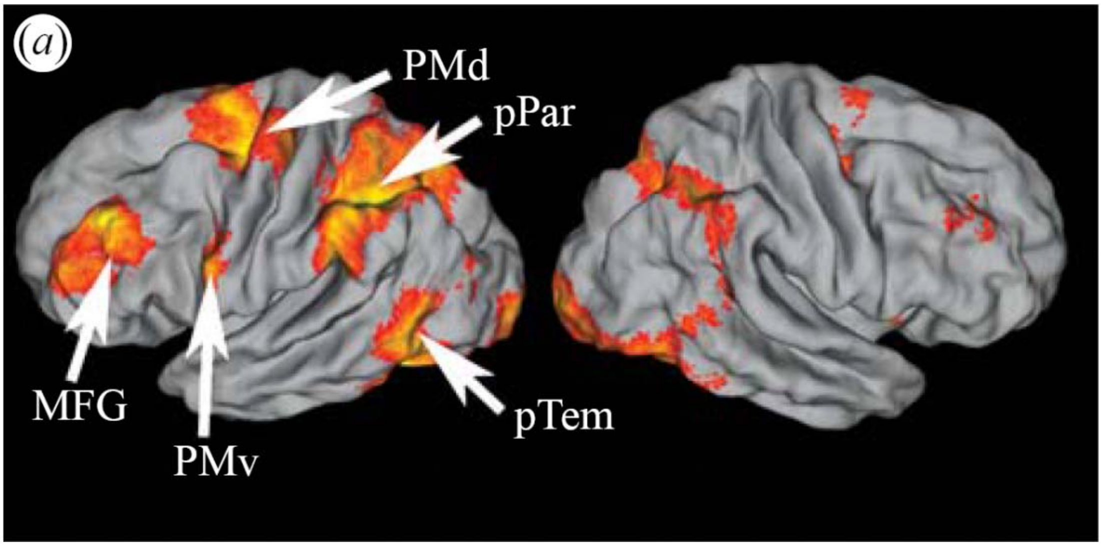

Figure 3. Areas of the cortex active in pantomiming and planning familiar pantomime tool actions in the left and right hemispheres when using the right hand MFG – Middle Frontal Gyrus; PMv – Ventral Premotor; PMd – Dorsal Premotor; PMd – Posterior Parietal; pTem- Posterior Temporal. (Reproduced with permission of The Royal Society, from Figure 1, Frey, S. H. 2008. Tool use, communicative gesture and cerebral asymmetries in the modern human brain. Phil. Trans. R. Soc. B. 363, 1951–1957).

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innovation could take place that allowed the advantages of group size to increasingly take effect. This may also be connected to the increased length of time the human brain requires to mature which allows motor and social skills to be acquired (Coward and Grove, 2010 this volume).

The Visual Template and Procedural Factors

Gowlett's (2007) emphasis on the importance of procedural demands for making stone tools and the playing down of the supposed mental template may reflect the practicalities required for knapping skills that depend mainly on the embodied dorsal pathway. Hallos (2005), however, has shown that the production of Acheulean tools also requires sophisticated planning procedures; a fact borne out by Pope's analysis and construction of the processes involved in tools produced by *Homo heidelbergensis* at Boxgrove (Pope 2004). Thus, although the *chaîne opératoire* (as mediated by the implicit processes of the dorsal stream) is important for making tools, in order to successfully manufacture an Acheulean biface, especially the later more sophisticated examples, a reliance on a visual template would have been increasingly necessary (Keller 2004, 92; Sharon 2007), a fact also demonstrated by ethnographic studies (Pétrequin and Pétrequin 1993); although such a direct correspondence with modern human groups is not always feasible yet such groups are often studied or cited accordingly e.g., Stout (2002), de Beaune (2004). This reinforces the importance of the integration of the various pathways identified and, as suggested by Gamble, "there was no separation between doing and thinking in the act of stone knapping" (Gamble 1999: 129). Moreover, Sharon et al. (2010) have indicated that a mental template would have been essential for the production of Acheulean tools, which may be related to what has been termed a "bauplan" (Lycett and Gowlett 2008).

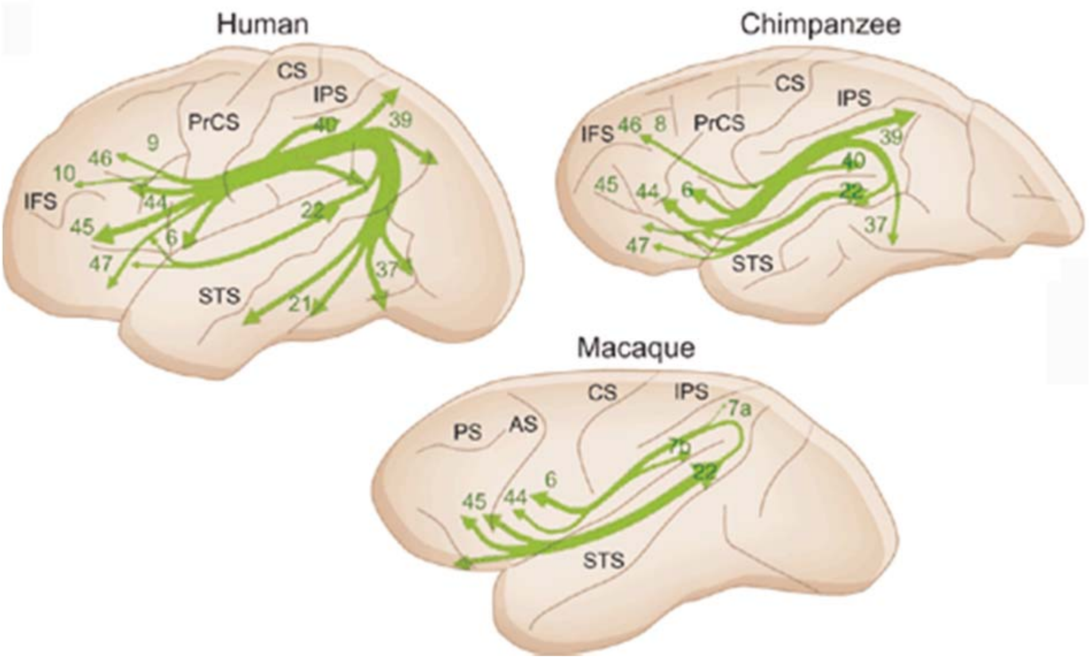

Figure 4. The various neural centres identified in the text showing how the connecting tracts become more extensive from macaques to chimps to humans. Note how the tract connecting the parietal area to the temporal region is either much smaller or absent in non-human primates. AS, arcuate sulcus; CS, central sulcus; IFS, inferior frontal sulcus; IPS, intraparietal sulcus; PS, principal sulcus; PrCS, precentral sulcus; STS, superior temporal sulcus. (Reproduced with permission of Nature Neuroscience from, Figure 1. Ghazanfar, A. A. 2008. Language evolution: neural differences that make a difference. Vol. 11 (4): pp. 382-384).

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Perhaps previous reference to a mental template has been over simplistic in suggesting that this is an all or none phenomenon when, in fact, there appears to be a graded response that can range anywhere from the implicit to fully explicit as is reflected in the growing interest in symmetry and standardised tools.

These observations can be assimilated with McNabb et al.'s (2004) analysis of early Acheulean toolmaking from the Cave of Hearths whereby an initial reliance on the natural shape of stone blanks dictated the final shape (as processed by the embodied dorsal pathway), yet several of these tools also seem to show a greater attention to actual form. Such "occasionals" may in fact constitute evidence of the beginnings of an overt conscious preoccupation with form that was mediated by aSMG and represented the initial coming together of the ventral and dorsal pathways, which was eventually realised in the prodigious symmetry of the late Acheulean handaxes referred to by Wynn (2002). This provides further evidence that there may have been an initial reliance on the "blind" procedural coordinates involving the "where/how" embodied pathway that was increasingly supplemented by the consciously disposed "what" stream. This tendency is highlighted in McNabb et al.'s sequence of events (which derive from a site dated sometime before 500,000 BP and therefore perhaps represents the onset of such a process) and Stout's observations regarding the increasing demands on brain functioning from Oldowan through to Acheulean toolmaking.

In sum, there must have been an incremental coming together of the abilities relating to visual, visuo-spatial and visuo-motor capacities so that increasingly complex tools types could be produced that was later furthered by the social scaffolding available through fronto-parietal mirror neurons (Binofski et al. 1999; Grove and Coward 2008). It would have been the interplay between these various pathways, which interacted with social learning, that eventually led to the more complex tool types subsequent to the Acheulean. It seems, however, that it was perhaps from approximately 500,000 BP (Wynn 2002;Wynn 2004; Saragusti et al. n.d.; Grosman et al 2008; Wenban-Smith 2004) with the appearance of the more refined Acheulean tools of *Homo heidelbergensis*, that the tight coupling between the cited neural circuits and toolmaking tended to become supplemented by social learning in that a greater range and more composite tools began to appear in the archaeological record. Figure 5 sets out the possible chronology where the initial dominance of biological determinants for the production of tools eventually became subject to more diverse cognitive influences thanks to the restructuring of the brain. From this it can be hypothesised that, from around 500,000 BP, Acheulean tools began to serve as non-functional socially-mediated objects connected to display involving increased levels of investment. These insights can be assimilated with McNabb and Cole’s Visual Display Hypothesis (McNabb, this volume) but only in so far as this proclivity began to become a more frequent, rather than merely occasional, aspect of behaviour during the later Acheulean.

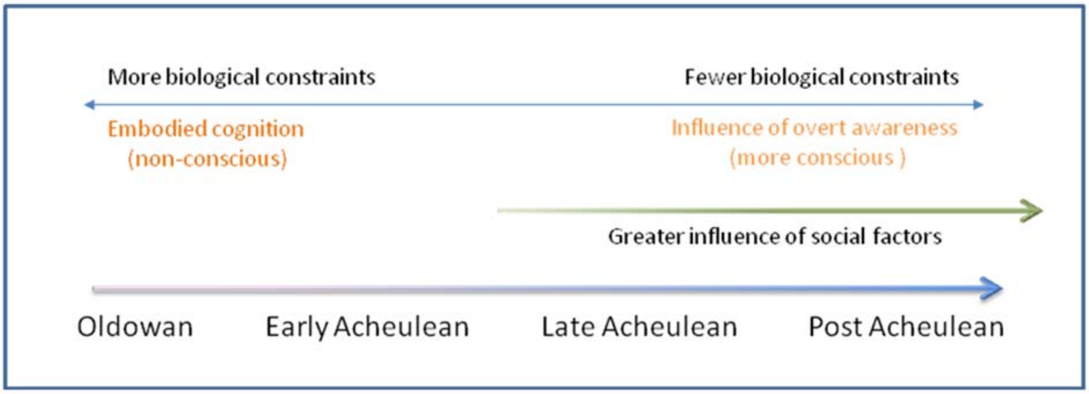

Figure 5. Influence of biological and cognitive factors on toolmaking (this format does not preclude the fact that Oldowan and Acheulean tools also appear at later dates than indicated as the scheme illustrated is based on minimum cognitive competence).

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Conclusion

Four phases of neurocognitive development seemed to have occurred related to toolmaking, 1) an enhanced primitive system relating to Oldowan tools that was mainly associated with developments in IPS, 2) augmentation of the enhanced primitive system relating to the early Acheulean associated with both IPS and ventral premotor cortex, 3) refinement of augmented enhanced system in IPS, premotor, and inferior parietal area relating to the late Acheulean, 4) addition of conceptual domain to [3)] relating to the appearance of composite tools during the Middle Palaeolithic that was mediated by the "what" ventral pathway that was later augmented by the fronto-parietal mirror pathway. In contrast to nonhuman primates, extra visual coordinates may therefore have been recruited in the IPS of *Australopithecus/Homo habilis* as part of a "primitive" ventro-dorsal pathway that led to the ability to produce Oldowan tools, which was later enhanced with further visual functions that allowed *Homo erectus* to produce the first Acheulean tools. As these increments increasingly became interconnected with the somatosensory and motor systems, hominins were thus able to manipulate and shape objects with greater acumen. The ventro-dorsal and dorsal-dorsal streams provided a means whereby information could be processed implicitly i.e., not available to immediate conscious awareness, which was closely tied to the object concerned in that these streams may be regarded as embodied and which led to the conservatism of Acheulean and Oldowan tools. Later Acheulean tools involved increasing enhancement of IPS and recruitment of IPL by way of aSMG that led to a greater concern for symmetry and coordinates relating to the processing of 3D shape from motion etc. The IPL subsequently began to play an important role in the production and ability to use more complex tools, which was mediated by conceptual imperatives linked to overt awareness of the ventral pathway that led to a reorganization of this part of the cortex, which probably reached a "tipping point" in *Homo heidelbergensis* (Dubreiul 2010). When the more consciously derived ventral steam began to engage more fully with the dorsal pathway, however, this eventually led to the ability to produce and use a greater range of tools. These abilities were further enhanced by the appropriation of mirror neurons that allowed more socially derived factors to increasingly affect how tools were made. Thus, thanks to the reorganisation of the neural pathways that occurred in response to the reciprocal processes associated with making tools, the human brain came to realise a distinctive architecture that allowed visual information on a number of levels to combine including visuo-spatial, visuo-motor, and overt (conscious) visual capacities, that was also supplemented with socially derived imitative capabilities.

Endnotes

[1] The underlying neural structures relating to how the brain processes visuo-spatial, motor, and pure visual information are highly complex and, therefore, a summary of the main thrust of the argument to be presented below is provided for convenience. Visual information first interfaces with the early visual cortex in the occipital area where certain basic aspects of form are processed. Subsequently, one pathway projects to the posterior parietal cortex (the dorsal "where/how" pathway) for processing visuo-spatial information with a second pathway projecting to the temporal cortex (ventral "what" pathway) where pure visual information is accommodated. The dorsal pathway also divides into two sub-streams where the dorsal-dorsal pathway projects to the superior parietal area, for online visuo-spatial control, and the ventro-dorsal pathway to the intraparietal sulcus (or IPS), where visuo-spatial and motor integration occurs. The processing in the dorsal stream is essentially implicit in being unavailable to conscious awareness whereas the ventral stream *is* available to such awareness. The dorsal stream, especially with respect to the IPS, allows nonhuman primates to grip objects using the entire hand whereas, in humans, the same area appears also to allow the employment of a precision grip with enhanced capabilities. This occurs thanks to the interfacing of the forward (anterior) part of IPS with the premotor and motor cortex (as well as somatosensory areas) that also contain canonical and bimodal neurons through which both the affordances accorded by objects and the extension of the body can be realised, respectively. This pathway forms an arch that is referred to as a "primitive" system (as cited by Stout and Chaminade 2007), which is shared by primates and is non-conscious in the sense that tasks can be performed without the need for conscious awareness i.e., the processing is essentially automatic but should not be confused with a lack of self-consciousness. Certain differences seem to exist in human IPS in that visuo-spatial coordinates not only operate at a more sophisticated level e.g., process 3D shape from motion and symmetry, but also interface more completely and effectively with the forward motor area. Initial increments along this pathway permitted early hominins to begin producing Oldowan tools. These, however, were subsequently augmented by *some* pure visual coordinates deriving directly from the early visual cortex that projected to the dorsal pathway, which meant that the visuo-motor system was able to benefit from greater control but still at a pre-conscious level, which thereby facilitated the first Acheulean tools. Thus, there was a reciprocal relationship between the underlying neural structures and tool production that led to changes in the way these pathways came to be structured that depended on the affordances embodied in objects, which led to the conservatism of Oldowan and earlier Acheulean tools. In other words, early toolmaking depended on a reciprocal dynamic that was closely linked to implicit cognitive processes that were tied to and scaffolded through a stepwise engagement that was intimately related to the materials being transformed (see discussion on the relationship between affordances and canonical neurons). In later Acheulean tools (after 500,000 BP), however, the dorsal pathway began to interface more with the ventral stream. As the ventral stream is concerned more with overt awareness/consciousness, this led to an expansion of the parietal area that allowed the ventral premotor, and corresponding dorsal pathway, to interface with conceptual aspects of tool use (part of the fronto-parietal system) which ultimately allowed a greater range of tools to be produced during the late Acheulean to Middle Palaeolithic period. Later developments involving composite tool use were probably also facilitated by mirror neurons that overlaid the aforementioned fronto-parietal system that allowed social learning to occur (see below for an explanation). Oldowan tools are thus held to be mediated by a neurostructure that remained tied to what will be referred to as an enhanced "primitive" visuo-spatial/visual motor system which, although essentially the same as in Pan, nevertheless, benefitted from a certain

"tuning" to the basic network. As the enhanced primitive system operated at an implicit/embodied level, the spatio-visual coordinates necessary for producing Oldowan and early Acheulean tools were dependent on the prevailing affordances inherent to the materials engaged with in that there was a close interconnection between making tools and implicit processes.

[2] The processing of 3D shape from motion has been found to demand much more processing capacity than is the case for 2D shape. According to Orban and associates (Orban et al. 2006) "Human IPS includes four motion sensitive regions, ventral IPS (VIPS), parieto-occipital IPS (POIPS), dorsal IPS medial (DIPSM) and dorsal IPS anterior (DIPSA), which are also sensitive to three-dimensional structure from motion (3D SFM). On the other hand, the monkey IPS contains only one motion sensitive area (VIP), which is not particularly sensitive to 3D SFM. The human IPS includes four regions sensitive to two-dimensional shape and three representations of central vision, while monkey IPS appears to contain only two shape sensitive regions and one central representation."

[3] Damage to the right inferior parietal area in humans—usually areas 39 and 40 and temporo-parietal junction (Halligan et al. 2003)—causes neglect involving an inability to attend to events in the left hemifield whereas damage to the equivalent left area leads to ideational apraxia (Husein and Nachev 2007). Crucially, monkeys do not seem to suffer neglect when similar areas of the brain are damaged though they may experience extinction that is regarded as a separate syndrome to neglect (Milner 1987; Milner and Goodale 2006, p. 193, 196). The fact that non-human primates fail to suffer neglect may be due to the fact that monkeys lack an equivalent inferior parietal area. This area has recently been implicated in tool use as an interface where perceptual and visuo-spatial/motor abilities converge that allows for global scrutiny of visual information in relation to sustained attention (Rushworth et al. 2006; Rizzolati and Matelli 2003; Hodgson 2005, 2009). Neglect also relates to the fact that the right parietal area is concerned with scanning or attending to a scene in a holistic way i.e., has a wide "searchlight" that encompasses a broad field of view covering both hemifields that does not apply when the corresponding left hemisphere suffers damage where only the right hemifield is affected (Farah 2000 p. 213). As the right inferior parietal area is privileged for the integration of allocentric object recognition and egocentric visuospatial coordinates within a broad spatial reference frame, this has implications for understanding the making of stone tools in that the left hand invariably serves to secure the tool to be struck that is positioned to the left of the mid-body line and therefore lies within the left visual field. Importantly, the right hand brings the hammerstone down towards the core to be knapped within the broader field of vision mediated by the right hemisphere. A wider field of view and the greater attentional resources required, concerning the integration of the ventral and dorsal streams, are therefore brought together in the left hemifield so that the whole scene can be observed in relation to the striking platform that would also help avoid potential injury to the left hand. This scenario receives corroboration in the finding that the left hemisphere (right hand) has been found to be specialised for movement trajectory control whereas the right hemisphere (left hand) is more concerned with position control (Haaland et al. 2004). It is likely that this asymmetry developed very early in hominin evolution that is supported by the investigation of Delagnes and Roche (2005) that found a different functional specialization required by each hand for the making of stone tools. This suggests that either *Australopithecus or Homo habilis* may have been endowed with cognitive abilities beyond that of modern day chimps that provided the cortical foundation on which later processing abilities for making tools were based.

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RETHINKING PHYLOGENY AND ONTOGENY IN HOMININ BRAIN EVOLUTION

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Abstract

Theories of hominin and human cognitive evolution have traditionally focused on the phylogeny of the human brain, and on comparisons of human and primate brains in relation to social or ecological variables. Far less attention has been paid to ontogenetic processes, despite the recognition that experience has a profound influence on adult cognition. In this paper we discuss the interplay between phylogeny and ontogeny by examining relationships between human brain size, developmental scheduling and cognition.

The correlates of large brains include not only altered subsistence and life-history strategies to meet associated energetic costs, but also on macro- and micro-scale structural adaptations required to meet increased processing costs. This means that larger brains are of necessity more highly interconnected brains, with higher degrees of folding of the neocortex (gyrification) and higher ratios of myelinated connections between neurons (white matter) to neurons themselves (grey matter). Here we argue that the combination of these evolutionary trends underpins the complexity of human behaviour, as the neural circuits involved in cognitive mechanisms such as the mirror neuron system (the system governing motor emulation and imitation) and theory of mind (fundamental in social cognition) mature only slowly, and require considerable socially-scaffolded experience to develop to their full potential. These abilities are likely to be fundamental in characteristically human behaviours such as the cultural transmission of complex forms of tool manufacture and use, attested to in the archaeological record. Their elaborated modern human forms, we argue, are possible only in the context of the evolution of relatively slower trajectories of brain growth and hence longer periods during which the growing brain can be influenced by experience among modern humans relative to other primates.

Here we review some of the differences in ontogenetic brain development between humans and other primates, and compare the rates and trajectories of neural development between ourselves and our closest living relatives the chimpanzees to suggest that the human pattern of expanded periods of growth coupled with slower trajectories of neural development is likely to have been of huge significance during hominin evolution. In addition, we discuss fossil and archaeological proxies which might allow the reconstruction of evolutionary patterns of development, suggesting that it is only post-*Homo erectus* and specifically among *Homo heidelbergensis* and *Homo neanderthalensis* populations that developmental patterns approximate those of modern humans, arguing for a similar – but not identical – role for socially-scaffolded learning of complex technical skills as among modern groups in these species.

Introduction

Theories of hominin and human cognitive evolution have traditionally focused on the phylogeny of the human brain in relation to socio-ecological variables. A prominent example of such research is the Social Brain Hypothesis, the central tenet of which suggests that the size of the neocortex places constraints on social cognition and hence the size of the social group (Dunbar 1992, 9). Far less attention has been paid to ontogenetic, developmental processes such as the effects of infant socialization within these larger and/or more complex social groups, despite the fact that many lines of evidence now suggest that length and intensity of development and socialization have a profound influence on adult cognition and particularly on social performance.

By arguing for a renewed focus on ontogeny we are not suggesting that phylogeny is not important. Experiments in raising chimpanzee infants in human households did not produce simply unusually hairy humans (Hayes 1952) – our genetic heritage is of course fundamental to the structure and function of our brains, and to our development more generally. Indeed, our argument below will be based on the premise that it is the phylogenetic evolution of crucial life history parameters that makes the role of ontogeny development and environment so important. Adult cognition and indeed brain configuration is the result of the *interplay* between phylogeny and genetics on the one hand and ontogeny and an individual's interactions with the physical and the social environment on the other. Even fully 'modern' *Homo sapiens* do not automatically become fully-functioning members of their societies, any more than other animals denied environmental input at critical periods of development acquire many of their own species-typical traits – even those often considered genetically 'hardwired' - such as birdsong - require experience and exposure to environmental stimuli to develop (e.g. Brainard and Doupe 2002). One of the aims of this paper is thus to argue that both phylogeny and ontogeny must be considered in any account of hominin evolution.

We will argue here that it is in fact the strong relationships between brain size and life history (Robson and Wood 2008; Barrickman *et al.* 2007; Smith and Tompkins 1995; Harvey *et al.* 1986) that are key to investigating hominin brains. We will examine the general ontogenetic trajectory of brain growth in humans relative to that in chimpanzees, and the relevance of these trajectories for social cognition, focusing particularly on two specific aspects of brain structure – gyrification and the ratios of grey and white matter in the brain – that are of particular importance during brain development. In the final section of the paper we consider the implications of a difference in trajectories between humans and chimpanzees for an increasing (phylo)genetic role for ontogenetic developmental processes of socialization during hominin evolution.

Ontogeny and phylogeny of human life history and growth

Modern humans have a larger than expected adult brain for our body size, relative to the ratio in other primates (Isler *et al.* 2008). In theory, encephalization could be achieved by either extending the period or increasing the rate of brain growth (or through some combination of the two; Robson and Wood 2008, 401). Either of these paths to encephalization will necessarily have significant implications for wider life history strategies.

Human life histories have much in common with those of the great apes. All great apes have relatively slow life histories, with long lifespans and slow growth (Charnov and Berrigan 1993). Slower life histories also correlate with larger adult body size (as energy can be invested in growth over a longer period), as well as with a constellation of other traits including larger babies (because larger mothers can invest in larger offspring), longer gestations and later age at first reproduction (Zollikofer and Ponce de Léon 2010; Robson and Wood 2008). Most elements of the human life history 'package' – with the interesting exceptions of age at first weaning and interbirth interval – see discussion in Robson & Wood (2008) are thus predictable from general primate trends, but are at the extreme end of the spectrum (Robson and Wood 2008). Our large body and brain size mean that we develop extremely slowly, with an extended period of juvenile dependence, late puberty and age at first reproduction, and years (even decades) of prolonged and intensive parental effort.

Pre-reproductive phases of human life are therefore absolutely and relatively longer than observed among other large-bodied apes with similar gestation lengths (Crews and Gerber 2003) and may even include evolutionarily novel stages of development such as adolescence (e.g. del Giudice *et al.* 2009; Locke and Bogin 2006; Bogin 1999; Schultz 1969). This unique human combination of life history traits has most frequently been explained in terms of selection for extended periods of development as an adaptation for the acquisition of complex ecological and/or technological foraging skills (e.g. del Giudice *et al.* 2009; MacDonald 2007), social skills (Joffe 1997), or indeed both (Walker *et al.* 2006).

A related possibility is that the human life history strategy may have been adaptive because it mitigates ecological risk or reduces mortality. Under this hypothesis juvenile growth rates are slow because energetic resources are directed towards brains and immune systems to reduce the risk of starvation, and because slower rates of growth free up resources that can be used to feed younger siblings (Crews and Gerber 2003). The resulting reduction in adult mortality among humans compared to other great apes (Robson and Wood 2008) may have reduced constraints on prolongation of growth, development and longer life spans in general, perhaps aided by cultural factors such as 'material culture, language, and socio-culturally elaborated life ways, including long-term care of family members and late-life reproduction by men' (Crews and Gerber 2003).

Although in this argument

'… juvenility did not evolve primarily for skill-learning, … it would nonetheless *permit* extensive learning ... once extended skills/social learning became possible thanks to a long juvenility, a self-reinforcing cycle could have ensued, in which the advantages of learning generated an evolutionary pressure to increase juvenility even further and promote the growth of even bigger brains' (del Giudice *et al.* 2009, 9)

As well as their derived life history strategies modern humans are characterized by a distinctive pattern of growth. While human gestations are not significantly longer than those of other anthropoids (Crews and Gerber 2003), they do demonstrate several differences in the allocation of energy to their foetuses, particularly in the last trimester when human foetal neurological development is fast-tracked at the expense of other tissues (Crews and Gerber 2003), contributing greatly to humans' secondary altriciality. This prioritization of brain growth continues throughout the first few years of life in humans: while brain growth continues at its rapid early pace for some time after infancy, bodily growth rates decline until the pubertal growth spurt corrects the imbalance (Bogin 1999).

Regardless of this rapid peri- and post-natal brain growth, at birth human infants have achieved a smaller proportion of their brain growth than other great apes, and this difference is maintained throughout their growth, as demonstrated clearly in Figure 1. Humans therefore reach their adult brain size more slowly than other primates. However, the differences have been exaggerated; the allometric exponent of neonatal brain size relative to adult brain size is negative (i.e. larger-brained species typically have smaller relative neonatal brain sizes), and human neonates have more or less the size of brain expected for an anthropoid primate of our brain size (DeSilva and Lesnik 2008), at ~29.9% of adult size compared to ~40.1% for chimpanzees (see DeSilva and Lesnik 2006 for a comprehensive review). Human infants also reach adult brain size earlier than usually claimed – on average 90% of adult brain size is achieved by around 5 years, only 1 year later than in chimpanzees (Robson and Wood 2008). While human mothers give birth to unusually large infants, then, those infants' brains are only slightly smaller than we would expect based on primate trends.

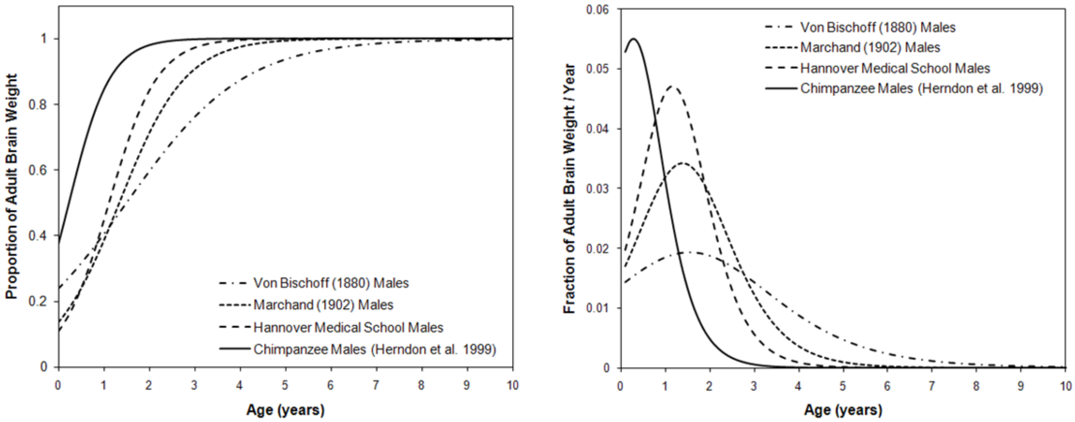

Figure 1. The trajectories of human and chimpanzee brain growth compared. The three human trajectories are from autopsy samples; the lines shown are the best-fit lines calculated by Kretschmann *et al.* (1979) from the raw data in each case. The chimpanzee line was calculated by fitting the growth equation of Kretschmann and colleagues, , to data published by Herndon *et al.* (1999).

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In addition, the overall trajectories of relative brain growth for both humans and chimpanzees are remarkably similar (Figure 1), suggesting that if humans were simply born later we would not deviate markedly from general great apes' gestational strategies – at least, in terms of brain development. As discussed above, when dental and somatic or bodily growth are also taken into account, human ontogenetic patterns deviate much more markedly from those of chimpanzees, being significantly slower; Zollikofer and Ponce de Léon 2010, 443. Nevertheless, in terms of the degree of neural development of our offspring relative to those of other primates, humans *do* appear to have an anomalously short gestation period. One potential selective pressure for this probably relates to the constraints imposed by the size of the female pelvic canal, itself reduced relative to that of other primates by the bipedal posture of humans (Franciscus 2009).

However, pelvic capacity is unlikely to be the only cause of these differences between humans' and other primates' brain development. Postnatal development is not linear, and while comparisons of neonatal and adult brain size are informative, consideration of patterns of growth at a finer scale reveal more differences between humans and other great apes that may have significant implications for adult cognition and behaviour.

While among precocial primates high gestational brain growth rates slow rapidly after birth relative to overall bodily growth, among (secondarily) altricial primates these rapid gestational rates of brain growth continue (Martin 1990). In humans these rapid growth trajectories continue for a full year after birth, compensating somewhat for our highly altricial offspring's small neonatal brain size. By a year after birth, human infants are pursuing a brain to body growth trajectory much like that of other primates – clearly demonstrated in Figure 2, in which we have 'shifted' a chimpanzee trajectory to be as altricial (i.e. small-brained) at birth as a human neonate.

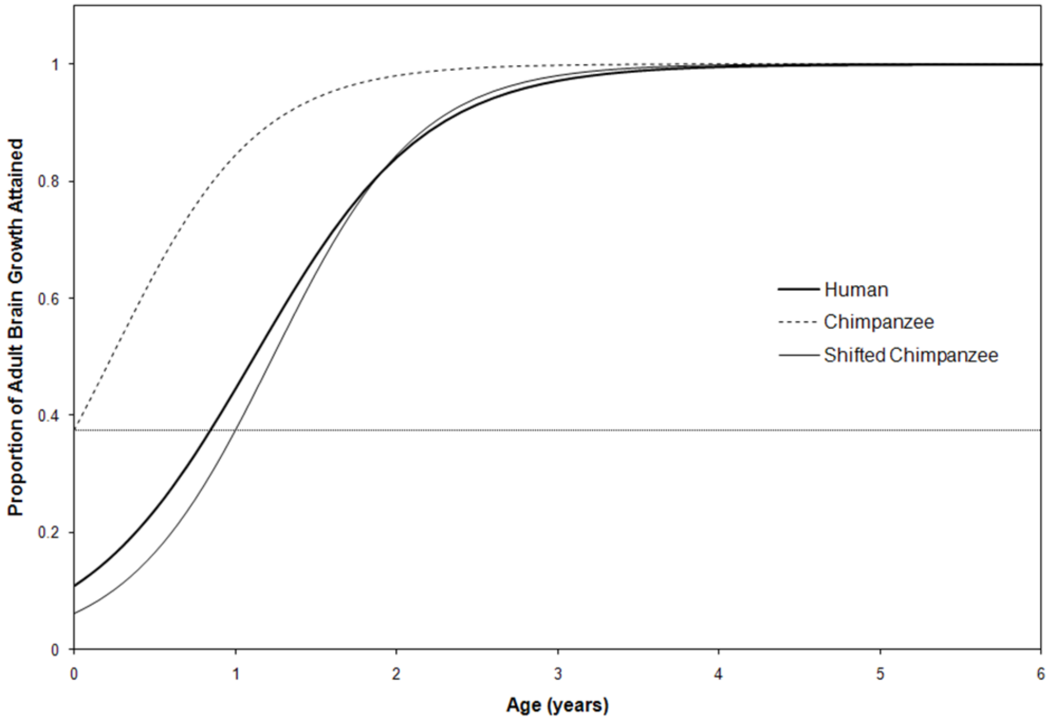

Figure 2. The similarity between the growth curves of chimpanzees and humans; the 'shifted chimpanzee' is born as altricial as a human, and follows a very similar trajectory. The curves show human data from the Hannover Medical School sample (Kretschmann et al. 1979) and chimpanzee data from the Herndon et al. (1999) database. Both curves show male growth trajectories.

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Thus, while trajectories of growth relative to adult brain size are not radically different among humans compared to other primates, growth *rates* do display some interesting differences. Figure 2 compares the growth rates of chimpanzees and humans over the first five years of life, and demonstrates that while rates of brain growth in chimpanzees peak no more than two months after birth, the human peak again occurs a full year later, at approximately 14 months. Note also that the peak growth rate in humans is somewhat lower than that in chimpanzees – meaning that despite our extreme altriciality, our brains never grow as fast postnatally (relative to their size) as do those of chimpanzees. Finally, it is also clear from this graph that the relative amount of brain growth occurring postnatally is substantially greater in humans than it is in chimpanzees (i.e. the area beneath the postnatal section of human curve is substantially greater).

Socialization, mirroring and Theory of Mind

Explanations of the specific advantages of extensive relative post-natal brain growth focus on the adaptiveness of a 'critical period' in which the brain can be 'tuned' to its environment during a relatively plastic growth phase. Some degree of neural plasticity continues well into adulthood (e.g. Merzenich 1987; Greenfield 1997, 115-118). However, the brain is particularly plastic early in life as the synapses develop between neurons ('synaptogensis'; Figure 3). Many of these developing synapses will be lost as the brain matures, due to competition for limited synaptic space and neural apoptosis ('programmed cell death'; Figure 3). Thus the synaptic capacity of immature neurons is almost 50% greater than that of adult cells

(Lenroot and Giedd 2006, 720). In the prefrontal cortex, peak synaptic density occurs at 3-4 years of age and declines as brains mature, particularly after puberty (Höistad *et al.* 2009, 6; Bear *et al.* 2007, 709), as those synapses that are reinforced by frequent use out-compete those that are under-utilized, and grow stronger to enable more efficient transmission of information between neurons that are frequently associated in particular recurrent tasks (Deacon 1997). 'Slower' trajectories of brain growth thus allow for a much longer period of 'experience-expectant information storage' (Greenough *et al.* 1987) over which these processes of synaptic proliferation, competition and pruning and neural apoptosis can occur (Figure 3), and during which they can be influenced by environmental stimuli (Bear *et al.* 2007; Westermann *et al.* 2006; see also Grove and Coward 2008 for further discussion). This long period of extreme plasticity in human children coincides with the development of 'higher-order' neurobehavioural cognitive functions, including highly developed motor and social skills (Courchesne *et al*. 2003: 343).

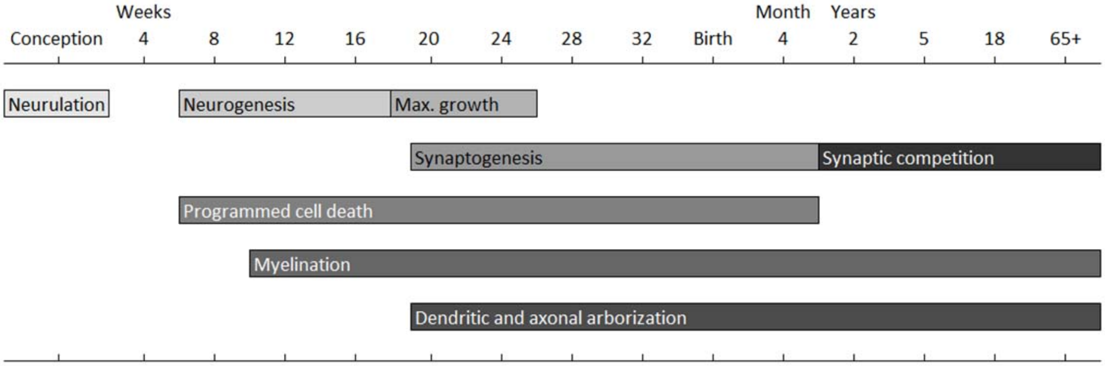

Figure 3. Sequence of events in brain maturation (redrawn from Lenroot and Giedd 2006 figure 1). Neurulation, the initial development of neurons, occurs first and is followed by multiple cycles of the production of new neurons (neurogenesis). New connections begin to be established between neurons (synaptogenesis), and the axons of different neurons 'compete' for space to synapse on the dendrites of recipient neurons and thereby establish a connection between those neurons (synaptic competition). Programmed cell death (apoptosis) prunes under-utilized neurons throughout these processes. Axons connecting neurons are ensheathed in fatty myelin to insulate and speed up action potentials travelling between those neurons, while further development and multiple branching (arborisation) of dendrites and axons and denrities continues throughout life.

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The mirror neuron system

Mirror neurons, which are activated by both performance and observation of specific, goal-directed actions (Rizzolatti and Craighero 2004), were first identified in macaques and only later in humans. Until very recently, most work has thus assumed an evolutionarily primitive heritage among primates for the basic mechanisms involved in motor emulation that were elaborated later in the hominin and human lines. However, more recent work has suggested that the information necessary to match observed with executed actions may not be (completely) genetically specified, but that sensorimotor learning during development may also have a vital role to play. Experimental work has demonstrated that the functioning of the mirror neuron system (MNS) in both monkeys and humans is strongly affected by training and experience (Catmur *et al.* 2008; Iriki and Sakura 2008; Catmur *et al.* 2007; Keysers and Gazzola 2006; Ferrari *et al.* 2005), suggesting that the 'mirroring' properties of the system are not completely innate. Instead, many are acquired through simple Hebbeian or associative learning processes, in which the temporal correlation of observation and motor performance activates both neural circuitries simultaneously, entraining the circuitries associated with both observation of others' actions (in multiple sensory modes) and kinaesthetic and sensory feedback from one's own actions and links them into a shared 'mirroring system', The Hebbeian maxim is thus, 'what fires together wires together' (Catmur *et al.* 2007; Keysers and Perrett 2004).

Neurological imaging and kinematic studies have demonstrated the vital role of sensorimotor functions and bodily 'know-how' in tool manufacture and use (Stout *et al.* 2008; Bril and Roux 2005; papers in Roux and Bril 2005) alongside - if not primary to - the 'higher-level' prefrontal and executive functions presumably involved in the broader contexts of action from the sourcing of raw materials to schemata of use. Among all tool-using primates, tool use is socially acquired and therefore likely to be reliant on MNS-mediated motor imitation – suggesting that it is the evolution and/or development of the MNS that underpins the appearance and elaboration of stone tools in the archaeological record. While the monkey MNS has now been demonstrated to respond to actions performed with tools (previously thought to be a human specialism), this has been demonstrated only after a long period of experimentation and familiarization of the monkeys to the tools and their use (Ferrari *et al.* 2005, 213, 221). In contrast, recent studies have suggested that in humans mere observation, or even simply *thinking about* motor actions may be almost equivalent to actual motor practice in improving motor learning (Heyes 2001, 256). While trained individuals do demonstrate stronger activations in response to others' actions (for example, trained pianists report finding it difficult to keep their fingers still while listening to piano music), even naïve individuals show some degree of neural activation when they observe others' actions (Keysers and Gazzola 2006, 389). This probably reflects the flexibility inherent in the varying selectivity of different neurons in the MNS, with some responding only to very specific motor actions and others more broadly, so that even novel actions can be extrapolated from the wide variety of motor skills that *are* within the observer's motor vocabulary (Keysers and Gazzola 2006, 389).

It is also notable that in monkeys, an MNS response to tool-actions was not sufficient for them to actually imitate the behaviour – given the opportunity to use a stick used in an experiment to access food left out of reach, the monkeys never attempted to do so (though at least one did pick up the stick and bite it; Ferrari *et al.* 2005). In fact, primates generally, while good *emulators* (being able to reproduce the physical results of actions in often very creative ways), are usually considered rather poor at *imitation*. In Horner and Whiten's 'puzzle box' experiments (2005), for example, juvenile chimpanzees shown how to access food inside the box performed only those actions relevant to retrieve the prize, while human children performed even the unnecessary actions they had observed. However, results of similar experiments designed to test apes' imitation skills have been mixed, and Heyes' review of the evidence suggest that chimpanzees 'can imitate to the extent that they have had prior experience of interacting with humans and/or explicit training to imitate' (Heyes 2001, 253; see also Iacoboni 2005). Animals deliberately exposed to particular forms of stimuli not frequently encountered in the wild routinely develop skills and behaviours not practiced by their wild conspecifics – hence the mismatch in a wide range of cognitive skills demonstrated by human-enculturated and wild chimpanzees (e.g. Ferrari *et al.* 2005; Heyes 2001, 253), suggesting that development of both the MNS and imitation are heavily scaffolded by experience .

A key observation here is that motor 'mirroring' among humans is also very closely linked to social skills. Humans tend to (non-consciously) imitate one another's facial expressions, gestures and mannerisms during social interactions (Frith 2008), with the degree of mirroring related to high scores on paper tests for empathy. Such mirroring inclines the 'imitated' party to perceive the interaction (and his/her interlocutor) positively (Heyes 2001, 256). Significantly, many of the motor actions involved in such social mirroring involve 'perceptually opaque' movements. For 'transparent' motor behaviours such as hand movements, others' and one's own actions can be perceived simultaneously and the neural pathways are thus amenable to simple associative learning processes. However, the movements of the face and trunk that are so crucial to social interaction are typically only visible using cultural artefacts such as mirrors, or through interaction with others (Catmur *et al.* 2007; Heyes 2001). Co-activation and entrainment of the motor and sensory neural circuits involved in these actions requires that we, 'watch others as they do what we are doing – whether they are deliberately imitating our movements, as adults imitate infants, or simply reacting in the same way to ongoing events, like fellow spectators at a sports match' (Catmur *et al.* 2007, 1529; see also Keysers and Gazzola 2006, 396; Heyes 2001).

The key to how the human MNS functions to imitate skilled behaviours such as tool manufacture and use is therefore to be found not only in phylogeny but also in ontogeny, as social skills and behaviours are critical to imitation and the acquisition of skilled motor actions. Chimpanzee tool use is of course highly skilled and socially acquired, particularly in the context of the mother-infant bond where infants have strong intrinsic motivation to copy behaviour and mothers to facilitate such copying (e.g. Matsuzawa 2007). However, this facilitation stops short of formal teaching (Tomasello 1999), and it has been argued that chimpanzee learning is based on a dyadic subject-object framework (mother-infant; mother-object; infant-object; object-object) focused on the emulation of actions on objects, rather than on socially-referenced triadic relationships among mothers-and-infants-and-objects (Matsuzawa 2007, 10; see also Sherwood *et al.* 2008, 435). In human children, such triadic relations commence from around 9 months of age (Sherwood *et al.* 2008, 435), and are strongly associated with other social skills, notably the capacities for joint attention and intentionality.

Individuals of many species may act together, either because their actions mutually affect one another and become coordinated or because of 'simultaneous affordances' in the environment that stimulate similar behaviours, for example a fresh carcass or indeed a buffet table (Knoblich and Sebanz 2008). However, higher levels of joint action may occur when individuals are able not only to perceive behavioural cues such as direction of gaze or bodily orientation but also to interpret them in the light of their own motor repertoire (via the MNS) and to attend to the same object(s) *together* - for example a parent pointing out things of interest (Knoblich and Sebanz 2008). Gaze following in particular has been widely studied in a variety of animal species, but studies on chimpanzees have produced mixed results (Sherwood *et al.* 2008, 430, 434 for review) while both dogs (e.g. Hare and Tomasello 2005) and goats (Kaminski *et al.* 2005) are consistently capable of following humans' gazes. This would suggest that domestication/socialization to (human) social systems in which joint attention is common may again be a key stimulus for the development of these abilities.

Once individuals are able to determine what someone is attending to, they may also be able to compare their own perceptions with those of the other to determine whether they are shared (Knoblich and Sebanz

2008). This level of joint attention clearly requires complex social cognitive skills, notably Theory of Mind (ToM - see below), and is likely to be the essential prerequisite for teaching, allowing the instructor to determine whether the learner has all the necessary perceptual attention or whether attention-guiding gestures such as pointing may be necessary (Frith 2008). While, as noted above, chimpanzee mothers *facilitate* infants' learning by making all the necessary equipment available, they do not direct attention to parts of the task they get wrong or correct their mistakes (Matsuzawa 2007; Tomasello 1999), and chimpanzees do not appear to use 'ostensive' gestures that would indicate the signal to follow will be a deliberate communication about something of relevance to the receiver. In contrast, human infants are very sensitive to these behavioural cues; for example, eye contact prior to demonstration of a novel action or the naming of objects dramatically improves a child's imitation of that action or recall of the name (Frith 2008).

Among humans, individuals are also usually able to move beyond this stage of behavioural cueing to model the *intentions* behind actions and to engage in complementary action to aid (or to hinder) others' actions – *joint intentionality*. In order to achieve this it is necessary to represent both their own and others' contributions to the final goal (Knoblich and Sebanz 2008, 2025). Among humans, of course, there is a questionmark over the extent to which the evolution of human language scaffolds the development of higher stages of joint attention during childhood, or indeed the evolution of the underlying cognitive mechanisms among our hominin ancestors. However, many of these behaviours have precursors in other primates and thus were probably inherited from a common ancestor, and language learning itself is hugely reliant on social interaction and cognition in general, and ToM (see below), joint attention and perhaps also the MNS more specifically, suggesting that these forms of fundamentally social cognition are primary to language, not results of it.

In short, far from being innate, genetically specified mechanisms for acquiring skilled behaviour, the MNS and skilled motor imitation more generally are hugely influenced by experience acquired during development, which is provided as much by the social as the physical environment. The acquisition of these skills, utilising genetically inherited basal capacities, is thus strongly associated with - and probably scaffolded by - fundamental mechanisms of social cognition such as ToM.

Theory of Mind

ToM is perhaps most usefully defined as the ability to understand that not only do others *think* in much the same way that you do, but also that *what* they think may differ. This appreciation that others have a different perspective from yourself, and to model that alternative perspective, underpins human social interaction, and sets us apart from most other primates in kind, and from all other primates in degree (see e.g. review in Emery and Clayton 2009). In modern human infants ToM emerges fully in infants by 4-5 years of age (Emery and Clayton 2009; Grove and Coward 2008 and references therein; Brüne and Brüne-Cohrs 2006, 440), i.e. during the period of extreme plasticity occurring during the key phase of ontogenetic brain growth discussed previously.

However, in some individuals ToM does not develop in the usual manner; autistic spectrum disorders (ASD), whose severe forms are sometimes known as Asperger's Syndrome, are characterized by deficits in social cognition and interaction and the avoidance of novel situations and behaviours of any kind. Although the specific nature of both the deficits and the neurological mechanism(s) involved in ASD remain the subject of considerable debate, one significant line of enquiry suggests that the condition can be defined, at least in part, by a lack of ToM abilities (Baron-Cohen *et al.* 1985) while many other cognitive capacities and 'non-social' forms of intelligence are preserved (Brüne and Brüne-Cohrs 2006, 446).

In addition, individuals with ASD often demonstrate difficulties with imitation that seem to represent a failure of the ToM capacities that would normally 'scaffold' the development of the MNS

'…resulting from early inattention to social stimuli (including adults imitating the autistic infant), and deficits in joint attention reducing the frequency of synchronous movement in response to a common stimulus' (Heyes 2001, 259,

such that Hebbeian processes responsible for the necessary neural connections do not occur, or occur to a lesser extent, in these individuals.

A growing number of researchers have also implicated abnormal neurological developmental processes in ASD. Current evidence suggests that the autistic brain grows substantially faster than that of normally developing individuals (Courchesne *et al*. 2003, 2004, 2007; Redcay and Courchesne 2005), reaching adult weight considerably earlier as a result. Yet the adult brain size of autistic individuals does not differ significantly from that of neurotypical individuals, implying that it is the *pattern* of growth that is the crucial factor.

In Figure 4 we plot rates of brain growth of both neurotypical children and those with ASD for comparison; the important point to note here is that the ASD phenotype involves a period of neural 'overgrowth' relative to neurotypical controls (Redcay and Courchesne 2005). As a result, children with ASD have substantially bigger brains than neurotypical controls between the ages of approximately 2 and 5, 'at the beginning of an important period of developmental neuroplasticity and learning' (Courchesne *et al.* 2003:343). Courchesne and colleagues argue that this more rapid growth of the brain in individuals with ASD shortens the critical period during which experience of the physical and social environments may influence synaptic proliferation and pruning.

One argument is that this reduction of the timeframe in which the selective effects of experience may 'shape' patterns of neural development means that ASD synaptic proliferation is explosive and random, resulting in early fixation of potentially anomalous connections and the subsequent inability of the apoptosis mechanism to achieve targeted pruning of maladaptive synaptic connections (Casanova *et al.* 2008; see below).

Further support for this position may be found in recent arguments that ASD individuals often experience sensory hypersensitivity. Individuals with ASD have much better eyesight (≈2.79x better than average) and more sensitive olfactory, haptic and auditory systems than neurotypical controls; furthermore, the degree of hypersensitivity correlates with scores on measures of ASD severity (Baron-Cohen *et al.* 2009). As Baron-Cohen *et al*. point out, such hypersensitivity could be the result of processing differences at multiple levels: sensory receptors could be denser or more sensitive, neural processing could be faster and/or top-down inhibition systems could be affected. This last might mean that the process of forming higher-level 'holistic concepts and meaningful labels' (Snyder 2009) that usually help structure perception of sensory information

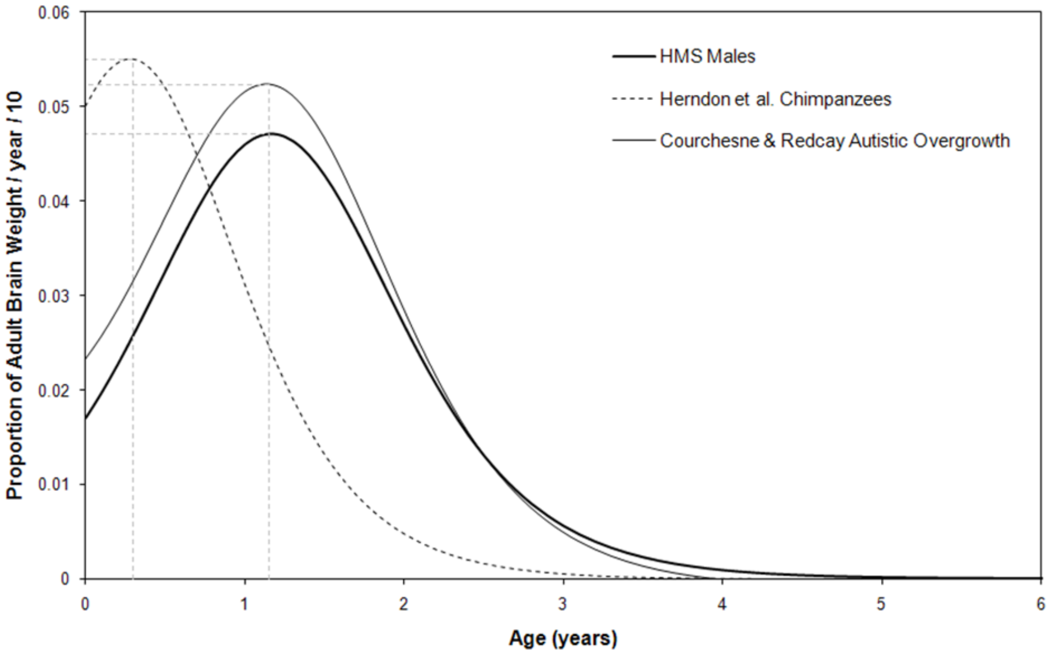

Figure 4. Chimpanzee, non-autistic, and autistic human growth rates over the first five years of life. Note all lines are scaled to proportion of adult brain weight; there is of course a vast difference between the sizes of chimpanzee and human brains, with ASD and non-ASD brains being virtually identical in size by adulthood. The human curve is calculated from Hannover Medical School data (Kretschmann et al. 1979), and the chimpanzee curve from the Herndon et al. (1999) database. The autistic overgrowth curve is calculated by multiplying the Hannover Medical School curve by age-specific values of the Redcay and Courchesne (2005) autistic overgrowth equation.

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and inhibit the costly processing of lower-level details does not occur (or occurs to a lesser extent) among individuals with ASD. These individuals would then routinely experience sensory 'overload', with reduced top-down processing constraints resulting in a low signal-to-noise ratio.

Neuroimaging of the brains of individuals with ASD does indeed appear to show reduced co-ordination of activity between association areas and those mediating perceptual and emotional processing. Brains are more connected between local regions, and differences in gyrification and in grey and white matter distribution (see below) suggest an increase in short-range relative to long-range connections (Casanova *et al.* 2008). One argument is that among children with ASD, short-range neural connections proliferate at the expense of long-range circuits and systems relating to top-down control and coordination during early development. Such a pattern of development might result from a failure of synaptic pruning mechanisms following early over-production and/or a disturbance in white matter production, such as in processes of myelination that would make long-range connections more efficient and competitive. (Casanova *et al.* 2008).

It therefore seems likely that the development and refinement of higher-order and particularly social cognition is intimately related to the evolution of slower trajectories of neural developmental trajectory in normally developing humans, relative to that in other primates and in our hominin ancestors, and that a focus on the interplay between ontogenetic and phylogenetic factors is therefore fundamental to understanding hominin brain evolution. Most studies of hominin brain evolution have focused primarily on gross brain size and/or the relative sizes of different brain and particularly neocortical structures. However, larger brains are associated not only with the energetic costs offset by changing life-history strategies, but also with significaitn processing costs, as increased brain (and body) size is associated with increased transmission times for nerve impulses. In addition, as the number of neurons increases, the number of connections between them increases exponentially, and thus, given already extremely high levels of connectivity between cortical neurons, larger brains are potentially highly costly and inefficient. The ways in which these costs are offset, and the ways in which these interrelate with solutions to large brains' energetic costs, have significant repercussions for large-brained species. Two of these adaptations to the increased processing costs of large brains – gyrification and the ratio of white to grey matter in the brain - are examined briefly in the following sections.

Gyrification

Perhaps the most obvious feature of the brain's gross anatomy is the wrinkled and folded surface of the neocortex. Viewed in section, it is clear that some parts of the neocortex bulge outward (gyri) while some are folded inward (sulci). The ratio of total cortical surface (i.e. *including* the surface area of cortex hidden in cerebral sulci) to exposed cortical surface (i.e. *excluding* the surface area of cortex within sulci; Rilling 2006) yields a 'gyrification index' (GI) which varies both phylogenetically and ontogenetically (Figures 5 and 6).

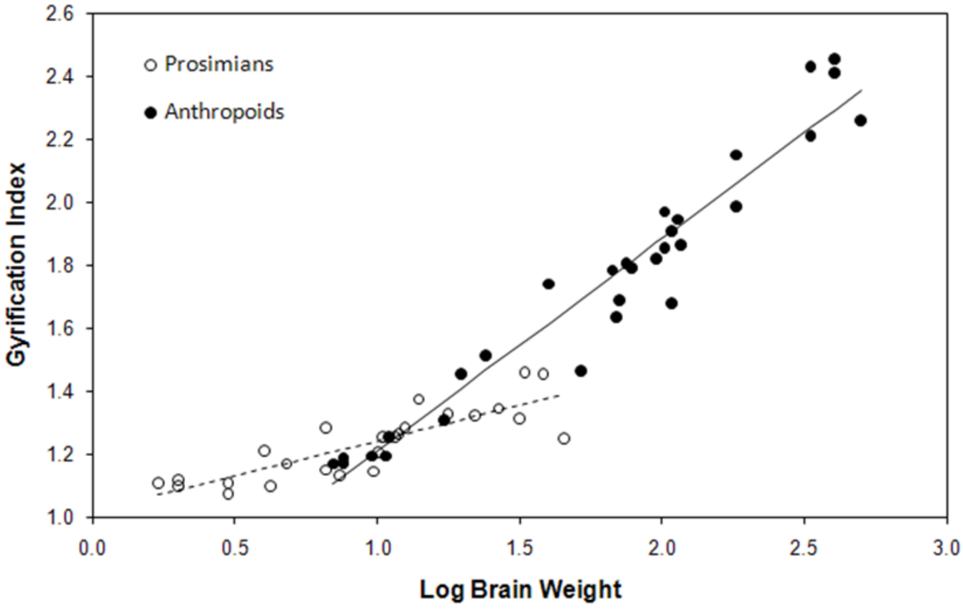

FIGURE 5. THE PHYLOGENY OF THE GYRIFICATION INDEX IN PROSIMIANS AND ANTHROPOIDS (DATA FROM ZILLES *ET AL*. 1989).

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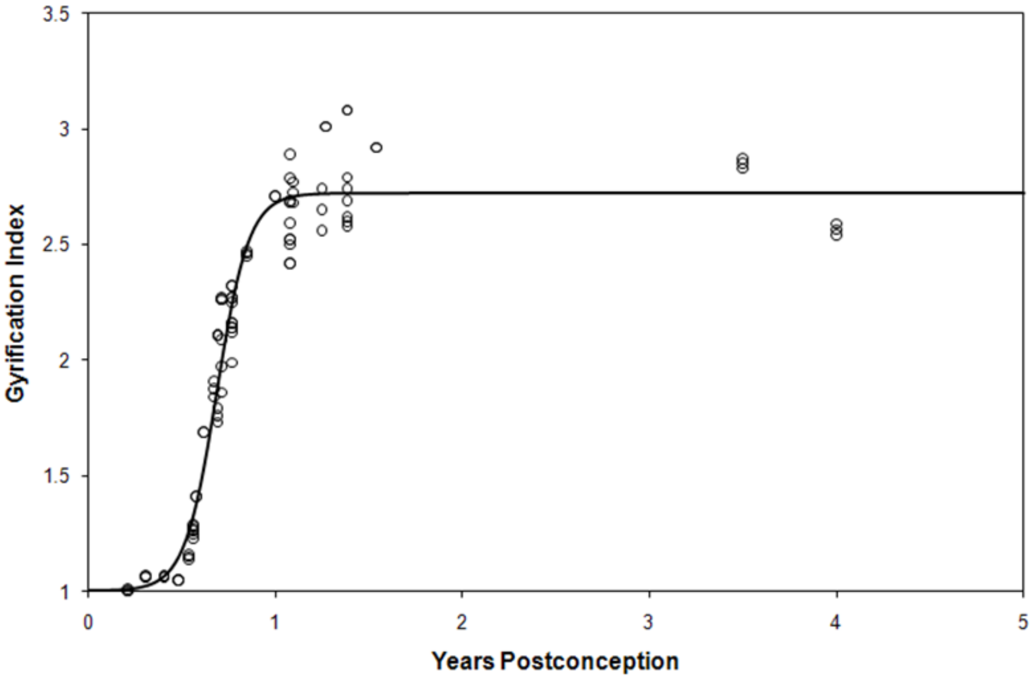

Figure 6. The ontogeny of the gyrification index in humans (data from Zilles et al. 1988; curve fit as per the Kretschmann *et al*. 1979 procedure - see caption to Figure 1).

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The traditional explanation for increased levels of gyrification in large-brained primates has centred on the need to fit a larger brain (or, more specifically, neocortex) into a semi-spherical skull. This explains why gyrification of the expanded surface of the neocortex is more pronounced in larger-brained species (White *et al.* 2009; Rilling 2006; Zilles *et al.* 1988) - Figure 5 demonstrates the existence of distinct evolutionary relationships between GI and brain weight in prosimians and anthropoids: the latter have substantially higher GIs than the former across much of the range of empirically documented brain weights, and GI increases with brain weight at a substantially higher rate in anthropoid primates (though it should be noted that the abscissa in Figure 5 represents a logarithmic scale, indicating that, although GI is *absolutely* higher in larger brained animals, GI as a ratio to brain weight is *relatively* higher in smaller-brained primates).

Among humans the degree of gyrification in some areas (notably temporal/parietal association regions and prefrontal cortex) is even greater than predicted from our larger brain size (White *et al.* 2009; Sherwood *et al.* 2008; see also Rilling 2006). This observation is better explained by newer theories of gyrification which argue that sulci and gyri develop as strongly connected regions are drawn together by the many axons linking them, reducing transit time for action potentials and enhancing the efficiency of specific circuits (White *et al.* 2009; Lenroot and Giedd 2006, 720). Such a mechanism would explain the general link between brain size and GI (as transit time and efficiency become increasingly significant costs as brains become absolutely larger), and the human deviation from general mammalian trends in this regard is of particular interest here, suggesting adaptations for processing efficiency over and above those required by encephalization *per se*.

The argument that gyrification relates to the development and elaboration of neural circuits also explains the ontogenetic changes in gyrification. Early stages of gyrification occur in the foetus only 10-15 weeks after conception (White *et al.* 2009, see Figure 5), but it is during the third trimester (when maternal resources are increasing directed towards foetal brain growth; see above) that GI increases dramatically and the brain begins to develop its adult morphology (White *et al.* 2009, see below; Lenroot and Giedd 2006). Although it was traditionally thought that gyrification plateaus after birth (i.e. matches the threefold postnatal volumetric growth of the brain), 3D techniques of assessing GI are now beginning to document changes in GI occurring throughout childhood and adolescence (White *et al.* 2009). In particular, gyrification appears to increase significantly in later-maturing regions such as prefrontal cortex between 6 and 16 years and declines thereafter, perhaps especially at adolescence (White *et al.* 2009).

Although individuals' patterns of gyrification do appear to be strongly heritable, there is considerable individual variation and monozygotic twins also show considerable differences. Deeper and earlier-developing sulci such as the Sylvian fissure (the two very deep sulci lateral sulci that are one of the most prominent landmarks of the brain) are more similar between twins (and thus likely to be more highly constrained genetically) than superficial sulci which develop postnatally and which may thus be more plastic in response to stimuli from the physical and social environments (Sherwood *et al.* 2006; White *et al.* 2009).

In short, then, the phylogenetic and ontogentic development of gyrification indices in the human brain suggest adaptations for greater connectivity to offset the potential inefficiency of larger brains – and, indeed, the evolution of gyrification indices greater even than this requirement in some parts of the human brain. Ontogenetically, the gradual development of gyrification among late-maturing parts of the brain may suggest a role for developmental experience in literally shaping the adult brain.

Grey and White Matter Ratios

The relative balance of 'grey' and 'white' matter in the brain provides an alternative perspective on these processes. Grey matter (actually a blood-suffused rosy colour in the living brain) is comprised of neural cell bodies, while 'white' matter is mainly comprised of supporting glial tissue such as astrocytes (which play a role in regulating neuronal energy uptake), oligodendrocytes and myelin (the former synthesizes the latter, which sheathes axons to facilitate long-range propagation of action potentials; Barton 2006).

The ratio of neurons to glia has long been known to vary phylogenetically (see Figure 7), with larger-brained (and bodied) species having lower neuronal densities (Barton 2006; Sherwood *et al.* 2006). However, in larger-brained species those neurons are larger and have longer and thicker axons (improving conduction velocity) which are increasingly myelinated (sheathed in fatty myelin), helping to insulate them and speeding up synaptic transmission), thus conserving processing speed in the face of greater transmission distances (Barton 2006). As brains grow larger across speciesthe volume of white matter thus rises disproportionately (Sherwood *et al.* 2006), and the ratio of grey to white matter in human brains is as expected for a primate of our brain size (Smaers *et al.* 2010; Schoenemann *et al*. 2005), making them *relatively* more connected than those of smaller nonhuman primates - perhaps especially in prefrontal areas (Höistad *et al.* 2009, 5).

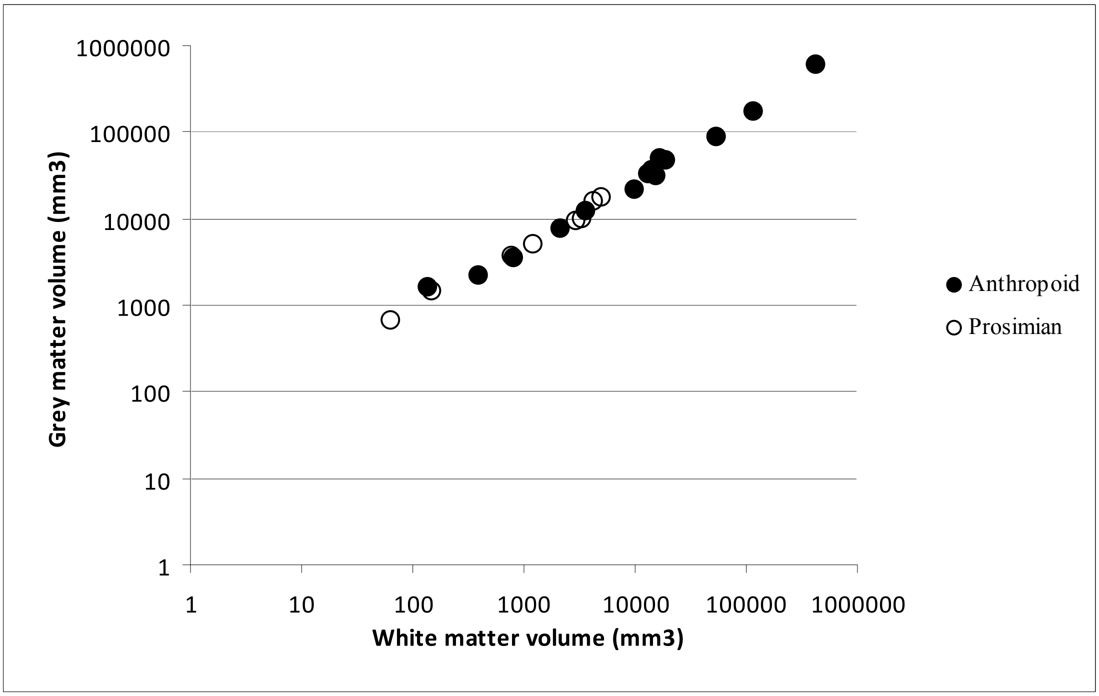

FIGURE 7. THE PHYLOGENY OF GREY AND WHITE MATTER RATIOS (DATA FROM FRAHM *ET AL.* 1982).

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However, ratios of white to grey matter also vary ontogenetically. Most of the neurons we will ever have are present by birth, and therefore volumes of grey matter do not change significantly post-natally. The rapid postnatal growth of the brain is instead due mainly to proliferation of synapses, maturation of the glial cells and myelination of axons (Höistad *et al.* 2009, 5), and white matter volume thus increases dramatically between birth and adolescence (see Figure 8), when considerable amounts of synaptic pruning occur. Myelination of cortical axons begins before birth. First to myelinate are the spinal cord and brainstem; the fibres linking the cerebellum to the cerebral cortex and which are necessary to the fine control of voluntary movement only begin to myelinate after birth, and do not mature until about 4 years of age (Höistad *et al.* 2009, 5; Grove and Coward 2008; Lenroot and Giedd 2006), while intra-cortical connections, particularly in prefrontal regions, continue to myelinate well into the third decade of life, and do not decline here until after 50 years (see Figure 3 and refs in Höistad *et al.* 2009, 401). In contrast, in humans grey matter growth declines after the age of 5, with volumes peaking at 10-12 years in frontal and parietal and 16-18 years in temporal regions (Höistad *et al.* 2009).

Both gyrification and white:grey matter ratios undergo significant changes during adolescence, when a variety of gross psychological and behavioural changes also occur and also when a number of psychiatric disorders such as schizophrenia first manifest. This may thus be another critical period for brain development, as growth patterns change and brains enter the later, less plastic stages of maturation. While ASD seems to relate to atypical early brain development trajectories (see above), schizophrenia has been argued to represent an exaggeration of 'normal' brain maturation mechanisms occurring during adolescence, such as reductions in grey matter volume, although myelin deficiencies and changes in white matter volume also often occur (Paus 2001; Paus *et al.* 2008, cited Höistad *et al.* 2009, 1, 6). While arguments continue to rage

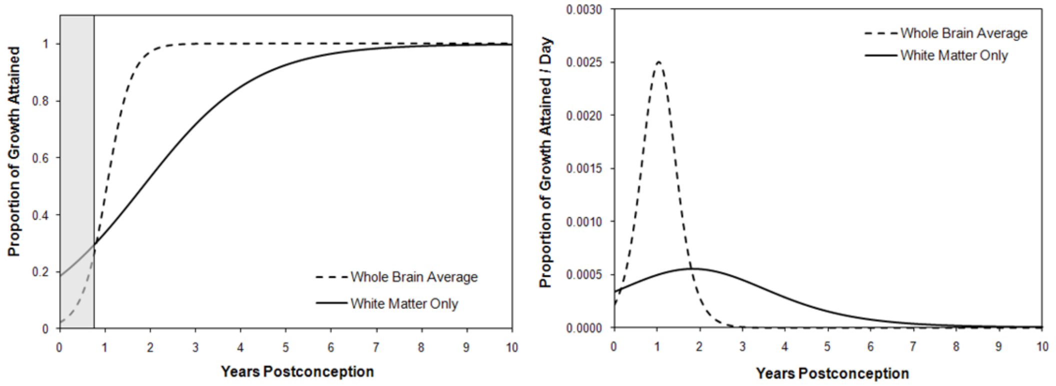

Figure 8. The white matter growth trajectory compared to the average growth trajectory for all brain elements in humans (equations from Klekamp *et al*. 1989).

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over the relative contributions of genetic inheritance and environment to conditions such as schizophrenia and ASD, genetic components do appear to be substantial (Picchioni and Murray 2007; Freitag 2006), suggesting high heritability of such developmental disturbances, which may be an unwelcome negative result of the extreme scaling of large brains. As discussed above, large brains – or, rather, enlarged neocortices – necessarily entail several functional correlates in order to maintain efficiency. They are increasingly dominated by disproportionately large late-maturing neocortices, which are increasingly closely inter-connected, with greater ratios of white to grey matter and larger gyrification indices. All of these features of large brains require concomitantly slower maturational schedules and thus longer 'critical periods' of plasticity during which they are influenced by social and physical environmental stimuli. The downside would seem to be that the complexity and prolongation of the process of 'wiring' the brain renders larger brains more vulnerable to a variety of developmental abnormalities such as ASD or schizophrenia, as well as to degenerative conditions such as Alzheimer's or multiple sclerosis (Sherwood *et al.* 2006), suggesting that humans' large brains may be near the functional limits of encephalization (see e.g. Hofman 2001 for discussion)

Discussion: the Evolution of Ontogeny

The complex relationship between the phylogenetical evolution of the human brain and its ontogenetic development merits serious consideration of the extent to which the two processes may have interacted throughout hominin evolution (see e.g. Zollikofer & Ponce de Léon 2010 for discussion). Relatively small variations in developmental patterns can have large effects both overall brain size and the relative sizes of brain components. One hypothesis is that encephalization may have been achieved via relatively simple single-gene mutations affecting the number of cycles of symmetric division precursor cells for neurons undergo before each cell begins to increase exponentially (Rakic 2009, 726): the more precursor cells that can be formed, the larger the structure that results, and as brain size increases, late-maturing structures such as the neocortex grow disproportionately larger via the same mechanism (Finlay and Darlington 2005; Finlay *et al.* 2001). Many of the genes thought to have been under selection in recent human evolution are believed to be regulatory genes governing the timing of developmental processes, and indeed regulatory genes may be fundamental to evolution more generally (Vaquerizas *et al.* 2009, 260).

Large brains are associated with many costs, including reduced efficiency and high energetic demands. Nevertheless, encephalization has clearly been adaptive among primates generally, and the hominin lineage in particular, indicating that these costs are adequately balanced on an evolutionary timescale by benefits. One obvious possibility is that large brains are adaptive because of a net cognitive gain of some kind, although the nature of the relationships between brain size, cognitive prowess and behavioural sophistication remains frustratingly unclear. Another possibility is that the wider constellation of adaptations surrounding large brains themselves are also adaptive.

As we have seen, comparison of human brains with those of other primates demonstrate clearly that the energetic and efficiency costs of larger brains have been met by evolutionary changes to the structure of the adult brain - for example through increasing gyrification and greater proportions of white to grey matter – as well as to broader life histories strategies such as longer, slower developmental schedules (Isler & van Schaik 2009). However, it is also highly possible that these 'side-effects' of larger brains were also adaptive in and of themselves, and contributed to a positive feedback loop during hominin evolution in which the ontogenetically selective effects of extended 'critical periods' of development, via which the structure of the brain itself can be at least partly fine-tuned to be optimal for the required functions, was also evolutionarily adaptive and therefore selected for in and of itself,

Larger brains are of necessity relatively more interconnected brains to maintain efficiency of signalling; however, the complexity of human (and indeed ape) behaviour and of the neural 'wiring' involved is such that our brains require extremely significant environmental input from both the physical and social environments if the individual is to function sufficiently well to survive and to negotiate a complex social world in order to reproduce. Thus, an increasing reliance on physical and especially social interaction to structure hominins' slower-growing brains is likely to have been adaptive not only as a means of offsetting the energetic and processing costs of larger brains, but also because it allowed the development of elaborated forms of hgher-order and social cognition possible *only* in the context of extended periods of growth and slower trajectories of neural development. Modern human patterns of brain growth and development trajectories may thus represent an extreme state of such a positive feedback loop, maximising the length of time during which environmental input can significantly influence the brain and allow the development of complex forms of cognition, to the extent that only small deviations are associated with conditions such as ASD and schizophrenia, which significantly impact on particularly social cognition, and reduce the likelihood of reproduction and thus evolutionary fitness (Avila *et al.* 2001; Walsh *et al*. 2008).

Clearly, such fine-grained neurological developmental processes as gyrification and white:grey matter ratios cannot be studied directly in fossil remains. Work is needed to establish the extent to which they may be estimated from proxies such as gross brain sizes ascertained from endocranial volumes or from the, many elements of the broaderlife-histories of extinct hominins which can be accessed in the fossil record, and allow tentative estimates as to the nature and timing of possible inflection points in the evolution of human developmental scheduling.

In a previous paper (Grove and Coward 2008) the authors argued for *Homo erectus* as a possible break-point in hominin developmental scheduling. More recent work, including a comprehensive review by Robson and Wood (2008) and work by Zollikofer and Ponce de Léon (2010) have since provided further data, and allow a more detailed consideration of the evidence.

Certainly in terms of overall brain size *Homo erectus* would seem to be a highly plausible candidate. 'Archaic' hominins (the pre-erectines, in Robson & Wood's terminology; 2008) remained relatively small-brained (with the larger brains of the robust australopithecines apparently a specialized adaptation related to their derived dental and jaw morphology; DeSilva and Lesnik 2008). DeSilva and Lesnik calculated that the brains of australopithecine neonates would have been around 38.1% of adult size at birth and those of early *Homo* 35.2%, compared to values of ~40% for chimpanzees and only 29% for humans (see refs in Franciscus 2009), suggesting a general lack of selection for secondary altriciality for both the australopithecines and the earlier *Sahelanthropus* and *Ardipithecus* (refs in Zollikofer and Léon 2010, 447; Robson and Wood 2008, 412-415). The rejection of derived life-history scheduling for these early hominins is also supported by dental data documenting a more rapid trajectory of growth (Robson and Wood 2008, 411), although dental analyses of the robust australopithecines underline the mosaic nature of life history among different hominins by suggesting a unique 'package' of dental ontogenetic scheduling (Zollikofer and Ponce de Léon 2010, 447).

Only among *Homo erectus* specimens (*sensu lato*) do brain sizes increase to nearer modern than chimpanzee values (DeSilva and Lesnik 2008; Leigh 2006; Walker and Ruff 1993), and a number of studies have suggested that *Homo erectus* brain sizes were consistent with modern human brain-growth, with only ~33.1% of adult brain size achieved by birth (DeSilva and Lesnik 2008; Robson and Wood 2008). Other anthropological and archaeological developments associated with late *erectus* have also been used to suggest a significant change in lifeways including increased body size (Robson and Wood 2008), a greater focus on dietary meat and longer limbs suggesting adaptations for more efficient bipedalism (O'Connell *et al.* 1999) as well as expansion into northern latitudes (see refs in Grove and Coward 2008, 396) that might relate to both dietary and social innovations in meeting the different energetic demands of human developmental schedules. The association of *erectus* with the handaxe in particular has been argued to suggest an increased role for cognitive mechanisms permitting the faithful imitation of skilled motor behaviours. Acquiring the skills of Oldowan core-and-flake technologies may require only a relatively straightforward extension of action repertoires and social skills (Knoblich and Sebanz 2008). However, more complex tool behaviours involving 'roughing-out' stages intended not to produce useful flakes but to prepare for later stages of manufacture may require higher levels of joint attention and intentionality to learn - the imitation, rather than emulation, of goal-directed rather than simply sequential motor sequences. Thus ToM is also likely to be significant here (Knoblich and Sebanz 2008) in order to translate between one's own and others' perceptions – from 'what *I* see' to 'what *s/he* sees' and vice versa) – even before considering the significance or otherwise of handaxe symmetry, symbolism and/or 'sexiness' (Hodgson 2009a, 2009b; Kohn and Mithen 1999 and comments thereafter; Wynn 1995; see also McNabb this volume for further discussion).

However, other research has suggested that *Homo erectus* may not have been quite so modern after all. In particular, interpretations based on two of the major fossil specimens for examining life history scheduling in *Homo erectus* - the Mojokerto and Nariokotome juveniles – remain controversial. A mismatch in age at death as calculated using dental and skeletal methods for the Nariokotome juvenile (Dean and Smith 2009; Walker and Leakey 1993) has been used to argue that the derived modern human pattern of delayed juvenile growth and catch-up adolescent growth-spurt had not yet become established (Smith and Tompkins 1995), and that the Nariokotome boy had already undergone an early growth spurt more similar to that known among chimpanzees (Zollikofer & Ponce de Léon 2010, 448). Several more recent analyses of the material have also argued for a primate-style growth trajectory (Dean and Smith 2009; DeSilva and Lesnik 2006; Leigh 2006).

Age estimates of the Mojokerto child vary much more widely, ranging from 0.1-1.5yrs to 4-6 years of age at death, and make it difficult to determine how much brain growth had occurred during gestation. If the Mojokerto child does fall at the younger end of this proposed age-range this would suggest a fast trajectory of growth more akin to that of modern non-human primates. However, if older a slower, more derived 'human' pattern is more likely (DeSilva and Lesnik 2006; Coqueugniot *et al.* 2004). Meanwhile, while the the subadult specimen from Dmanisi apparently developed faster than modern humans based on its degree of skeletal maturation, it nevertheless fell within the 95% range of modern human variation (Zollikofer & Ponce de Léon 2010, 446). Zollikofer and Ponce de Léon's recent review concluded that early brain growth in *Homo erectus* was likely to have been fast (i.e., more 'modern'), but that these rates were not sustained for long (i.e., more 'primitive'; 2010, 446).

In short, the *Homo erectus* material does not provide unambiguous evidence of a shift towards derived human life history and developmental scheduling. Perhaps this is not surprising given the wide geographical and temporal distribution and variability of specimens.

It is therefore worth expanding on the arguments put forward previously (Grove and Coward 2008) to consider the later pre-modern *Homo* species more thoroughly. Although *antecessor*, *heidelbergensis* and *neanderthalensis* share considerable similarities with modern *Homo sapiens* in both postcranial and cranial morphology, insofar as it is fair to judge from the archaeological record they appear to have demonstrated several differences in behaviour and perhaps also cognition. Body masses and brain sizes among these species are statistically indistinguishable from those of modern *Homo sapiens*, and DeSilva and Lesnik (2008) calculate that ~29.5% of brain growth would have been completed prenatally among Middle Pleistocene *Homo*, compared to a figure of 29.9% for modern humans. Zollikofer and Ponce de Léon (2010) suggest that while postnatal brain growth rates were higher among Neanderthals than modern humans, their larger adult brain sizes meant they took the same amount of time to develop as in modern humans.

However, a variety of other lines of evidence have also been used to investigate patterns of gestation and development in these mid- Pleistocene species. Studies on dental development, including crown and root formation and eruption times, have given mixed results (perhaps not surprising given the small sample sizes of many of the studies and the variability of modern human dental developmental schedules). Studies have variously argued that Neanderthals:

1. Developed on faster and more rapid trajectories than *Homo sapiens* (e.g. Smith *et al.* 2007);

2. Had shifted towards the derived slow growth rate characteristic of humans relative to the shorter, more rapid periods of growth of *Homo antecessor* and *Homo heidelbergensis* (e.g. Bermúdez de Castro *et al.* 1999);

3. Developed on a trajectory almost indistinguishable from modern humans (Machiarelli *et al.* 2006; Guatelli-Steinberg *et al.* 2005; Ramírez Rossi and Bermudez de Castro 2004; Dean *et al.* 2001), and

4. Shared with *all* pre-modern *Homo*, including *erectus* (s.l.) a similar pattern of dental development, in contrast to non-human primates and archaic hominins, with *Homo ergaster* representing the evolutionary link between the two (e.g. Bermúdez de Castro *et al.* 2003; see review in Robson and Wood 2008, 414).

The much better preserved fossil record of the Neanderthals (including many finds of juveniles and two neonates (Holloway *et al*. 2004) also allows consideration of other skeletal traits that might inform on life history strategies, notably the dimensions and shape of the pelvis. Trinkaus (1984) had suggested that Neanderthal pubic morphology was consistent with a longer period of gestation in this species, but this suggestion was strongly refuted by Rak and Arensburg (1987) and Rosenburg (1988). More recently, Weaver and Hublin (2009), based on the pelves of the Tabun female and Kebara male, concluded that Neanderthals retained a more primitive birth mechanism than modern humans, but that obstetric difficulty would have been about the same in both species.

In addition, the stage of skeletal growth attained by the adolescent Neanderthal skeleton Le Moustier 1 by 10.5-13yrs of age would locate it in the lower part of the modern human bodily growth trajectory - although its height was only slightly less than that of modern humans, suggesting that Neanderthal adolescents probably underwent a similar growth spurt to modern humans (see e.g. Zollikofer & Ponce de Léon 2010, 448 for refs).

This admittedly brief survey of work on life history evolution in later *Homo* indicates a number of variable adaptations with no simple dichotomy between 'fast'/primate and 'slow'/human strategies (DeSilva and Lesnik 2008; Robson and Wood 2008, 417; Crews and Gerber 2003, 13), but nevertheless a gradual development of the characteristic modern human condition of expanded juvenile period of development, , with *Homo erectus* (s.l.) perhaps pushing the boundaries of non-human primates strategies, and *Homo heidelbergensis* and *neanderthalensis* approaching, if not quite matching, modern human developmental schedules (cf. Hodgson this volume).

The significance of this slower developmental scheduling lies in its association with extended periods of brain growth, and hence the greater degree of environmental influence the growing brain was subject to during the critical periods of synaptogenesis and synaptic competition.

Conclusions

Investigation into the evolution of modern human cognition has focused primarily on insights from phylogenetic comparison of gross brain size and structure of human brain and those of other primates. The role of ontogenetic and developmental factors has not been accorded the significance it deserves in studying the evolution of cognition, and particularly of technological and social behaviours.

The implications for archaeology are significant. Two of the most significant elements of modern human cognition, the Mirror Neuron System and Theory of Mind, are both strongly reliant on social and kinaesthetic experience scaffolded by social interaction for full realization in human infants, and their elaboration in modern humans may be related to our much longer periods of development and particularly dependent childhood relative to other primates. During this time brains continue to develop and mature in the context of social and physical environments which impact on the processes of synaptic competition and pruning and myelination, as documented by changing patterns of gyrification and ratios of grey to white matter. These ‘slower’ trajectories of growth (relative to those of other primates) are of course part and parcel of wider life-history strategies related to the re-structuring of energetic budgets across the whole lifespan necessitated by encephalization. At the same time, adaptations to the processing costs of larger brains - in particular, the phylogenetic patterns of gyrification and the ratio of white to grey matter – led to increasing interconnectivity of hominin and human neocortices, and these processes also had significant effects on cognition. It is the scale and complexity of those connections, and the structuring role of environmental input in their development - that both allows the elaborations of the MNS and ToM seen among modern humans, and their interaction, and that renders humans more vulnerable to developmental and/or degenerative disruption of normal processing.

It is possible that this role of ontogenetic experience in shaping the brain was a fortuitous by-product of encephalization adaptive for other reasons. However, the potential adaptiveness of the neural and cognitive plasticity that results may also have been adaptive in and of itself, and an alternative possibility may be that large brains are a by-product of selection for increasing neural plasticity achieved through delayed maturation of the brain. The modern human brain and cognition is likely to be the result of a complex constellation of selective pressures and releases linking encephalization, long,slower life histories and delayed maturation of the brain, larger and more complex social groups and subsistence practices etc. (see e.g. Coward & Grove submitted figure 1), and there is no reason why selective pressures should have remained constant or equal throughout hominin evolution, but it does seem clear that ontogenetic processeses of neural development, and the structuring experience of and interaction with the social and physical world are likely to have been extremely significant throughout hominin evolution.

Early developments in the hominin line, notably the habitual use of stone tools in the extraction of animal protein (only appearing themselves at 2.6mya (Semaw *et al*. 1997) but attested to by cutmarks on bones from 3.3mya (McPherron *et al*. 2010)), would seem to represent significant behavioural changes from panin lifeways. Not only are these stone tools used in rather different ways, but they also seem to demonstrate enhanced levels of motor skill relative to those known among even enculturated and trained chimpanzees (Delagnes & Roche 2005) – possibly related to the adoption of bipedalism and the release of locomotive selective pressures on wrist and hand anatomy (Ambrose 2001, 1750; Hodgson this volume). However, these early tools do not seem to be accompanied by any obvious fossil indicators of changed life histories (Robson & Wood 2008), and appear to be explicable in terms of more skilled forms of motor emulation, rather than goal-level (socially-scaffolded) imitation, and it is not until the appearance of Mode 2 and subsequent technologies that it is clear that at least precursors of the cognitive skills involved in fine-grained imitation and social interaction had become established at a level distinguishing hominins from other primates. However, these early changes in lifeway may represent the earliest elaborations on a basic primate theme, establishing the selective environments which made the later elements of the modern human cognitive suite adaptive.

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