
From Individual Neurons to Social Brains

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The manufacture of stone tools is an integral part of the human evolutionary trajectory. However, very little research is directed towards the social and cognitive context of the process of manufacture. This article aims to redress this balance by using insights from contemporary neuroscience. Addressing successively more inclusive levels of analysis, we will argue that the relevant unit of analysis when examining the interface between archaeology and neuroscience is not the individual neuron, nor even necessarily the individual brain, but instead the socio-cognitive context in which brains develop and tools are manufactured and used. This context is inextricably linked to the development of unique ontogenetic scheduling, as evidenced by the fossil record of evolving hominin lineages.

In this article we will argue that the relevant unit of analysis when examining the interface between archaeology and neuroscience is not the individual neuron, nor even necessarily the individual brain, but instead the socio-cognitive context in which brains develop and tools are manufactured and used. This is not to say that the burgeoning field of neuroanatomy is not important to archaeology: far from it. Studies shedding light on the neural processes underlying behaviour can hardly fail to impact on research into ancient cognition. Nevertheless, we wish to stress that such a fine-grained examination of the individual brain is relevant to archaeology only within a wider physical and social context. The data available following recent advances in neuroscience are most significant archaeologically for examining the wider cognitive adaptations that have made humans highly social, tool-making animals.

Beginning with the finest level of analysis, that of the individual brain and its specific neural components, this article will address successively more inclusive levels of analysis that stress the importance of context by situating the brain in the body — the level at which individual acts of tool use are traditionally investigated by the archaeologist. We conclude by examining the individual body in its context of multiple and interacting brains, bodies and tools, focusing on the importance of development within the human social milieu. Particular attention will be paid to those

aspects of human development that differ from those of other animals as a result of our uniquely extended ontogenetic schedule.

A central question in early prehistory, with its limited archaeological record comprised largely of stones and bones, is how stone tool use relates to cognition, and how lithic evidence can be used to inform on the evolution of distinctively human forms of thought. At the heart of this debate is the issue of whether stone tool use is a result of or a stimulus to a more flexible intelligence, and for this reason we ask whether social interaction precedes and surrounds tool use or whether, in certain circumstances, the artefacts themselves act as the media of social interaction (e.g. Mithen 2000a; Henshilwood *et al.* 2001; Wynn 2002, and comments thereafter). These are not mutually exclusive solutions — any one single monolithic scheme for the evolution of tool behaviour would underestimate the complexity of such behaviour in both modern humans and other animals (Beck 1980; Whiten *et al.* 1999; 2005). Nevertheless, it is a useful heuristic to imagine tools as being not only products of certain social behaviours but also as potential reinforcers of such behaviours (Gosden 2005; Gosden & Marshall 1999).

Gosden (2005), building upon an argument initiated by Gell (1998), has been a strong proponent of the argument that artefacts might possess an agency independent of their makers. Examining recurrent

forms in the pottery of Roman Britain, Gosden argues that, once given form by a manufacturer, an artefact imposes its own rules on the future production of similar forms. In a sense, a norm is produced during a certain initial phase to which future artefacts must conform in order to be regarded as appropriate for a particular function. This conformity is, at least in part, enforced by previous 'generations' of similar objects.

While we are not convinced that artefacts themselves possess agency when divorced from their makers, we do see evidence in the archaeological record of embedded social processes that are necessarily repetitive or 'normalized' in nature. Almost without fail these processes involved the interaction of several individuals and were mediated by the artefacts that were manufactured and used. It is in the reconstruction of the specific neural functions involved in these interactions that we feel neuroscience has most to offer archaeologists. In particular, three recently discovered classes of neurons would seem to offer considerable insights into the complex socio-cognitive web of technological evolution that we envisage.

Individual brains

At the finest level of analysis — that of individual neurons — three recently discovered classes of neurons are of particular interest to the archaeologist in elucidating the links between cognition, tool behaviour and the social world. These are bimodal, mirror and canonical neurons, and are discussed individually below.

Bimodal neurons

Bimodal neurons respond to information from both the somatosensory Receptive Field (sRF) and the visual Receptive Field (vRF) adjacent to it (Maravita *et al.* 2001; 2002; 2003; Maravita & Iriki 2004). Distal type bimodal neurons (DBNs) code for information from the hand area and, crucially, are not only activated by objects within the immediate grasp of the hand but also register changes within the area of space that hand can potentially reach given the arm's current position and orientation. Proximal type bimodal neurons (PBNs) code for similar information from the shoulder area (Fig. 1); the area covered by the vRF encompasses everything within reach of the hand — including those areas that the hand could reach via movement of the arm. Bimodal neurons thus allow for the anticipation of interaction with objects; the signature of *anticipation*, as depicted in the activation patterns of these neurons, is identical to that which occurs during the *execution* of the actions themselves.

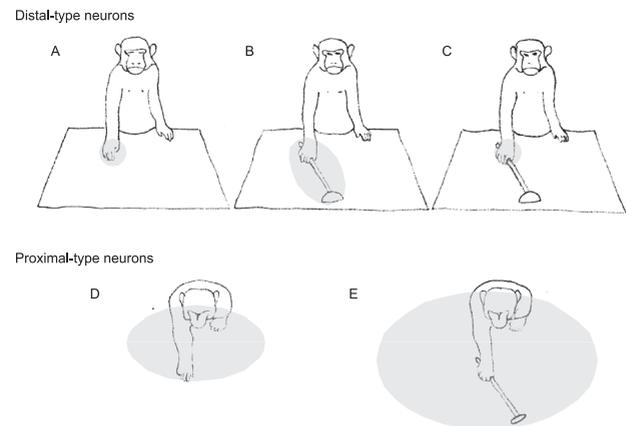


Figure 1. Distal-type bimodal neurons related to the hand area (A) code not only for objects in contact with the hand (the somatosensory Receptive Field), but also for the area immediately surrounding the hand (the visual Receptive Field). The vRF is extended during tool use (B), but not during passive holding of the tool (C). Proximal-type bimodal neurons related to the shoulder area (D) code for a vRF that radiates from the shoulder, as well as the sRF of currently accessible objects. Proximal-type neuron codings for the vRF are also extended during tool use (E). (Redrawn after Maravita & Iriki 2004, 80.)

For an archaeologist, the significance of bimodal neurons is that the areas for which they code are extended by the use of tools. For example, the PBNs of a macaque allowed to use a simple rake in order to retrieve food code for the area immediately encompassing the hand *and the rake*, whilst the monkey's DBNs code for the total area within reach of the arm/rake (Maravita & Iriki 2004). The neural information regarding the action capabilities of the hand and arm in space is therefore directly modified by the use of tools. In this way, tool use can be seen to have direct, rapid effects on the way in which the brain represents the capabilities of the body in space, demonstrating a level of plasticity in this area that is clearly hugely relevant to the investigation of links between the evolution of the human intellect and the manufacture and use of tools.

The nature of the tool itself is also vital to the extension of the body image in the brain. Use of an unsuccessful tool, or the *passive* holding of a perfectly useable tool, will not extend the area coded for by bimodal neurons. The monkey must experience successful tool use in order for the neurons to assimilate the new-found capability. However, short periods of tool use — on the order of five minutes — are sufficient. The effects of tools are also transient; further

activity without the tool quickly returns the body image to its normal state (Maravita & Iriki 2004). The modification of the area to which bimodal neurons respond is therefore both temporary and dependent on the tool being useful in the attainment of a particular goal (i.e. reaching for an object). Modification of the body image during tool use is thus context-dependent, suggesting that neural substrates serving tool behaviour are sensitive to inputs beyond the level of the individual brain.

Mirror neurons

Mirror neurons have received considerably more attention in the literature beyond neuroscience than bimodal neurons, with which they share certain features. Mirror neurons are so-called because they fire both when an agent executes a particular action and when that agent observes (or hears, Kohler *et al.* 2002; Gazzola *et al.* 2006) another agent executing the same action (Rizzolatti & Craighero 2004). Discovered initially in the premotor cortex (area F5) of the macaque (Rizzolatti *et al.* 1996; Gallese *et al.* 1996), the human mirror system includes, but is not necessarily limited to, the insula, amygdala, limbic system and supratemporal sulcus (Iriki 2006, 3).

The direct homologue of the macaque F5 region in humans is Broca's area, which has inevitably led to speculation regarding the role of the mirror system in the evolution of vocalization, speech and language (Arbib & Rizzolatti 1997; Rizzolatti & Arbib 1998; Arbib 2002). Indeed, there has been much speculation about the potential role of the mirror neuron system as a basic mechanism underpinning many aspects of human social cognition including empathy and, potentially, theory of mind. Essentially, the possession of 'theory of mind' (a phrase coined by Premack & Woodruff (1978) during speculations about interpersonal cognition in chimpanzees), allows an agent to appreciate that another may have thoughts and desires different from his own. In human children, this appreciation is found to be present from the age of approximately three and a half years (Wimmer & Perner 1983; Gopnik & Astington 1988).

It is argued that mirror neurons may be vital to the development of a theory of mind since they allow an agent to predict (or, perhaps more accurately to 'retrodict') another's thought processes via their behaviour (Hesslow 2002). This amounts to the simplistic process of putting oneself in another's shoes and asking 'What would I do in that situation?' (prediction of action from thought) or 'Which thoughts would have caused me to act like that? (retrodiction of thought from action). This is clearly an important

skill in social situations, and one which is sometimes argued to have sparked the so-called 'big bang' of human culture (Mithen 2000a; Ramachandran n.d.).

Canonical neurons

The final class of neurons discussed here, canonical neurons, is often thought of as part of a package with mirror neurons, as both are located in area F5 of the premotor cortex. Whilst there are functional similarities, however, there are also some important differences. Canonical neurons are activated during the execution of goal-related movements *and* during object observation, where coding is specific to the type of grip required to interact with the object (Grèzes & Decety 2002; Grèzes *et al.* 2003; Pacherie & Dokic 2006). For example, a small, light object that would require a precision finger grip to lift activates a particular set of neurons, whilst a larger, heavier object, requiring a stronger whole-hand grip, activates a different set. In this way an object is assessed for a potential interaction pattern before tactile contact is made. Such a process is obviously highly goal-dependant; for example, it requires a quite different level of precision to pick up a pencil from among a collection of fifty than it does to sweep them all onto the floor. It could be suggested that canonical neurons allow the monkey to evaluate what, in Gibsonian terms, a given object *affords* (e.g. Gibson 1979); on the basis of these affordances and the individual's goals, it then shapes the appropriate hand and/or arm movements. The aforementioned area F5 of the premotor cortex as well as the anterior intraparietal area are both thought to be implicated in this process of translation from object appearance to potential action (Jeannerod *et al.* 1995; Rizzolatti & Fadiga 1998; Grèzes *et al.* 2003).

In short, canonical neurons are capable of representing not only goal-directed actions (in much the same way as mirror neurons) but also the potential for such actions based on the objects to hand. Thus, in the same sense that bimodal neurons do not code for regions of extension for a tool when that tool is ineffective, mirror and canonical neurons do not fire when basic actions are observed. They are both highly goal-dependent; in the case of mirror neurons those goals can be the goals of another agent, whilst in the case of canonical neurons the physical requirements of the goal are identified before (or even in the absence of) execution.

Bimodal, mirror, and canonical neurons: the three systems together

In summary, it seems that mirror neurons are concerned with the goal-directed behaviours of the self

and others, canonical neurons relate to the potential for and specific requirements of interaction with an object, and bimodal neurons are associated with the spatial sphere of influence of a given system of agent plus object. By examining the links between the activities subserved by these three functional groups of neurons, we can begin to examine evolving systems of interacting agents and objects of the kind represented in the archaeological record. These separate but related neuronal systems are likely to have evolved to facilitate an agent's interactions with both inanimate objects and other agents: thus new data from recent advances in neuroimaging technology inform on the evolution of the cognitive capacity for tool behaviour itself, as well as the advantages that tool use might subsequently confer in other areas of the cognitive domain. However, significant as these neural mechanisms may be, they need to be placed in the evolutionary context of individuals engaged from the first in multiple ongoing social interactions which have equally important ramifications for the development and transmission of tool behaviours.

Technology and the brain in society: imitation, simulation, and theory of mind

The majority of the early hominin archaeological record is composed of stone tools. Some aspects of these tools change with time and across space whilst others persist and are widely distributed in the archaeological record. What mechanisms might contribute to the transmission of these tool 'types' between toolmakers? Considerable evidence is available from neuroscientific studies of primates and humans; for example, imitation is central to sophisticated social learning processes because, unlike emulation or social facilitation, imitation necessarily involves the cause-and-effect understanding of a specific action *as a means to an end* — an understanding that Johnson-Frey (2003; 2004) has suggested may be of particular importance in human tool behaviour.

The scale of imitation seen in humans appears greater than that of other great apes, a difference which manifests relatively early in development. Horner & Whiten (2005) showed that, when an experimenter removed a prize from a simple 'puzzle box' by performing a series of causally irrelevant actions followed by a series of necessary actions, juvenile chimps allowed access to the box performed only the necessary actions to retrieve the prize, while human children performed all the actions. While such fine-grained 'over-imitation' may at first appear to be a handicap in achieving the necessary goal, it could be

argued that faithful reproduction of others' actions may be vital during the learning of detailed, precision skills such as flint knapping.

This capacity for imitation may also be present in primates other than the great apes. Iriki (2006) found that, among macaques, those that could be trained to use tools were afterwards more capable of imitating other behaviours. She suggests that this latent capacity, which is rarely expressed in the wild, is released among primates through habitual tool behaviour, to the subsequent benefit of other socio-cognitive domains (Iriki 2006, 660). The potential implications for hominin evolution in the context of tool use are clear: with specific cognitive mechanisms liberated by the advent of stone tool behaviour from at least 2.6 million years ago (Semaw 2000; Semaw *et al.* 2003), human technological abilities have blossomed to produce more varied and complex forms of material culture than those of any other species.

As mentioned briefly above, a capability of modern *Homo sapiens* often considered crucial to our cultural development is the possession of a theory of mind (ToM) (Mithen 1998; 2000b; Brüne & Brüne-Cohrs 2006), the ability to attribute mental states to ourselves and to appreciate that these may conflict with those of others. There is disagreement, however, as to the way in which this 'theory' develops and is implemented. Some researchers believe that ToM is literally a theory in the scientific sense; according to the somewhat unfortunately named 'theory theory', we accrue empirical knowledge of others via social experience, and gradually extrapolate general rules from consistencies in the data we accumulate, building along the way a theory of other minds (Carruthers 1996). Alternatively, 'simulation theory' suggests that we employ the far more pragmatic heuristic of simply using our own minds as models for those of others. In other words, we internally simulate likely outcomes based on our own experiences (Gordon 1986; 1996).

A potential benefit of the simulation theory is that it would allow the repeated simulation of trial-and-error alternatives without the expensive trials and potentially dangerous errors, offering a considerable selective advantage (Hesslow 2002, 244; Fig. 2). The discovery of mirror neurons may also provide us with a clear neural mechanism for simulation (Gallese & Goldman 1998). Adopting the perspective of another agent — simulation in the basic sense — is the covert, mental equivalent of the cognitive process involved at the overt level in imitation. As we have seen above, investigations of the properties of mirror neurons have provided a key insight into imitative processes. The existence of mirror neurons could thus be argued to

support simulation theory over the alternative (Gallesse & Goldman 1998; Hesslow 2002).

It is also interesting to note in this context that a predominant explanation for autistic spectrum disorders (ASDs) suggests they are due to deficiencies in the neural substrates that support social cognition (Baron-Cohen *et al.* 1985; Baron-Cohen 1995; Happé 1994a,b). It is therefore no surprise that a number of researchers have hypothesized there may be a link between mirror neurons and autism (Hamilton *et al.* 2007; Oberman *et al.* 2005; Oberman & Ramachandran 2007; Williams *et al.* 2001; 2006). One recent study on imitation in ASD patients has shown that, when asked to copy experimenters holding their hands up with the palms facing away from their body, autistic subjects tended to hold their palms towards themselves — recreating the view of the hands *they* had seen instead of translating the perspective the *other* had seen (Perner 1996). Such basic malfunctions of the imitative system may have profound effects on social development.

The imitation of hand actions is of particular importance in addressing the evolution of tool use. Imitation of the hands, and of tool use more generally, is a highly cognitively transparent task; tools can be used in identical ways for identical purposes by self and others and, more importantly, due to the position of the hands as relatively distal effectors, the visual stimulus provided by 'you using a tool' will look much like that of 'me using a tool'. This has led Iriki to argue that 'tools become a medium for realizing equivalence among agents and of self-other compatibility' (Iriki 2006, 663). She goes further to suggest that, via the bimodal neurons discussed earlier, agents are able to establish parity between body parts and tools, and that the flipside of this process enables us to objectify parts of the body, and eventually the self entirely.

Brains in context

As exciting as these new developments are, the neuroanatomical foundations of such changes in body plan and cognitive representation cannot be studied separately from a consideration of the particular contexts which might select for them. Interactions between individual agents and tools are necessarily inherently social in nature and so implicate a more inclusive level of analysis that takes into account the social context as well as the ontogenetic development of hominin technological evolution.

In fact, the developmental plasticity of the brain is considerable: it is argued that redundant architectonic information in the mammalian genome is minimized by a reliance on Darwinian processes to structure

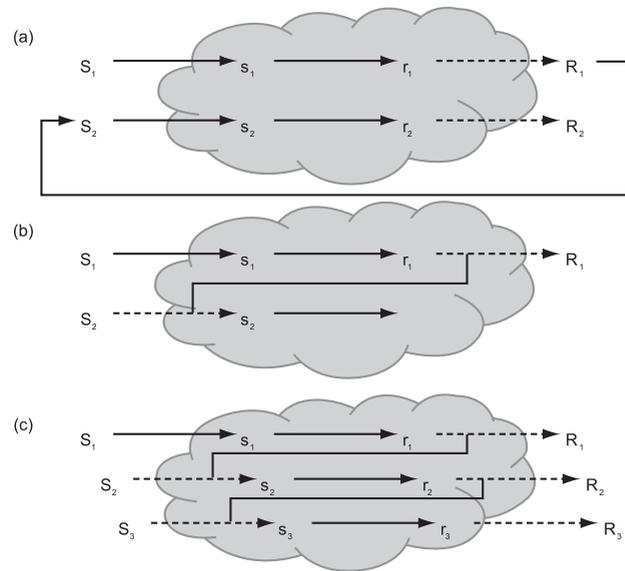


Figure 2. The development of internal simulation: (a) shows the scenario without simulation, where a stimulus S_1 elicits activity in the sensory cortex s_1 , leading to a response decision r_1 and, finally, the overt motor response R_1 . This response leads simply to the generation of a second stimulus S_2 , and so on. (b) The onset of simulation allows the likely effects of responses to given stimuli to be evaluated internally. (c) Ultimately, this leads to the possibility of internally simulating extended loops of responses and stimuli. (Redrawn after Hesslow 2002, 244.)

brain development (Deacon 1997). Transplantation experiments would seem to demonstrate that, rather than being genetically 'hardwired', much variation in the neuroanatomical connectivity of mammalian brains is achieved by overproduction of neurons and underspecification of axonal growth and connectivity, so that brain structures are established through a process of axonal competition for limited synaptic targets and programmed cell death for those that fail. In short, the young brain proliferates new connections, with only a subset surviving the selective effects of experience (Fig. 3; Donald 1991; Deacon 1997).

Most of the neurons we will ever have are already present at birth. Post-natal brain growth is largely due to a vast and rapid increase in the number of connections, a process which is highly adaptable to changing circumstances. Even within specific brain regions, the most electrically and metabolically active circuits — i.e. those *used* most — grow at the expense of others (Greenfield 1997, 110–15). As a result, there is considerable plasticity in intraspecies development, as demonstrated by the highly variable response to

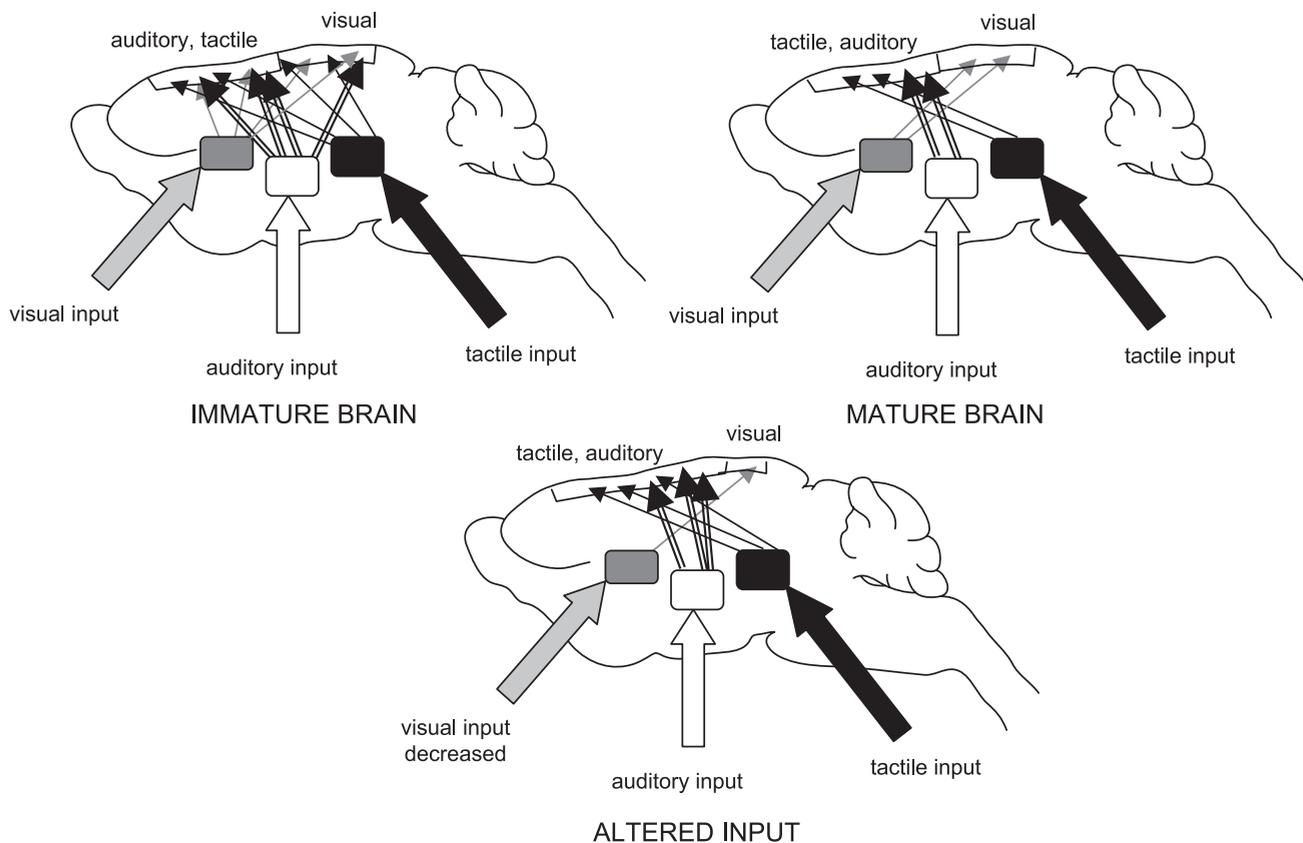


Figure 3. Brain growth through axonal competition and the effect of altered environmental input. (Redrawn after Deacon 1997, 208 fig. 7.6, 210 fig. 7.7.)

brain injuries among children. For example, loss of left-hemisphere language circuits during childhood does not inevitably result in impaired language processes, as the brain structures involved parasitize on corresponding right hemisphere structures normally associated with spatial functions — to the latter's detriment (Wills 1993; Gibson 1996; Bradshaw 1997).

Epigenetic influences on the brain are now known to occur pre- as well as post-natally, and 'foetal programming' has recently become an important area of research in developmental biology (e.g. Barker 1998). In addition to metabolic disorders such as obesity, diabetes and cardiovascular disease and respiratory conditions such as asthma (Barker 1998; Reynolds *et al.* 2001; Vickers *et al.* 2003), susceptibility to psychological conditions and brain disorders such as schizophrenia, depression and post-traumatic stress disorders have also been related to this dynamic relationship between genes and the environment (Holtman *et al.* 1999; Halligan *et al.* 2004; Yehuda *et al.* 2005).

Nor is such plastic reorganization and reworking of synapses limited to critical perinatal developmen-

tal periods, as was previously thought. The adult brain too is capable of dynamic structural change in response to trauma such as limb amputation, after injury or stroke — or even merely after extensive training. For example, the cortical sensory region for the hand is known to expand and contract with demand even in adults (Merzenich 1987; Donald 1991; Wills 1993; Bradshaw 1997; Greenfield 1997, 115–18), and after loss of a finger, sensorimotor control of adjacent fingers is enhanced by 'taking over' the newly available areas.

Controversially, continuing production of brain cells has also been identified in adults, with rates of neural regeneration strongly affected by environmental factors (Eriksson *et al.* 1998; Gage 2002; Gould & Gross 2002 — though see Rakic 2002 for arguments *contra*). Rates of regeneration in adult rats have been estimated at over 270,000 new brain cells a month (c. 9000 a day: Gould & Gross 2002), although research on humans (post-mortem) has suggested a much lower figure of around 500–1000 (Eriksson *et al.* 1998). Set against a total of c. 100 billion neurons and perhaps

ten times that number of glia in the average adult brain (Williams & Herrup 2001), with an average neuron loss of *c.* 9000 neurons a day (a rate increased by, for example, the use of alcohol and other drugs: Hefti 2002), this is certainly a low figure. Nevertheless, it does argue for the continuing possibility of change in response to the environment in the adult brain, a conclusion strengthened by the presence of other processes also contributing to the brain's ability to respond to the effects of experience. The process of myelination, for example, speeds up and makes more efficient the movement of impulses along nerves (e.g. Hardcastle 1976; Marieb 1991), and many brain structures are known to continue to myelinate well into adulthood (e.g. Giedd *et al.* 1996; Paus *et al.* 1999).

The results of experience may also facilitate repeated behaviours: 'once an impulse has succeeded in passing through a synapse the threshold to future excitation at that synapse is lowered. This means it is then easier for future impulses to pass through the synapse; they are facilitated' (Hardcastle 1976, 8). Thus rehearsed actions set up proprioceptive feedback loops between the Central Nervous System — the brain — and the peripheral nervous system — the limbs — enabling very fast 'mindless' reactions with very little conscious effort (Craik 1947; Lashley 1951). The classic example of this is the ability of sportsmen and women to catch e.g. cricket/tennis balls despite the physical impossibility of processing the trajectory and velocity of the missile fast enough for an effective response to be made (e.g. Rose 1997).

In short, environment has a huge effect on neuroanatomy, particularly during early development but throughout life. Neuroanatomists such as Kathleen Gibson have argued that in fact the plasticity of the mammalian brain in response to environmental input is so significant and integral to its functioning that they could well be considered bio-environmental or bio-social organs (Gibson 1996).

In terms of primates and humans, it is obvious that both may exhibit quite different cognitive styles in different environmental circumstances. For example, apes raised in captivity are often capable of more complex linguistic, tool-using, imitative and mirror-recognition behaviours than those reared in the wild. Similarly, many behaviours that are fundamental parts of modern human lives today were un-thought of even a century ago, such as driving cars, riding bicycles, using tin openers and playing computer games. All of these behaviours affect our thought processes without being reliant on any recent change in the genes responsible for brain growth (Gibson 1996, 36) — for better or for worse (Greenfield 2008).

This is not, however, a question of crowning nurture over nature. Experiments in bringing up chimpanzees alongside human children did not see them develop completely human cognitive styles (e.g. Hayes 1952). Rather, as Matt Ridley has argued (2003), the issue is one of nature *via* nurture, with both genetic and environmental factors playing a part. For example, the young of many mammals must be exposed to light during the first few weeks after their eyes have opened for those structures of the brain subserving light reception to develop. After this period, the animals can no longer become sighted (Ridley 2003, 164–5; see also Greenfield 1997, 114). A similar critical period is thought to exist for language acquisition among humans; children not exposed to language during this period never acquire fluent language skills (e.g. Hurford 1991; Lightfoot 1999; Komarova & Nowak 2001). A genetic underspecification of brain development and 'final' structure is therefore clearly the result of natural selection: a selection, it has been suggested, for rapid adaptive responses to environmental change (e.g. Deacon 1997).

The 'channelling' properties of the environment, therefore — and not simply the natural environment but also the technological and social environment — are a significant structuring element in terms of brain development and adult cognitive style.

Hominin life history and its social ramifications

Humans demonstrate some very distinctive developmental characteristics that could inform on the evolution of this flexibility of neuroanatomical response to the environment. Among mammals more generally, two distinct developmental styles can be determined among mammals, who can be divided between those with altricial young, born in relatively large litters in a less-developed state after a relatively short gestation, and those with precocial young — usually singletons or twins born after a relatively long gestation who are well developed and able to locomote soon after birth. Primates as a whole are a precocial order — but, interestingly, one with delayed motor development. In modern humans, this motor delay is so extreme that we have been dubbed 'secondarily altricial'. It takes a human neonate a year to reach the stage of motor development equivalent to those of a newborn great ape (Fig. 4; Smith & Tompkins 1995).

In terms of brain growth, while the brains of apes in general are 40 per cent of adult size at birth and 80 per cent at one year, the brains of human neonates are 25 per cent of adult size and only 50 per cent at one year old. By four years old, when a chimpanzee's brain

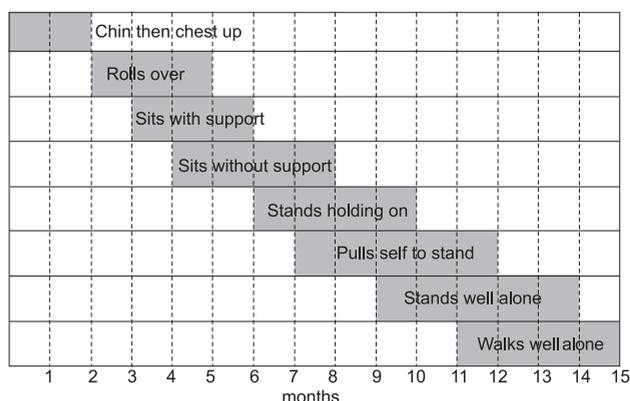


Figure 4. Human motor development milestones. (Redrawn after the Introductory Psychology Image Bank: (<http://www.mhhe.com/socscience/introlibank/set1.htm>.)

reaches adult size, human brain size is still only 84.1 per cent of full size — even at age 10, there is still some 5 per cent of growth remaining. It is not until around the age 16 that the brain reaches its maximum size (Foley & Lee 1991; Smith & Tompkins 1995; Coqueugniot *et al.* 2004). Of course, correlations between brain size and crude measures of intelligence such as IQ remain weak (e.g. Rushton & Ankney 1996; Simonton 1999; Heilman *et al.* 2003), although certain measures of brain volume (particularly that of the ‘executive brain’, the combined volumes of the neocortex and striatum) do appear to correlate positively with cross-species frequencies of social learning, innovation and tool use (Reader & Laland 2002). Such findings indicate that cognitive flexibility, a hallmark of modern human cognition, may be influenced by both the evolutionary and ontogenetic growth trajectories of specific brain areas. However, the costs, benefits and ramifications of encephalization *per se* are discussed in detail elsewhere (Barrickman *et al.* 2008; Aiello & Dunbar 1993; Coward & Grove submitted). For the purposes of our argument here, the significance of the distinctively human pattern of brain growth lies rather in its relative timing and impact on cognitive development.

While in most mammals the brain grows at its fastest in utero, with rates dropping off sharply after birth, among primates high foetal growth rates continue after birth (Smith & Tompkins 1995). But for chimpanzees and macaques this rapid growth lasts for only about a month or so after birth, while human neonates maintain it for a full year. This is not a result of shorter gestation; humans have absolutely and relatively long gestations and large neonates for body weight, and energetic investment in gestation is about

average for a primate of our size (Smith & Tompkins 1995). It is really only postnatal costs that exceed those of the more precocial chimpanzee neonate: the energetic cost of the brain of modern humans is some three times that of chimpanzees overall (Foley & Lee 1991).

An extended period of immaturity necessarily entails significant costs that would seem on the face of it to reduce overall reproductive fitness; as Joffe has detailed (1997), energetic and time costs lower maternal reproductive rates, while the offspring themselves delay reproduction and must negotiate the most dangerous portion of their lifespan for longer (among primates juvenile mortality is much higher than adult). Clearly, there must be some considerable adaptive benefit to the extended period of immaturity seen among primates and particularly humans.

The main hypothesis forwarded as to the nature of these benefits suggests that an extended juvenile phase of life allows the acquisition of the large body of knowledge and skills that must be acquired prior to adulthood among species with highly complex social and foraging skills. Joffe’s review of the evidence (1997) favoured the prior explanation, concluding that in contrast to social skills, foraging skills appeared to be acquired relatively easily and quickly by juvenile primates (see also Barrickman *et al.* 2008, 581). It is debatable how far social and foraging skills can really be separated out from one another, particularly among modern humans, whose complex hunting practices rarely reach peak efficiency until at least maturity (Barrickman *et al.* 2008, 581; see also Coward & Gamble 2008; MacDonald 2007; Coward & Grove submitted).

Nor is an extended period of immaturity and growth among humans matched by a residual enlargement of body size relative to other primates; it has been suggested, therefore, that humans can be regarded as *growth suppressed* during most of their development, with the adolescent human growth spurt representing catch-up growth at sexual maturity. There is some controversy as to whether this is a uniquely human characteristic, but at the very least it is clear that the human adolescent growth spurt is significantly more pronounced than that of non-human primates (Bogin 1999). The most plausible explanation for this is argued to be a prolongation of ‘young’ physical form to elicit parental behaviour — care rather than competition — from adults (Smith & Tompkins 1995).

The significance of this rescheduling of brain growth and development thus lies in the fact that, unlike other primates, most human brain growth takes place while the individual is already interact-

ing with the extra-maternal environment. Given the significant role of epigenetic factors in ontogenetic brain development discussed above, this prolonged post-natal growth period massively extends the time-frame during which the selective effects of experience of the physical and social environment can impact on processes of brain development (e.g. Coqueugniot *et al.* 2004) including synaptic competition and pruning, myelination and facilitation. A relative underspecification of brain development clearly also necessitates highly developed learning abilities among species occupying niches reliant on complex foraging and social skills: cognitive evolution in general has been argued to be driven by selection for increased learning abilities, particularly as regards novel manual skills in feeding contexts which would enable species to process more difficult foodstuffs (Byrne 2007).

Such an increased focus on learning undoubtedly impacts on the complexity and cultural transmission of technological skills such as lithic manufacture and use. Underpinned by a primate heritage of the basic cognitive mechanisms discussed in the first half of this paper, the extended juvenile period among humans allows for absolutely more time for cognitive development in the face of environmental (both social and ecological) stimuli which relate to their capabilities for learning the relevant skills for a niche characterized by extreme flexibility in the face of ecological variability (Coward & Grove submitted). In a recent review of the anthropological literature, of 24 case studies where information was available on the length of time it took to master craft skills, all but six required longer than one year, and more than half (14 cases) took more than five (Hosfield in press).

Furthermore, this complexity of technology relates not only to changes in life history discussed above, but also to associated developments in hominin sociality. The necessary changes in developmental and life history strategy may be highly adaptive — but, crucially, they can only occur as part of a constellation of other behaviours. Increased parental care is clearly vital as larger brains require high-quality, protein-rich diets in early development, and given already high levels of investment in offspring by mothers, the extra investment must come from elsewhere, be that pair-bonded males or older relatives. It is interesting to note that the prolongation of life spans beyond reproductive stages makes little sense outside a way of life where the handing down of complex skills learnt over a lifetime is adaptive (Fig. 5; Peccei 1995; Hawkes *et al.* 1998; O'Connell *et al.* 1999).

While this article focuses on lithics, the arguments extend to other technological domains and

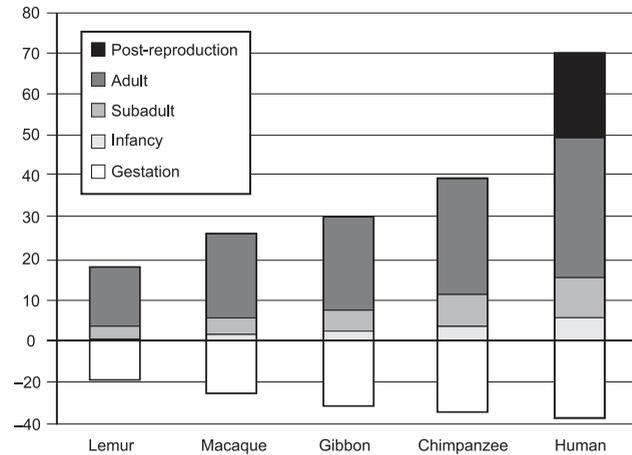


Figure 5. Hominoid life histories. Positive scale is in years, negative scale in weeks. (Redrawn after Schultz 1969, 149.)

skilled behaviours: for example, complex hunting and gathering and food-processing practices. This observation brings us full circle, as more sophisticated foraging and processing skills and more complex social networks for food-sharing and care-giving allowed hominins to target even higher quality resources such as meat more efficiently, further fuelling brain expansion and development and creating positive feedback/ratcheting effects between the costs and benefits of encephalization and altered life-histories (see e.g. Aiello & Wheeler 1995; Barrickman *et al.* 2008; Kaplan *et al.* 2000; Coward & Grove submitted). Although it may seem blatantly obvious, it is worth emphasizing the point that simple linear causalities are unlikely to be sufficient for investigating the evolution of human cognition.

Locating the changes in hominin evolution

Evidence for developmental histories is of course difficult to assess in the fossil record of extinct hominin species. Pelvic inlet size and cranial capacity of fossil hominin and hominid species are of particular interest here. Of course, head size at birth is not a direct measure of learning-dependency and/or life-history; nevertheless, as discussed above, the trade-off between the adaptive constraints of pelvic size/parturitional mortality and the benefits of encephalization are particularly important variables in the constellation of physical and social adaptations that combine to make human cognition unique. Comparisons of the pelvic inlet size and cranial size are thus salient markers of the degree to which the derived pattern of human development — longer, slower, brain maturation in

more complex social environments — had established itself among fossil hominin populations.

On this basis, the balance of evidence currently suggests that *Homo erectus* is the locus of many of these changes. The pelvis of *Australopithecus afarensis* specimens are sufficiently spacious that selective pressure for secondary altriciality seems unlikely (Smith & Tompkins 1995) given cranial capacities not significantly greater than those of living hominoid apes (Foley & Lee 1991), although the robust australopithecines have yielded confusing results perhaps related to their highly specialized dental adaptations (Smith & Tompkins 1995). In contrast, the large brain and reduced pelvic inlet of Neanderthals are very similar in dimensions to those of modern humans and suggest similar patterns of perinatal growth (Foley & Lee 1991; Smith & Tompkins 1995; Coqueugniot *et al.* 2004).

Sadly, lack of evidence precludes viable reconstruction of *Homo habilis*'s development (Smith & Tompkins 1995), although it has been noted that encephalization — a characteristic of the genus *Homo* particularly — is likely to require a shift towards secondary altriciality (Foley & Lee 1991). But it is the data from *Homo erectus* which is most interesting. Although the pelvis from Nariokotome is very narrow compared to modern humans, this specimen is that of a juvenile male (Smith & Tompkins 1995). In contrast, the Mojokerto *Homo erectus* child from Java, estimated to have been around 1 year old at death, has an endocranial capacity of 72–84 per cent adult size, arguing for a rapid 'ape-like' rather than slow modern human pattern of postnatal brain development. The conflict between the dental and skeletal age of the Nariokotome skeleton could also suggest that the derived modern human pattern of delayed childhood growth followed by an adolescent growth spurt had not yet become established in *Homo erectus* (Smith & Tompkins 1995), although Foley & Lee have argued that all members of the genus *Homo* display extended maturation, being dentally advanced for a given chronological age (Foley & Lee 1991). Nevertheless, *Homo erectus* has very modern human-like limb dimensions and was thus probably fully bipedal, which may imply that pelvic constraints were exercising some selective pressure on birth-size and thus delaying maturity (O'Connell *et al.* 1999).

Given a strong correlation between brain size and longevity among primates, it also seems likely that the increased size of *Homo erectus*'s brain was associated with an increased lifespan. The link between increasing maternal body size and delayed maturity also argues for *Homo erectus* as a break point in developmental schedules — estimated *Homo erectus* body weights of 55–60 kg are a 55 per cent increase (70

per cent for females alone) on the c. 35–40 kg average among australopithecines (O'Connell *et al.* 1999).

Some of the behavioural and social correlates of changing life histories can also perhaps be detected in the archaeological record associated with *Homo erectus*. A larger body size is highly correlated with the broader foraging range necessary for exploiting the patchier high-quality foods which allow an increase in brain size. Similarly, a smaller thoracic capacity suggests a simpler gut as a result of a shift to a higher-quality diet requiring less gastric processing — resulting in more metabolic energy available for encephalization (Aiello & Wheeler 1995; O'Connell *et al.* 1999). The earliest evidence for such a dietary shift — the faunal remains of large animals, often with cutmarks — appears in the archaeological record of *Homo erectus* (Foley & Lee 1991). Evidence for larger site sizes, more diverse assemblages and the exploitation of a broader range of habitats and wider geographical spread at around this time (*Homo erectus* is the first hominin to appear outside Africa, as far north as Georgia) would also seem to point towards increasing behavioural flexibility, perhaps relating to the development of modern developmental histories in which longer juvenile periods were adaptive because of the ways in which longer-term immersion in highly social post-natal environments could influence epigenetic development of cognitive mechanisms derived from our primate cognitive heritage and enable individuals to learn the skills associated with more and more complex social and ecological niches.

These physical, skeletally-based lines of evidence are not immediately linked to the changes in neurons and brains we surmise occurred during hominization. Nevertheless, they do represent convenient and informative ways in to the constellation of physical and social adaptations without which the developments underpinning modern human cognition could not have occurred — and it is with *Homo erectus* that we can begin to see some of the many necessary developments come together in something that begins to resemble the derived modern human lifeway.

Conclusions

In conclusion, we have argued here that cognition cannot simply be identified at the level of the individual neuronal system or even the individual brain. The brain cannot be separated from the body; the sensory and motor modalities that structure primate life and cognitive and technological achievement are the property of both central and peripheral cognitive and motor systems.

Nor can individual agents — brains in bodies — be separated out from one another. Mirror neurons potentially provide a mechanism by which individuals structure their social interactions through an innate cognitive equivalence of physical actions by oneself and by others. The manufacture and use of tools provides a further means by which individuals may associate with one another: imitation or outright teaching of knapping behaviours will necessarily encourage cognitive empathy. Not only do tools extend the body schema of the individual, but through exchange and re-use among hominins, they encourage the perception of self-other equivalence, together with the observation of those important differences that exist between individuals.

The individual brain, then, is shaped by its embodied experience of the world and by the other embodied brains around it from a very early stage. New developments in neuroscience are now beginning to allow us to address the functional neuroanatomy of the individual brain, with huge potential for addressing the neural bases of the behaviours we see in the 2.6 million years of the archaeological record. Equally, these new developments are highlighting the complexity of the linkages between brain and body, as well as those between individuals and between individuals and the social and physical environments in which they are immersed. We must choose our level of analysis with care.

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