The Evolution of Cognitive Control

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Abstract

One of the key challenges confronting cognitive science is to discover natural categories of cognitive function. Of special interest is the unity or diversity of cognitive control mechanisms. Evolutionary history is an underutilized resource that, together with neuropsychological and neuroscientific evidence, can help to provide a biological ground for the fractionation of cognitive control. Comparative evidence indicates that primate brain evolution has produced dissociable mechanisms for external action control and internal self-regulation, but that most real-world behaviors rely on a combination of these. The archeological record further indicates the timing and context of distinctively human elaborations to these cognitive control functions, including the gradual emergence of increasingly complex hierarchical action control.

Keywords: Executive function; Prefrontal cortex; Brain evolution; Social brain; Paleolithic archelogy; Oldowan; Acheulean

1. Introduction

Every species is unique, and humans are no exception. Distinctively human characteristics include such oddments as small canines, a broad pelvis, and an extended life span, all of which may only be properly defined and understood in a comparative, evolutionary context. As Darwin (1958, p. 449) himself pointed out, the same is true of human intelligence. Intelligence is perhaps *the* defining characteristic of humanity, but it is notoriously hard to define.

Boring (1923) famously defined intelligence as whatever it is that intelligence tests test. In this spirit, an evolutionary biologist might define intelligence as whatever it is that

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humans do best. Unfortunately, this circular definition is both too broad and too narrow. Distinctive human abilities in domains like language and tool use certainly seem intelligent but are enabled in large part by specific sensorimotor and somatic adaptations (Bril & Roux, 2005; Hauser, Chomsky, & Fitch, 2002; Marzke, 2005) that fall outside conventional ideas of ''intelligence.'' At the same time, animals like dolphins and crows that share little with humans in terms of habitat, behavior, anatomy, or phylogeny nevertheless appear quite intelligent to us (Emery & Clayton, 2004; Marino, 2002). This has led some to suggest that what we really mean by intelligence is flexibility in the production of adaptive, goal-oriented behavior (e.g., Byrne, 1995; Lefebvre, Reader, & Sol, 2004; Roth & Dicke, 2005). Cognitive scientists generally explain such flexibility in terms of cognitive control.

Cognitive control might be loosely defined as the use of internal representations (e.g., goals) to select, modulate, and coordinate subordinate cognitive, motor, and perceptual processes. Such control is made possible (and necessary) by evolutionary changes in brain size and structure that increase the length of synaptic chains linking sensation to action (Mesulam, 1998; Miller & Cohen, 2001). But is this simply a question of ''more is better,'' reflecting enhancement of a unitary capacity for cognitive control? Or is there a diversity of independent mechanisms for cognitive control that might be differentially developed in particular species and individuals?

2. Fractionating cognitive control

Cognitive control is widely viewed as synonymous with frontal lobe function, and particularly with the prefrontal cortex (PFC). Other brain regions contribute to neural networks enacting cognitive control, but PFC plays a distinctive ''executive'' role by modulating activity in posterior and subcortical structures (Fuster, 2001; Miller & Cohen, 2001). More than 150 years of neuropsychological research has led to the identification of three classic syndromes associated with damage to orbital, medial, and lateral PFC. Such damage is thought to produce more or less independent deficits in emotional regulation, attention, and action planning, respectively. This broad characterization is supported by evidence of functional imaging, cytoarchitectonics, and neural connectivity (Fuster, 2001; Miller & Cohen, 2001; Wood & Grafman, 2003). However, it remains unclear to what extent conventional descriptions like ''attention'' and ''action planning'' actually capture PFC functional contributions. Where should hypothetical categories of executive function come from and how should they be tested?

Information processing models (e.g., Baddeley, 1986; Norman & Shallice, 1980) can suggest well-defined candidate functions, but they risk circularity if functional categories are both inspired by and tested against performance on ''executive'' tasks that are themselves not well understood (Barkley, 2001; Miyake et al., 2000). Neuroanatomy provides an additional line of evidence to help constrain cognitive models, although it would be a category error to propose purely anatomical definitions for cognitive functions (cf. Baddeley, 1996). Patterns of cortical connectivity do suggest the presence of multiple functional networks in PFC, with a particularly robust distinction between ventromedial and lateral PFC (Fig. 1).
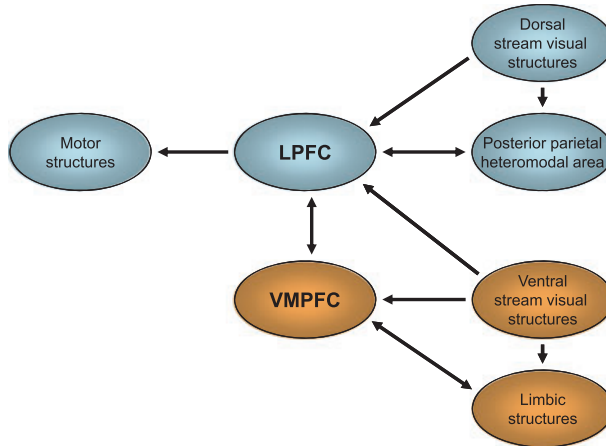
Fig. 1. Simplified representation of connectivity between prefrontal cortex and other brain structures. Drawn after Wood and Grafman (2003).

Ventromedial PFC (VMPFC: including medial and lateral orbitofrontal, medial frontal, and cingulate gyri) is dominated by reciprocal connections with limbic structures involved in regulation of the internal milieu, and with posterior temporal lobe visual association cortex involved in the ventral stream of object perception. In contrast, lateral PFC (LPFC: including superior, middle, and inferior frontal gyri) is characterized by extensive connections with sensory and motor structures involved in interactions with the external environment. These patterns suggest a distinct role for VMPFC in the regulation of affective and somatic states and for LPFC in the regulation of action (including cognitive action). This distinction can usefully inform information processing models, for example, by suggesting the need to include affective process like ''energisation'' and ''attentiveness'' as well as action control processes like ''task setting'' (Shallice, Stuss, Picton, Alexander, & Gillingham, 2008).

Despite the importance of affective and somatic regulation to cognition (Damasio, 1994), most attempts to fractionate cognitive control have focused on the control of action in LPFC. For example, the ''central executive'' of working memory is thought to rely on separable mechanisms for controlling attention and for maintaining/integrating working memory representations, both linked with the dorsal LPFC (Baddeley, 2003). Commonly postulated executive functions such as shifting between tasks or mental sets, updating and monitoring of working memory representations, and response inhibition (Miyake et al., 2000) similarly focus on action regulation, and likely rely on LPFCs extensive reciprocal connections with posterior sensory association cortices (Collette et al., 2005; Fuster, 2001). However, these putative functions are not associated with clearly separable neural networks (Collette et al., 2005) and have been considered unlikely candidates for the ''fundamental units'' of cognitive control from a processing standpoint (Miyake et al., 2000).

Cognitive neuroscientists seeking inspiration from functional anatomy rather than explicit information processing models have often fractionated LPFC function into levels in an

action control hierarchy (Badre, 2008). This is consistent with evidence of rostro-caudal architectonic, connectional and developmental gradients in PFC (Badre & D'Esposito, 2009). However, the exact *functional* nature of the gradient, which might relate to differences in domain specificity (Petrides, 2005), relational complexity (Christoff & Gabrieli, 2000), temporal context (Koechlin & Summerfield, 2007), and/or representational hierarchy (Badre & D'Esposito, 2007), remains controversial. Part of the difficulty is that functional characterizations inevitably depend on the use of diagnostic behavioral tasks that are themselves theory laden. As in cognitive psychology, this raises the danger of simply defining cognitive functions in terms of the tests designed to test them. Is there any principled way to fractionate cognition that is not ultimately based on subjective intuitions about how to carve brain function into its natural kinds? Perhaps not, but the use of multiple, converging lines of psychological, neuropsychological, and neuroscientific investigation seems to provide our best chance of breaking the hermeneutic circle. Recent interest in the use of evolutionary evidence to further constrain hypotheses of brain function (e.g., Ardila, 2008; Barkley, 2001; Wood & Grafman, 2003) provides another promising avenue of investigation to add to this set.

3. Evolutionary evidence

It is a truism that the structure of the modern brain is a product of its evolutionary history. However, the potential for evolutionary evidence to inform our understanding of brain structure and function remains underdeveloped. This likely reflects the inherent difficulty of cross-disciplinary research and the challenge of truly integrating the vast fields of cognitive and evolutionary science. With this in mind, the following sections review some of the major forms of evolutionary evidence that are available to cognitive scientists and their potential contributions to an evolutionarily principled fractionation of cognitive control.

3.1. Comparative evidence

Over the past 30 years, evolutionary biology has entertained a vigorous debate over whether brain size variation is better explained as an adaptation for social (Byrne & Whiten, 1988; Dunbar & Shultz, 2007; Humphrey, 1976) or for ecological (Clutton-Brock & Harvey, 1980; Milton, 1988; Parker & Gibson, 1979) problem solving. As a result, many commentators now advocate a less dichotomized view, noting that ecological skills are often socially transmitted and that social cohesion serves ecological functions (Reader & Laland, 2002; Zuberbühler & Byrne, 2006). The key question is whether these interwoven socioecological pressures have led to a similarly integrated general intelligence, or whether individual species display idiosyncratic combinations of independently evolved executive functions.

In support of the former, it does appear that ''intelligent'' species like chimpanzees, dolphins, and crows tend to be intelligent across the board, displaying a wide range of capacities for tool use, cultural transmission, complex communication, and social problem solving

(Emery & Clayton, 2004; Krützen et al., 2005; Marino, 2002). It is striking that birds, cetaceans, and primates display such a similar range of abilities despite dramatically different neuroanatomy, and this is consistent with evolutionary convergence on a ''general problem solving ability'' (Lefebvre et al., 2004). On the other hand, behavioral abilities like ''tool use'' are not themselves executive functions, and it is not clear that different species always solve similar problems using the same cognitive strategies. For example, it seems likely that mechanisms of social problem solving differ between anthropoid primates and pair-bonded birds (Emery, Seed, von Bayern, & Clayton, 2007) and that the tool use of dolphins (Krützen et al., 2005) involves less complex action sequences than that of crows (Emery & Clayton, 2004) or apes (Byrne, 1997). A great deal of comparative behavioral, cognitive, and neuroanatomical research remains to be done on this subject.

For the moment, the primate evidence appears most directly relevant to understanding human cognitive control, and here at least there does seem to be some evidence of independent evolution. Data remain extremely limited, but independent variation in the size of dorsal (lateral as defined here) (Schenker, Desgouttes, & Semendeferi, 2005), polar (Semendeferi, Armstrong, Schleicher, Zilles, & Van Hoesen, 2001), and orbital (Semendeferi, Armstrong, Schleicher, Zilles, & Hoesen, 1998) frontal cortex across hominoids (bonobos, chimpanzees, gorillas, orangutans, and humans) has been observed. This variation correlates with behavioral differences between species and suggests a degree of evolutionary independence between LPFC and VMPFC.

3.1.1. VMPFC

Among hominoids, orangutans stand out as having an unusually small and undifferentiated orbitofrontal cortex as well as a solitary lifestyle and relatively simple social organization (Schenker et al., 2005; Semendeferi et al., 1998). The social sequelae of damage to VMPFC in humans are also well documented (Bechara, Damasio, & Damasio, 2000) and, together with the comparative evidence, suggest that social problem solving may have been an important pressure driving the evolution of this region. Furthermore, this interpretation helps make sense of VMPFC's connections with temporal lobe visual cortex, as the ventral stream of visual perception (Milner & Goodale, 1995) plays a key role in the perception of social signals like facial expression, posture, and gaze direction (Brothers, 1990; Frith, 2007). In fact, the volume of portions of the lateral geniculate nucleus projecting to the ventral stream correlates with social group size in primates (Barton, 1998).

It thus seems likely that primate VMPFC evolved together with the ventral stream as part of an integrated system for the cognitive control of social interactions. However, this system should not be mistaken for a dedicated social cognition ''module.'' VMPFC and the ventral stream each participate in nonsocial tasks such as object recognition (Milner & Goodale, 1995) and decision making under uncertainty (Bechara et al., 2000), whereas additional structures make key contributions to social cognition. LPFC, for example, is recruited during the suppression of prejudicial reactions to other individuals (Cunningham et al., 2004). Social problem solving may be an important selective pressure, but it is not itself an executive function. This leads to the question of what the executive demands of sociality actually are.

Byrne and Bates (2007) argue that social life places a premium on three abilities: (a) recognizing different individuals and social signals, (b) focusing sustained attention on relevant stimuli, and (c) rapid learning of (a large number of) social associations. To this, humans add a facility for the prediction of behavior through mentalizing (''theory of mind''). All of these abilities share a clear association with VMPFC, and particularly with its role in relating internal emotional or somatic states to visual stimuli. Attention and perception (Phelps, Ling, & Carrasco, 2006), rapid learning (Hamann, 2001), and the recognition of individuals (Hirstein & Ramachandran, 1997) are all facilitated by the affective marking of stimuli in VMPFC (Damasio, 1994), whereas mentalizing is supported by the same regions of VMPFC recruited during introspection (Frith, 2007; Ochsner et al., 2004). This suggests that mechanisms of self-knowledge play an important role in understanding others. In sum, primate VMPFC appears to have evolved to play a central role in the regulation of internal states and their association with external stimuli, most likely in response to the pressures of group living. This is a relatively discrete ''function'' that might be included in an evolutionarily principled attempt to fractionate cognitive control.

3.1.2. LPFC

It has been argued that LPFC evolved as an anterior extension of motor cortex and that it continues to play a central role in the regulation of action, including covert ''cognitive action'' (Ardila, 2008; Fuster, 1997; Wood & Grafman, 2003). This suggests that hypothetical functional gradients within LPFC might also reflect a posterior-to-anterior sequence of evolutionary elaboration. In fact, it is the more anterior portions of frontal cortex that are expanded and reorganized in humans (Rilling, 2006), whereas frontal cortex as a whole is no larger than expected for an ape brain of human size (Semendeferi, Lu, Schenker, & Damasio, 2002). The most anterior portion of PFC (frontopolar cortex, i.e., area 10p of Öngür, Ferry, and Price, 2003) in particular is dramatically enlarged in humans and contains less densely packed cells that leave more room for intrinsic and extrinsic connections (Semendeferi et al., 2001).

In humans, area 10p extends over both medial and lateral cortex, which might suggest a breakdown of the LPFC/VMPFC dichotomy at this high level of processing. However, it is now clear that medial and lateral 10p play dissociable roles in cognitive control consistent with this dichotomy. Medial 10p appears to be involved in maintaining focused attention to task-relevant stimuli (Gilbert, Spengler, Simons, Frith, & Burgess, 2006), while lateral 10p is involved in switching between different cognitive tasks or processes (Gilbert et al., 2006; Koechlin & Summerfield, 2007; Ramnani & Owen, 2004). Unfortunately, the comparative data needed to determine whether lateral and medial 10p have evolved in a coordinated or independent fashion are not yet available.

There is, however, evidence that lateral frontal cortex as a whole has evolved independently of orbital and medial sectors (Schenker et al., 2005). In fact, the lateral sector is relatively large in orangutans and chimpanzees and small in bonobos. This is a highly suggestive finding, considering that chimpanzees and orangutans routinely manufacture and use tools in the wild (van Schaik, Deaner, & Merrill, 1999), whereas bonobos do not. Tool use is a prime example of the kind of complex, instrumental action typically associated with

LPFC, and one of the more demanding forms of ''extractive foraging'' (Parker & Gibson, 1979) known in primates. Extractive foraging of embedded or encased foods commonly requires animals to learn abstract stimulus-response mappings and to assemble these into hierarchically structured action sequences (Byrne & Russon, 1998). Such operations depend on multilevel integration of sensory and motor representations across time in LPFC (Fuster, 2001; Passingham & Sakai, 2004), suggesting that primate LPFC function may have evolved at least partially in response to selection on foraging abilities (cf. Byrne, 1997).

This hypothesis predicts that variation in the degree of abstraction and/or hierarchical complexity involved in foraging by different primate species should correlate with the size and structure of corresponding subdivisions of the LPFC functional gradient. Unfortunately, the necessary neuroanatomical data are not yet available and adequate methods for quantifying the complexity of primate foraging techniques have yet to be developed (but see Byrne, 2007). Nevertheless, the hypothesis is testable in principle and consistent with the available evidence (Byrne, 1997; Schenker et al., 2005). If further supported, it would suggest that LPFC has evolved to serve a relatively discrete role in the cognitive control of instrumental action. LPFC provides the natural locus for this form of processing because of its extrinsic connections with sensory and motor structures (Fuster, 1997), extensive intrinsic connectivity (Badre & D'Esposito, 2009), and physiological capacities for sustained activity across time and events (Fuster, 2001; Passingham & Sakai, 2004). ''Multilevel sensorimotor integration'' by LPFC might thus be considered as a second element in an evolutionarily informed fractionation of cognitive control.

Again, this hypothetical function would not constitute an encapsulated ''foraging module.'' Real-world foraging implicates VMPFC in the facilitation of attention, perception, and learning, whereas LPFC properties supporting instrumental action with objects are also recruited in social problem solving. Examples include the intentional suppression of expressive behaviors (Goldin, McRaea, Ramela, & Gross, 2008), the strategic reappraisal of emotional associations (Ochsner & Gross, 2005), and the production of intentional communicative gestures (Arbib, 2005). Even if primate VMPFC and LPFC have evolved somewhat independently, they are still very closely integrated with one another. Variation in their relationship is likely to produce relatively subtle differences in cognitive style, rather than dramatic differences in general problem-solving ability. For example, the dorsolateral frontal sector of bonobos is relatively small compared to chimpanzees and orangutans and, unlike these apes, bonobos are not known to use tools in the wild. Nevertheless, captive bonobos can develop highly proficient tool skills if provided with a supportive social environment (Savage-Rumbaugh & Fields, 2006), and they display high levels of social tolerance that allows them to outperform chimpanzees on cooperative tool use tasks (Hare, Melis, Woods, Hastings, & Wrangham, 2007). This suggests a bonobo cognitive style more dependent on VMPFC self-regulation than LPFC sensorimotor integration but achieving similar ''general problem-solving'' capabilities. Conversely, it appears that orangutans, with their relatively small and undifferentiated orbitofrontal cortex, may be less proficient at inhibitory self-control than are chimpanzees and humans (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007). This might help to explain the apparent contradiction between orangutans' poor performance on some laboratory tests of physical cognition (Herrmann

et al., 2007) and their demonstrated facility with physical problem solving (e.g., Russon et al., 2008) in the wild, where conditions may be more suitable to the expression of an evolved LPFC-dominant cognitive ''style.''

3.2. Human evolution

Comparative evidence provides insight into the deep evolutionary origins of human cognition, but it cannot reveal details of the timing and context of more recent developments. Such evidence comes instead from the physical remains comprising the human paleontological and archeological records. Paleoneurological investigation of hominin cranial remains provides direct, if limited, evidence of brain evolution, whereas archeology provides evidence of past behavior.

3.2.1. Paleoneurology

Hominin cranial fossils preserve evidence of (a) overall brain size, (b) cerebral asymmetry, and (c) cortical sulcal patterns that leave impressions on the endocranial surface. As reported by Holloway, Broadfield, and Yuan (2004), currently available fossils suggest three major stages of hominin brain evolution. Stage 1, from approximately 3.5–2.0 million years ago (mya), consists of brain reorganization without substantial expansion and includes the relative expansion of posterior parietal association cortex at the expense of occipital visual cortex. This reorganization may have been an important precondition (Stout & Chaminade, 2007) for the emergence of stone tool making by 2.6 mya (Semaw et al., 2003). Stage 2, from 2.0 to 0.5 mya, begins with a sudden increase in brain size (500–750 ml) associated with the appearance of *Homo habilis,* followed by more gradual expansion (800–1,000 ml) related to body size increases in *Homo erectus. Homo habilis* also sees the first appearance of modern-human-like cerebral asymmetries, including enlargement of the Broca's cap region of left LPFC. Stage 3, from 0.5 to 0.02 mya, consists of a rapid but continuous increase in brain size (1,000 to 1,500 ± 200 ml) without associated changes in body size. Finally, over the past 15,000 years, decreasing body size has brought human mean brain size down to around 1,400 ml.

Aside from enlargement of Broca's cap in *Homo habilis*, evidence of frontal lobe size and organization from paleoneurology is limited. The fact that modern human frontal lobes are no bigger than expected for an ape brain of comparable size (Semendeferi et al., 2002) strongly suggests that this was also the case for ancestral hominins; however, much less can be said about the volume of specific regions of prefrontal cortex. There is some suggestion that Stage 1 involved a change in prefrontal lobe shape (Falk et al., 2000), perhaps indicative of functional reorganization, but this remains a tentative assessment (Holloway et al., 2004). The functional implications of an enlarged Broca's cap in Stage 2 are also unclear, they but might suggest adaptations for language, gesture (Arbib, 2005), and/or instrumental action with objects (Stout & Chaminade, 2009). Paleoneurology thus provides invaluable evidence for broad patterns in hominin brain expansion, but it leaves many details about the evolution of particular systems and abilities unanswered. To some extent, these gaps may be filled through consideration of behavioral evidence from the archeological record.

3.2.2. Archeology

The archeological record of human evolution is dominated by durable stone artifacts that have survived to be recovered by modern researchers. Fortunately for us, these tools and the refuse from their production can provide a surprisingly detailed record of individual actions and goal-directed sequences (e.g., Delagnes & Roche, 2005) going back as much as 2.6 million years. Somewhat less fortunately, there is no generally accepted method for inferring the cognitive processes underlying these reconstructed behaviors (Wynn, 2009), and widely divergent interpretations of the same evidence persist (e.g., Mithen, 1996; Noble & Davidson, 1996; Read & van der Leeuw, 2008; Wynn, 2002; Wynn & Coolidge, 2004). One response has been to develop an additional empirical basis for interpretation by using functional brain imaging to identify the neural correlates of particular Paleolithic technologies (Stout & Chaminade, 2007, 2009; Stout, Toth, Schick, & Chaminade, 2008; Stout, Toth, Schick, Stout, & Hutchins, 2000).

At first glance, the cognitive and behavioral complexity of Paleolithic tool production is easily underestimated. For example, the earliest known (Oldowan) stone tools consist of nothing more than sharp stone flakes struck from river cobbles (Semaw, 2006; Toth, 1985). However, even this simple technology requires substantial visuomotor coordination that must be developed through practice. Typically, flakes are produced by striking a cobble ''core'' held in one hand with a ''hammerstone'' held in the other. This requires visual evaluation of core morphology (e.g., edge angles, location of convexities and concavities) in order to select appropriate targets for percussion, as well as precise bimanual coordination to deliver highly forceful blows to small targets on the core. When these aspects of Oldowan skill are underdeveloped, as in trained apes or humans with insufficient experience, the products are diagnostically different from those found in the early archeological record (Stout & Chaminade, 2007; Toth, Schick, & Semaw, 2006).

In keeping with these behavioral observations, functional imaging studies indicate that proficient Oldowan flaking is especially reliant on posterior parietal mechanisms for object perception and bodily awareness and on ventral premotor control of manual prehension (Stout & Chaminade, 2007; Stout et al., 2008). This includes activation of portions of dorsal intraparietal sulcus that comprise a phylogenetically new functional area in humans, with novel response properties to central visual field stimuli and three-dimensional forms that are absent in monkeys (Orban et al., 2006). This leads to the conjecture that the emergence of Oldowan technology at 2.6 mya may have been enabled at least in part by the expansion of posterior parietal cortex in Holloway's Stage 1. In contrast, imaging results do not indicate any exceptional demands of Oldowan flaking on PFC.

This likely reflects the fact that Oldowan action sequences are relatively simple and can be fully accounted for in terms of the following: (a) responsiveness to current core configurations and (b) a simple (Markovian) chaining together of flake removals in which the location of the next removal is determined from the previous one according to a simple rule (e.g., vertically adjacent, horizontally adjacent, alternate face) (cf. Delagnes & Roche, 2005; Wynn & McGrew, 1989). This suggests that the need for control processes like task shifting or the updating of working memory representations should be quite

limited. Unfortunately, such interpretations are difficult to test given the lack of well-defined behavioral or neural criteria for identifying the recruitment of these putative cognitive functions. Alternatively, one might characterize Oldowan flaking as involving action selection based on sensory information and immediate context without the need to consider more temporally extended contingencies relating to past behaviors or ongoing subgoals. This assessment implicates the ''sensory'' and ''contextual'' levels of processing specified in the PFC model of Koechlin and Summerfield (2007), and it is in close agreement with the experimentally observed activations in motor (Brodmann area [BA] 4) and premotor (border between BA 6 and 44) cortex as well as the absence of activation in PFC.

Both interpretations support earlier characterizations (Bril & Roux, 2005; Wynn & McGrew, 1989) suggesting that Oldowan flaking does not directly implicate cognitive control demands beyond those seen in ape extractive foraging (e.g., Byrne & Russon, 1998). However, Oldowan flaking and ape foraging both exist in a broader behavioral context. For Oldowan and later stone technologies, this minimally includes the initial selection and transport of raw materials (Stout, Quade, Semaw, Rogers, & Levin, 2005), the effective use of tools after production (Schick & Toth, 2006), and the prior acquisition of relevant technological skills and knowledge (Stout, 2005). The details and cognitive implications of this broader context are not well known, but skill acquisition stands out as a key issue.

Available evidence indicates that it takes more than a few hours of practice to master even simple Oldowan flake production. Although novice flakers rapidly learn to identify and select appropriate targets (Stout & Chaminade, 2007), it takes much longer to develop the bodily techniques needed to reliably deliver forceful and accurate blows (Stout et al., 2008). Such skill acquisition requires the discovery of appropriate techniques through behavioral experimentation (Ericsson, Krampe, & Tesch-Romer, 1993) with various different grips, postures, and angles of percussion, as well as with hammerstones of varying size, shape, and density. Discovery of optimal techniques can be facilitated by explicit instruction or imitation of an expert model, but it minimally requires focused attention, self-monitoring, and the inhibition of automatic reactions during repetitious practice (Ericsson et al., 1993; Rossano, 2003). The necessity of such practice implies additional demands on both VMPFC and LPFC to support the full range of Oldowan behavior.

Functional imaging studies have not yet addressed the next major technological development in human evolution: the appearance by ~1.7 mya (Roche et al., 2003) of intentionally shaped ''large cutting tools'' characteristic of the early Achuelean (Clark, 1994). The earliest Acheulean tools come in a variety of forms, including pointed, trihedral ''picks'' made from large cobbles and flatter, two-sided ''handaxes'' made by trimming the edges of very large (>15 cm) flakes produced from boulder cores. Both methods require a new level of hierarchical control over individual flake removals, which must be subordinated to the broader goal of shaping the piece. This might be expected to involve LPFC in the assembly of individual removals into a coherent action ''chunk'' (Koechlin & Jubault, 2006) and/or the management of increasingly abstract relations (Badre & D'Esposito, 2007) between individual flake removals and overall core shape. The latter could also be thought of as an

increase in demands for the updating (sensu Miyake et al., 2000) or active use (Passingham & Sakai, 2004) of working memory representations. These intuitions make specific predictions regarding patterns of LPFC activation that should be testable in future research. It is also possible that the production of handaxes from large flakes produced in a previous technological operation implies an additional level of temporally extended ''episodic'' control (Koechlin & Summerfield, 2007). Unfortunately, this is likely to be much more difficult to test.

Brain activation data have recently become available for later Acheulean tool making, and they do provide evidence of associated LPFC activation (Stout et al., 2008). Later Acheulean handaxes, clearly present by ∼0.5 mya (e.g., Roberts & Parfitt, 1999), are much more refined than earlier examples, with sharper, more regular edges and a thinner cross-section. Such characteristics are very difficult to produce and clearly reflect intentional effort on the part of tool-makers (Edwards, 2001). There is some debate over the cognitive and/or functional implications of the symmetry seen in these forms (Machin, Hosfield, & Mithen, 2007; Wynn, 2002 and comments); however, it is the thinning of the cross-section that seems to present the greatest challenge for modern knappers (Winton, 2005). Thinning requires tool makers to strike very long flakes traveling more than halfway across the core surface. This in turn requires the careful preparation of edges and surfaces (platform preparation) through abrasion and/or micro-flaking before flake removal. Such platform preparation introduces a new subroutine into tool production, further increasing its hierarchical complexity and likely implicating additional demands for task shifting and inhibition of common actions that are inappropriate in a specific context. As expected for this level of hierarchical processing (Koechlin & Jubault, 2006), later Acheulean handaxe making is associated with activation of right BA 45 (i.e., the right homolog of anterior Broca's area).

Although this brief review merely brushes the surface of the Paleolithic archaeological record, it is clear that technological changes over the past 2.6 million years provide evidence of increasing demands for cognitive control. These changes are consistent with a gradual evolution of LPFC function, although the role of technological change as cause, consequence, or indirect correlate of cognitive change remains unclear. Implications for VMPFC are less clear but should not be underestimated. Levels of tool-making performance evident by later Acheulean times are achieved by modern practitioners only after hundreds of hours of practice, and they are clearly indicative of well-developed capacities for self-regulation. Although perhaps not decisive, the expression of such skills strongly suggests learning facilitated by the instruction and/or imitation of an expert model (Stout, 2005). For example, independent rediscovery of effective later Acheulean thinning techniques can take years (Callahan, 1979) if it ever happens at all. Increasingly skilled technical performance in prehistory thus provides strong evidence of multilevel sensorimotor integration and somewhat weaker evidence of the social (Stout, 2005) and cognitive (Rossano, 2003) skills needed to establish, maintain, and learn from interactions with expert models. LPFC and VMPFC may make dissociable contributions to human cognitive control, but it appears to be their synergistic interaction that enables the complexity of modern human cognition and culture.

4. Conclusion

Neuropsychological, neuroscientific, and evolutionary evidence all point to a fundamental distinction between the roles of LPFC and VMPFC in cognitive control. There may be additional distinctions to be made, for example, between dorsal and ventral LPFC (Passingham, Toni, & Rushworth, 2000), but this broad division seems a safe place to start. LPFC and VMPFC work together quite closely to produce flexible behavior across a wide array of social and ecological domains, but comparative evidence nevertheless indicates that they can evolve independently. This may give rise to distinctive cognitive styles in different species, for example, in the more socially mediated problem solving of bonobos versus chimpanzees (Hare et al., 2007) or the more action-oriented physical problem solving of orangutans.

Human evolution specifically appears to have produced coordinated enlargement of LPFC and VMPFC (Schenker et al., 2005), and distinctively human behavioral capacities are clearly supported by contributions from both. Human technological performance, for example, requires hierarchical action organization and the management of abstract environmental relations by LPFC but also self-regulation by VMPFC to enable deliberate practice in a social context. Similarly, human social problem solving requires cognitive control of overt communicative gestures as well as covert mentalizing and emotional regulation. These interactions suggest that evolutionary changes in one aspect of cognitive control could quite easily produce a new cognitive niche favoring evolution of the other, much as proposed by classic models of biocultural feedback in human evolution (Holloway, 1967; Washburn, 1960). It remains to be seen whether it will be possible to identify an ''initial kick,'' such as enhanced social tolerance (Hare & Tomasello, 2005) or sensorimotor control (Bril & Roux, 2005), that began this generative process.

Acknowledgments

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