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Possible Relations between Language and Technology in Human Evolution

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ABSTRACT

Complex tool use and language are distinguishing characteristics of the human species, yet the existence and nature of evolutionary relations between them remain controversial. Current thinking highlights three possible types of coevolutionary interaction involving shared neural substrates, shared social context, and shared reliance on general capacities. Evidence reviewed here supports the relevance of all three types of interaction and illustrates the contribution that detailed studies of archaeologically visible, technological behaviors, like stone knapping, can make to the study of human cognitive evolution. First, recent functional brain imaging studies of Lower Paleolithic tool making demonstrate an overlap with cortical language circuits that is consistent with motor hypotheses of speech and language origins. Second, ethnographic and developmental evidence highlights the role of joint attention and intentional communication in the social reproduction of both stone knapping and language skills. Finally, growing appreciation of the importance of hierarchical cognition—not simply in language but across domains of human action—is consistent with shared reliance on general information processing capacities.

INTRODUCTION

Complex tool use and language are distinguishing characteristics of the human species. For this reason alone, it is tempting to posit evolutionary connections between them. For archaeologists, the possibility that Paleolithic stone tools might shed light on language evolution is even more appealing. But are human language and tool use really related in any more meaningful way than that both are products of an expanded hominin brain (Hewes 1994)? Everyday experience does not suggest obvious links between the two. In fact, stereotypes like the bumbling professor or the hopelessly confusing some-assembly-required instruction manual suggest exactly the opposite. Archaeologists considering this question have similarly posited important differences between language and tool use, including the presence of innate and/or "domain specific" elements in language processing (Wynn 1993) and the absence of language-like syntax and semantics in tool use (Graves 1994). In this view, tool use and language are linked by nothing more specific than a few general cognitive abilities and the overarching context of cultural transmission (Graves 1994; Wynn 1993).

Along these lines, it is important to recognize that human language is a complex phenomenon, incorporating a wide array of sensorimotor, conceptual, and grammatical components. It remains controversial which of these might actually be unique to language (Hauser, Chomsky, and Fitch et al. 2002; Pinker and Jackendoff 2005); however, it is clear that many are shared with other behaviors. Working memory, for example, represents a likely point of overlap between language and tool use, insofar as both activities require the construction, production, and analysis of complex sequential action (Gibson 1999; Lieberman 2002; Wynn and Coolidge 2006).

Other potentially informative relations arise from the shared social context of human language and technology. Although the apparent innateness of human language acquisition has been cited as an important difference from tool use (Wynn 1993), the relative importance of innate capacities, heritable predispositions, environmental context, and social learning in each case has yet to be fully resolved (Lockman 2000; Pinker 1995; Tomasello 1995). Less controversial is the fact that social interaction plays at least some role in language acquisition, as well as in tool use and the acquisition of complex skills generally. For this reason, species that excel at tool use tend to be those that also possess rich social and communicative repertoires (Emery and Clayton 2004; Reader and Laland 2002). Formal modeling further indicates that selection for increased sociability and/or social learning ability is the most likely consequence of fitness benefits associated with the expression of complex skills (van Schaik and Pradhan 2003).

In humans, complex skill acquisition is facilitated by cultural learning (Tomasello, Kruger, and Ratner 1993) involving mental state attribution ("theory of mind") and joint attention. These are, of course, critical components of human linguistic communication in the broad sense (Hauser, Chomsky, and Fitch 2002) and central to the normal course of language acquisition (Carpenter et al. 1998). At the same time, language itself plays an important role in human technological learning and performance, providing a means of directing attention and action during shared activities (Reynolds 1993). This is particularly important in apprenticeship learning, where language can mediate aspects of meaning, motivation, and identity critical to the learning process (Lave and Wenger 1991; Rogoff 1990; Stout 2005).

But could tool use also have played a more direct role in language evolution? Motor hypotheses of language evolution (Greenfield 1991; Kimura 1979; Lieberman 1984; MacNeilage 1987; Rizzolatti and Arbib 1998) have variously proposed that speech, syntax, and semantics all have their origin in prior adaptations for motor coordination and/or object manipulation. Greenfield (1991) in particular has argued that language and object combination (including tool use and making) are constructive, hierarchically organized activities with a common developmental and evolutionary foundation in Broca's area of the left inferior frontal gyrus. More recently, this region of frontal cortex has also been identified as a major node in the mirror-neuron system of action understanding, a cortical network hypothesized to have provided a pre-adaptive substrate for intentional communication (Rizzolatti and Arbib 1998). Such work increasingly supports a direct evolutionary link between language and tool use.

Current thinking thus highlights three sets of possible relations between language and tool use in human evolution. Each implies a certain degree of coevolution and, importantly, makes predictions that are at least theoretically testable with respect to specific linguistic and technological behaviors. These possible relations are listed here.

1. Shared reliance on general capacities, such as working memory. This relationship implies coevolution in the sense that increases in these general capacities, for whatever reason, would tend to benefit both language and tool-using abilities. Its key prediction is that both linguistic behavior and Paleolithic technologies should be demanding of these general capacities.
2. Shared social context, including cognitive capacities for mental state attribution and joint attention, as well as the pragmatic contribution of language to complex skill learning and cooperative activity. This relationship implies coevolution in the sense that evolving language and tool-use capabilities would provide a complementary context for one another. Its key prediction

is that linguistic behavior and Paleolithic technologies should depend on similar cultural learning mechanisms for their reproduction.

3. Shared neural substrates underlying more specific aspects of language and tool use, including hierarchical combination in the inferior frontal gyrus and action understanding in the cortical mirror-neuron system. This relationship implies coevolution in the stronger sense that tool use would actually have provided a preadaptive foundation for specific aspects of the human language faculty. Its key prediction is that linguistic behavior and Paleolithic technologies should recruit overlapping neural substrates and processes.

These three possibilities are not mutually exclusive and each might be more applicable to some technological and linguistic behaviors than to others. For example, the manufacture of an Acheulian handaxe might be more demanding of working-memory capacity than is the production of Oldowan flakes, just as working memory might play a greater role in sentence parsing than in phonological processing.

In order to evaluate the actual evolutionary significance of these possible relations, it is necessary to test their predictions with reference to specific behaviors. Stone tool making is one such behavior that is archaeologically visible and exhibits a great time depth. The following sections draw on currently available evidence to examine the possible relations between stone tool making and language in human evolution, beginning with the strongest claims of specific neural and functional overlap.

SHARED NEURAL SUBSTRATES

Brain Activation during Oldowan Tool Making

Holloway (1969:404) provided an early examination of similarities between stone tool making and language, concluding that "selection favored the cognitive structures dependent on brain organization and social structure which resulted in both language and tool-making." More recently, Wynn (1993) suggested that the strongest link between tool behavior and language would come from evidence that the two "make use of the same neural structures or functions." In the same volume, Toth and Schick (1993) proposed that functional brain imaging might be used to look for precisely such points of overlap. This suggestion has now been implemented for Mode I (Oldowan-style) (Stout and Chaminade 2007; Stout et al. 2000) and Mode II (Acheulian-style) (Stout et al. 2008) stone knapping.

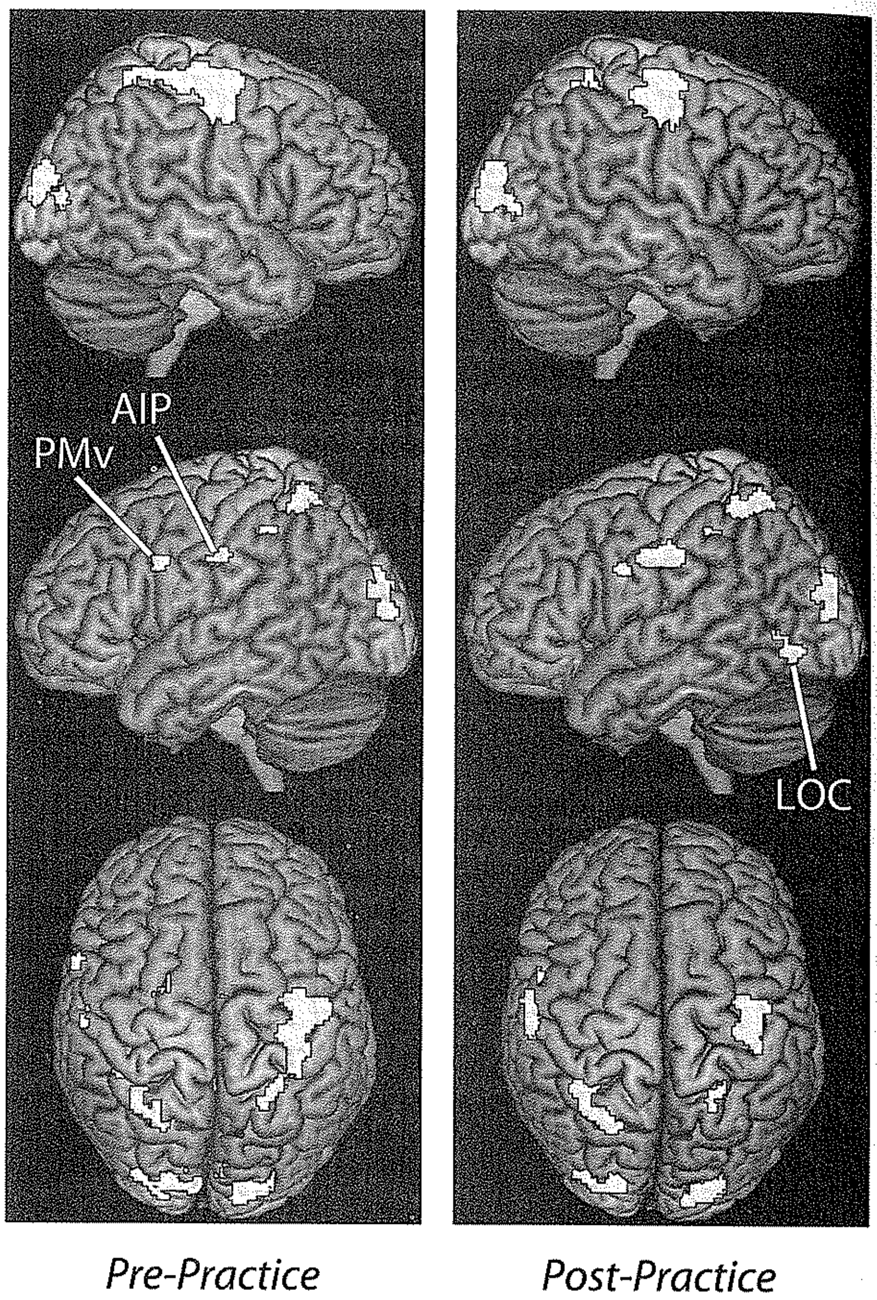
In one study (Stout and Chaminade 2007), positron emission tomography (PET) was used to collect brain activation data from six right-handed subjects producing Mode I flakes. Subjects had no prior knapping experience and were imaged both before and after four hours of practice. Data from these experimental knapping conditions were contrasted with a control condition in which subjects simply struck cobbles together without attempting to produce flakes. This allowed for the identification of activation specific to the requirements of flake production as opposed to more generic object manipulation and percussion.

Results from both naïve and practiced knapping conditions (Figure 8.1) indicate, among other things, increased activation of a parietofrontal action system including the anterior intraparietal sulcus (AIP) and ventral premotor cortex (PMv). These regions are homologous to cortical areas recruited during object prehension (Rizzolatti, Luppino, and Matelli 1998) and tool use (Obayashi et al. 2001) in monkeys, and their preferential recruitment during Mode I knapping thus indicates increased demands on an evolutionarily conserved cortical system that performs sensorimotor transformations for object manipulation (Maravita and Iriki 2004; Rizzolatti, Luppino, and Matelli 1998). This is particularly interesting for the current investigation because PMv, located directly adjacent to Broca's area, is a major locus of potential overlap with language processing.

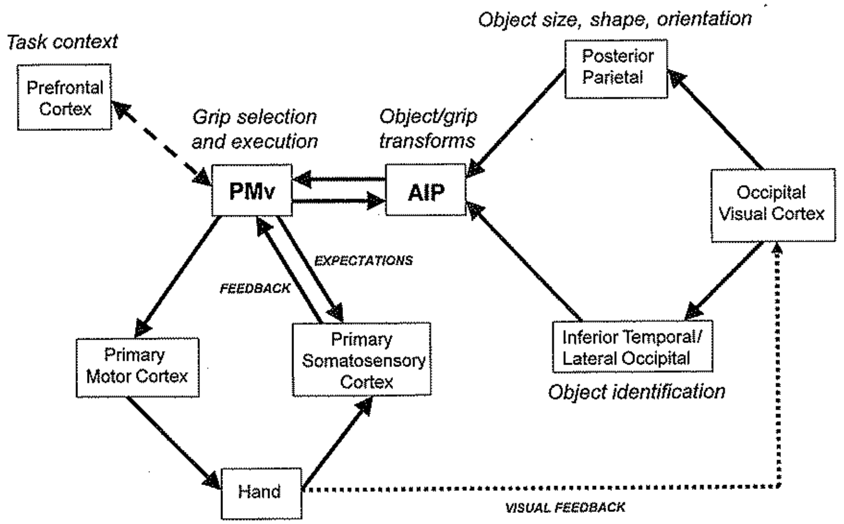
Shared Neural Functions in Language and Tool Making

Effective tool use, including tool making, requires dexterous manual prehension. This in turn requires the transformation of sensory information about object shape into appropriate grasping configurations of the hand (Frey et al. 2005). As in macaques (Rizzolatti, Luppino, and Matelli 1998), the human AIP is a visual-motor association area that plays a critical role in visually guided grasping (Frey et al. 2005) by providing information about object affordances to the PMv. According to the Fagg-Arbib-Rizzolatti-Sakata (FARS) computational model of grasping, in AIP-PMv (Figure 8.2) (Fagg and Arbib 1998) visual information presented to the AIP is used to derive a set of potential grasps; these grasps are passed to the PMv, which selects among them on the basis of additional constraints such as task goals; this decision is communicated back to the AIP, which shunts the non-selected grasp affordances; and the PMv is then responsible for the execution of the selected grasp as a sequence of functionally unified action components (e.g., extension, flexion, hold, release).

This specific model is consistent with a more general computational account of motor control known as HMOSAIC (Hierarchical Modular Selection and Identification for Control) (Haruno, Wolpert, and Kawato 2003). In simple MOSAIC (Wolpert and Kawato 1998), the sensorimotor system achieves consistent performance across variable environmental conditions by generating and



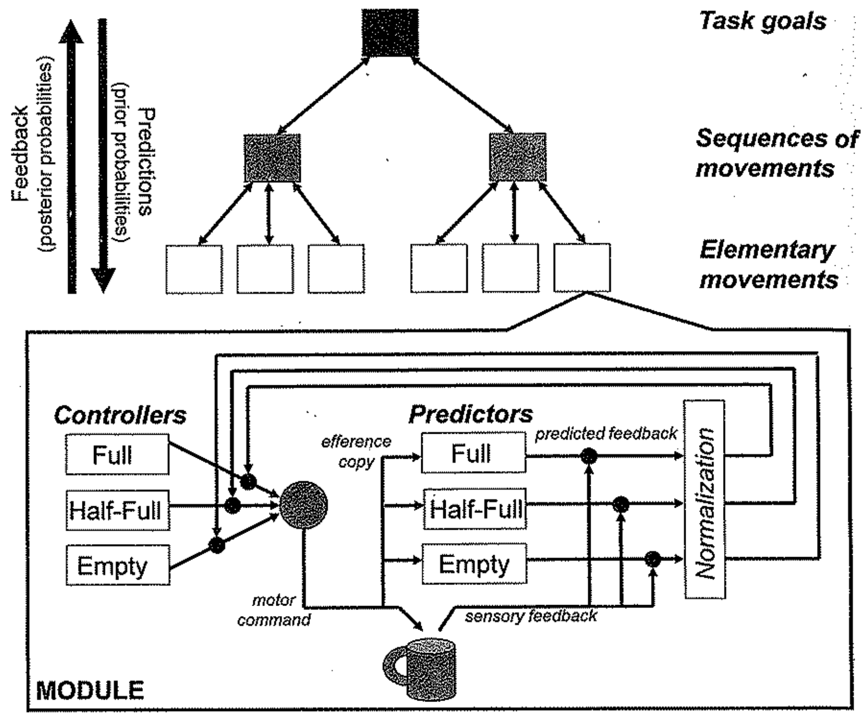
8.1. Brain activation during naïve and practiced Oldowan knapping by novices. Note activation of the AIP-PMv circuit in both conditions and enhanced activation of visual association cortex (LOC) following practice.



8.2. The Fagg-Arbib-Rizzolatti-Sakata (FARS) computational model of grasping in AIP-PMv (drawn after Fagg and Arbib 1998).

selecting among multiple motor plans on the basis of sensory feedback. More specifically, motor plans ("controllers") are used to make sensory predictions that are tested against actual feedback (Figure 8.3, lower part). In this way, rapid adaptation is achieved. However, actual motor behavior also displays higher-level regularities relating to conserved motor sequences and overall task goals. For example, most people can write a recognizable letter *A* with various different pens, with their left or right hands, or even by grasping the pen between their toes (Manoel and Connolly 1995).

HMOSAIC accounts for this consistency across conditions by employing multiple, interacting levels of predictor-controller pairings ("modules") corresponding to increasingly abstract aspects of the behavior (e.g., elementary movements, sequences of movements, goals of sequences). Higher levels generate predictions (Bayesian prior probabilities) used to prioritize module selection at lower levels, which return feedback (posterior probabilities) on outcomes to the higher levels. This hierarchical architecture (Figure 8.3, upper part) combines bottom-up and top-down processing in a way that allows HMOSAIC to learn both elementary movements and their higher-level sequencing through sensorimotor learning (Wolpert, Doya, and Kawato 2003).



8.3. The HMOSAIC (Hierarchical Modular Selection and Identification for Control) model of motor control (drawn after Wolpert et al. 2003). Efferent prediction and sensory feedback are used to select appropriate motor commands in low-level modules controlling elementary movements. These elementary movements are assembled into coherent sequences and adaptive, goal-oriented behavior through a combination of top-down and bottom-up processing. The production of hierarchically organized sequences in this model is formally similar to that required in language processing.

Following two these models, the role of the PMv in grasping may be described as the selection and sequential unification of action components with respect to object affordances provided by AIP and higher-level representations of task context and goals provided by the prefrontal cortex (Fagg and Arbib 1998). This form of hierarchical processing, involving the selection and unification of discrete elements to produce coherent higher-level structures, bears intriguing similarities to recent accounts of language processing based on the recursive combination of lexical elements through selection acting on intrinsic structural features (Jackendoff 2002; Vosse and Kempen 2000).

In these accounts, traditional distinctions between combinatorial rules (grammar) and lexical elements (the lexicon) are largely eliminated (Bates and Goodman 1997) in favor of a single process of unification acting on content-rich lexical items containing information about their own combinatorial possibilities. Similar processes of unification have been hypothesized to operate throughout the tripartite structure (phonology, syntax, and semantics) of human language (Hagoort 2005). As in both FARS and HMOSAIC, competition and selection between elements provide the proposed mechanisms for unification. For example, the use of lateral inhibition between competing unification links to generate a single, successful syntactic tree, as proposed by Vosse and Kempen (2000), may be explicitly compared with the use of inhibitory connections in FARS to ensure the emergence of a single, adaptive grasp.

Neuroanatomical Overlap

But does this computational similarity indicate a true evolutionary homology between object manipulation and linguistic processing or merely an interesting analogy (Wynn 1993)? After all, recursion and selection are powerful general mechanisms that might easily be used by many different cognitive systems. Additional support for a homology would come from evidence that PMv is in fact recruited for both tool making and language functions. This does appear to be the case. At least one recent review (Hagoort 2005) has concluded that anterior PMv plays a role in unification during phonological processing; this is the location, near the posterior border of Brodmann area 44 (classic Broca's area), that is activated during Mode I tool making.

The functionality of any brain region is largely determined by its pattern of connections with other brain regions (Passingham, Stephan, and Kotter 2002). Anterior PMv in particular is a major point of convergence for inputs from parietal sensory association cortices (Rizzolatti, Luppino, and Matelli 1998) and prefrontal area 46 (Takada et al. 2004). In turn, it sends outputs via the more posterior PMv to the manual and orofacial regions of the primary motor cortex (Takada et al. 2004). Consequently, it plays a key role in multiple neural circuits supporting sensorimotor transformations for action across a variety of modalities. Macaque PMv, for example, displays overlapping responsiveness to visual, tactile, and auditory stimuli (Graziano, Reiss, and Gross 1999) and has recently been found to coactivate with the perisylvian auditory cortex (a putative Wernicke's area homologue) in the perception of species-specific calls (Gil-da-Costa et al. 2006). In humans, the PMv is loosely divided into inferior and superior fields, which are responsive to auditory and visual stimuli, respectively (Schubotz and von Cramon 2003). This division, which mirrors the superior/inferior organization of hand and orofacial regions in the primary motor cortex, is also evident during action observation, with the superior PMv field responding to observed hand actions and the inferior portion to observed mouth actions (Buccino et al. 2001).

Although the extent of functional overlap between PMv fields is not well-known from imaging data, behavioral evidence indicates close interaction. One obvious example is the interdependence (Rauscher, Krauss, and Chen 1996) of manual gestures and speech in human communication (McNeill 1992). This relationship is present even in congenitally blind speakers talking to blind listeners (Iverson and Goldin-Meadow 2001). Kinematic studies have further demonstrated that grasping movements with the hand affect concurrent movements of the mouth, with larger manual target objects being associated with wider, faster opening of the mouth and with increased power of the voice spectrum during syllable pronunciation (Gentilucci et al. 2001). Finally, it seems that manual and oral control are even less well-differentiated during development, as exemplified by the Babkin reflex of newborns in which pressure to the palm results in mouth opening (Babkin 1960).

These observations are broadly consistent with the evolutionary-developmental hypothesis of Greenfield (1991), who proposed that discrete manual and linguistic circuits in the posterior inferior frontal lobe emerge through postnatal developmental differentiation of a common neural substrate. Such differentiation is thought to result from the exuberant growth and subsequent pruning of synaptic connections, driven by neuronal competition, intrinsic gene expression gradients, and extrinsic stimuli (Deacon 1997; Edelman 1987). In the case of the PMv, these processes would be expected to result in the differentiation of multiple neuronal populations playing similar roles in different neural circuits. The overt functional characteristics of these partially overlapping populations would then be a function of their particular patterns of connectivity with other (sensory, cognitive, and motor) brain regions.

Greenfield (1991) further argues that linguistic grammar and manual object combination in particular are homologous expressions of the hierarchical information-processing capabilities of Broca's area. The evidence of functional and anatomical overlap discussed above does support such a link between phonological processing and elementary object-oriented actions (e.g., grasping) but does not extend to the more complex multi-object and grammatical combinations ultimately invoked by Greenfield's hypothesis. The units of analysis involved are thus closer to those employed in scenarios linking manual specialization to speech production (Kimura 1979; Lieberman 1991; MacNeilage 1987), although Greenfield's more general argument regarding the developmentally differentiated hierarchical unification functions of inferior frontal cortex is clearly corroborated. In fact, more recent investigations (Stout et al. 2008) have shown more anterior activation of the right hemisphere homolog of Broca's area during Mode II tool making. This activation during more sophisticated tool making is perhaps unsurprising considering that a posterior-to-anterior gradient of phonological, syntactical, and semantic processing clearly exists in the linguistic functions of the inferior frontal cortex (Bookheimer 2002; Hagoort 2005) and that a similar gradient appears to be present for increasingly abstract levels of action observation (Nelissen et al. 2005). In any case, it provides further corroboration for Greenfield's hypothesis.

The Mirror-Neuron System

Another major reason for interest in PMv activation during Oldowan tool making is the role this region plays in the mirror-neuron system for action understanding. Mirror neurons, initially identified in the premotor cortex (area F5) of macaques (Di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996), are a special class of visuomotor neurons that discharge both during the execution of a particular action and during the observation of a similar action being performed by another individual (Rizzolatti and Craighero 2004). These highly specific response characteristics indicate that neural networks involved in the execution of actions are also spontaneously recruited by their observation. This automatic internal simulation of observed actions in the mirror-neuron system is thought to constitute a neural mechanism for recognizing the action goals and intentions of others (Fogassi et al. 2005; Rizzolatti and Craighero 2004) and has led to the hypothesis that mirror neurons provided a preadaptive foundation for understanding intentional communicative gestures (Rizzolatti and Arbib 1998).

Necessary differences in research methods make it impossible to record from individual mirror neurons in human subjects; however, noninvasive imaging has amply demonstrated overlap between action observation and execution in the inferior frontal/precentral gyrus (i.e., Broca's area / PMv) and the anterior part of the inferior parietal lobe (Rizzolatti and Craighero 2004). This corresponds closely with known locations of mirror neurons in macaques (Di Pellegrino et al. 1992; Fogassi et al. 2005) and is strongly suggestive of homology. Interestingly enough, these regions also show some degree of overlap with language processing (Hamzei et al. 2003, and above).

Of course, macaques do not speak, so the really interesting question with respect to language evolution is how the human mirror system might differ from that of monkeys (and other apes, although such comparative evidence is lacking). For example, whereas the responsiveness of monkey mirror neurons is specifically limited to transitive (object-directed) actions, transcranial magnetic stimulation (TMS) and magnetic resonance imaging research indicate that the human mirror-neuron system is also responsive to intransitive finger flexion (Patuzzo, Fiaschi, and Manganotti 2003) and to pantomimed actions toward imaginary objects (Buccino et al. 2001). This apparent broadening of response characteristics is consistent with the hypothesis that derived characteristics of the human mirror neuron might support intentional communication (Rizzolatti and Craighero 2004), although further research is clearly needed. This is also the case with TMS studies suggesting a similar "echo-neuron" system for human speech perception (Fadiga et al. 2002; Watkins, Strafella, and Paus 2003).

PMv activation during Oldowan tool making is located in left anterior Brodmann area 6, bordering area 44, in a region that has been identified as homologous to monkey area F5 (where mirror neurons are found) on the basis of sulcal anatomy (Rizzolatti, Luppino, and Matelli 1998), quantitative architectonics and electrophysiological response characteristics (Petrides, Cadoret, and Mackey 2005). This approximate location has also been identified as a point of overlap among action observation, action execution, and language production in humans (Hamzei et al. 2003). This suggests that elements of the mirror-neuron system may be preferentially recruited by Oldowan knapping as compared to simple percussion. However, this hypothesis has yet to be directly tested by experiments involving knapping action observation.

Potential Evolutionary Implications of Knapping-Related Brain Activation

Functional imaging studies with modern humans cannot directly reveal the mental capacities of prehuman ancestors but can shed light on the relative demands of evolutionarily significant tasks. For example, activation of the AIP-PMv circuit during Mode I knapping indicates that this technology is more demanding of sensorimotor transformations for object manipulation than is bimanual percussion without flake production. This most likely reflects the importance of deploying effective grips for hammer and core that expose the desired impact surfaces at an appropriate angle, provide sufficient support to absorb a powerful impact, and place fingers close to the point of impact in order to absorb shock and provide a kinesthetic guide for percussion (e.g., Stout 2002:698–699).

Although many animals combine objects for percussion (Marchant and McGrew 2005), only hominins seem capable (cf. Schick et al. 1999) of the control necessary for the efficient flake production seen at early Oldowan sites (Delagnes and Roche 2005; de la Torre 2004; Semaw 2000). In this context, comparisons of knapping with simple percussion bring into relief the truly distinctive neurobehavioral characteristics of stone tool making and highlight those brain regions most likely to have been relevant to evolving tool-making capacities. More specifically, functional and anatomical overlap between Oldowan knapping and phonological processing in the anterior PMv suggests that selection on tool-making abilities could also have contributed to an evolving hominin language capacity.

The relationship between size and function of cortical areas is not well-understood; however, one plausible outcome of selection acting on PMv functions involved in tool making would be expansion of this area. In fact, the premotor cortex as a whole does seem to be expanded in humans (Blinkov and Glezer 1968), although not to the same extent as prefrontal and temporo-parietal association cortices (Deacon 1997; Rilling 2006). The KNM-ER 1470 endocast from Koobi Fora, Kenya, provides direct evidence of a more complex and modern-human-like Broca's area (i.e., third convolution of the inferior frontal gyrus) dating back approximately 1.9 million years (Holloway 1999), although PMv itself cannot be resolved.

Many such characteristics of human neocortical organization may simply reflect the effects of extended development (Finlay and Darlington 1995), allometric expansion, and resulting design constraints (Deacon 1997). Nevertheless, comparative studies also document substantial residual variability suggestive of species-specific adaptation (Rilling 2006). Such adaptations, in the PMv or elsewhere, would necessarily be driven by changes in the more proximate mechanisms governing the formation of functional areas within the developing cortical plate.

Researchers are only now beginning to understand this process of cortical arealization, which appears to be regulated in large part by the influence of axonal projections from the thalamus. These axons, originating in the sensory nuclei of the dorsal thalamus, are a major source of sensory input throughout the neocortex and play an important role in inducing anatomical and functional differentiation (O'Leary and Nakagawa 2002). These projections are in turn guided by a combination of extrinsic neural stimulation and intrinsic chemical gradients produced by regional variations in gene expression (O'Leary and Nakagawa 2002). These mechanisms provide a large degree of plasticity. For example, the relatively common evolutionary phenomena of gene duplication might easily alter the expression of intrinsic gradients in such a way as to produce a real expansion or contraction (Deacon 1997). Alternatively, changes in neural stimulation derived from other cortical, subcortical, or somatic sources might alter neuronal survivorship during development, resulting in a net size increase or decrease. This latter process is referred to as displacement by Deacon (1997).

The potential for interaction between these mechanisms also suggests possible knock-on effects of PMv expansion. For example, gene duplication resulting in an expanded premotor cortex would increase the number of potential connections to and from the PMv during development and provide new raw material for displacement. Expanded neuronal populations in PMv might thus be recruited by various different circuits in a relatively plastic fashion. Interestingly enough, it has recently been shown that tool-use training leads to the extension of new functional connections from the visual and prefrontal cortex to the anterior intraparietal sulcus of adult macaques (Hihara et al. 2006). Comparable plasticity in an evolving speech circuit involving auditory, ventral premotor, and orofacial motor cortex would provide a potential mechanism for Baldwinian evolution (Deacon 1997) through genetic assimilation (Waddington 1953). In this way, behavioral changes that increased the fitness benefits of intentional vocal communication could lead to the developmental canalization of previously plastic responses, helping to produce the enhanced articulatory control so central to human language evolution (Deacon 1997; Lieberman 2002; MacNeilage 1995; Studdert-Kennedy and Goldstein 2003). One major candidate for such behavioral change is increasing reliance on the social learning of complex skills, including stone tool making (Stout 2005).

SHARED SOCIAL CONTEXT

Technical skill acquisition (Stout 2002, 2005) and collaborative performance (Reynolds 1993) are far from being the only behavioral contexts that might have favored intentional vocal communication in hominin evolution and may not even be the most important (Dunbar 1996). However, technological performance is the only context for which a substantial body of direct paleo-behavioral evidence currently exists. Happily, such performance does have the potential to be a rich source of information about social and communicative capabilities.

It has been argued that vocal communication is relatively unimportant relative to physical demonstration in the transmission of tool-making skills (e.g., Dunbar 2003); however, this is a narrow view that neglects the importance of intentional vocalization in directing attention during joint action (including pedagogy) and of language generally in establishing the social context for technological reproduction. In fact, a strict division between the technological and the social appears untenable in both human (e.g., Dobres 2000) and nonhuman (van Schaik et al. 2003) primates. Dunbar (2003) has proposed that the selection on the social cohesive functions of language preceded any eventual technological benefits; however, this becomes a bit of a chicken-and-egg problem when it is recognized that facilitation of the social reproduction of technical skills was likely to have been an important factor favoring the formation of larger and more cohesive groups in the first place (van Schaik and Pradhan 2003).

Stone knapping in particular is distinguished from other manual activities by its requirements for combined force and accuracy of percussion. Experimental and ethnographic studies (Bril, Roux, and Dietrich 2000; Roux, Bril, and Dietrich 1995; Roux and David 2005; Stout 2002) have shown that mastery of elementary flake removal is a necessary precondition for the emergence of structured and effective knapping strategies and that sufficient perceptual-motor skill is only achieved through dedicated practice over a prolonged period—often years. Knapping experiments (Stout and Chaminade 2007) corroborate these observations and show that, even in Mode I tool making, novice performance is highly constrained by the difficulty of combining force and accuracy in percussion. Four hours of practice were sufficient for subjects to advance from uncontrolled fracture to the preferential exploitation of favorable knapping surfaces, realized through small, marginal flake removals from acute platforms. This strategy minimized demands for force and accuracy in percussion but led to edge rounding, low productivity, and premature core exhaustion.

Interestingly enough, this strategic shift was accompanied by increased activation of visual association areas (the lateral occipital complex [LOC] and intraparietal transverse occipital [IPTO]) involved in object recognition and visual search, most likely relating to increased attention to technologically relevant aspects of core morphology but not with any modulation of prefrontal activity, which might suggest increased demands for motor planning and problem solving (e.g., Dagher et al. 1999). This is contrary to the pattern seen in the acquisition of less demanding motor skills, such as figure tracing and sequential button pressing, in which initial learning of task strategy / organization is "scaffolded" by activation in prefrontal and posterior parietal association cortices before shifting to more automatic execution in primary sensorimotor cortices (Kelly and Garavan 2005). These observations further emphasize the unusual perceptual and motor demands of stone knapping and illustrate the bottom-up emergence, rather than top-down imposition, of strategic regularities during skill acquisition (see also Roux and David 2005). More recent core-shaping, prepared-core, and blade technologies are clearly even more demanding of acquired perceptual-motor skill, although detailed experiments are required to quantify these differences.

Trends toward increasing skill and refinement evident in the archaeological record of the past 2.5 million years thus provide evidence of increasing investments in perceptual-motor skill acquisition. In modern humans, such investments

8.4. A traditional stone tool-making apprenticeship situation in Langda, New Guinea. Vocal and gestural instruction combine to provide "coaching" that dramatically reduces the trial and error involved in skill acquisition.

are supported by social and cultural structures that both support and motivate deliberate practice. For example, among modern stone adze makers in the New Guinea village of Langda, learners participate in a semiformal system of apprenticeship that provides opportunities for instruction, observation, and assisted action (i.e., social "scaffolding"), as well as motivation related to economics, prestige, and identity (Stout 2002, 2005). Linguistic communication plays a key role in this system of apprenticeship by facilitating joint action and the cultural construction of identity.

During interactions between novice and expert knappers, gesture (usually pointing) and vocalization are frequently combined to convey meaning and shape behavior (Figure 8.4). Common utterances include phrases like "do it here," "don't do that," "look here," or "wait, you have to do this [e.g., hit this side] first," which serve to direct attention to important aspects of action that might otherwise be quite difficult for novices to discern. This enables a form of coaching that can dramatically reduce the trial and error involved in skill acquisition. Although such linguistic utterances may not be strictly essential to the cultural reproduction of knapping skills, it is nevertheless clear that they greatly facilitate communication and learning by modifying or adding to the meaning of accompanying gestures. Language also plays a more fundamental role in establishing the cultural context that supports skill learning in Langda. This includes linguistically constructed kinship ties that cement relations between teachers and learners; myths, stories, and specialist terminology that create craft identity and a sense of belonging; and even the small talk, gossip, and joking that makes knapping an enjoyable social activity. In other words, language provides a social glue (Dunbar 1996) holding together the structures that support the reproduction of complex knapping skills. For these reasons, increased reliance on complex, socially facilitated skill learning over the course of hominin evolution would be likely to increase fitness benefits associated with intentional vocalization and (proto)linguistic communication.

Socially facilitated technical skill learning might also plausibly contribute to the preadaptive context of language evolution, insofar as learning in both domains is supported by capacities for joint attention. The kind of coaching and interactive skill learning described above clearly rely on shared attention to particular task features and a causal/intentional understanding of both technical and communicative actions. This is consistent with a substantial body of work detailing the importance of joint attention, scaffolding, and "cognitive apprenticeship" in human learning generally (e.g., Lave and Wenger 1991; Rogoff 1990; Wood, Bruner, and Ross 1976). This same ability to focus on objects and events being attended to or indicated by adults is critical to language learning, and joint attention skills have in fact been shown to correlate with individual variation in the development of both language and gesture (Bates and Dick 2002; Carpenter et al. 1998). At this basic level, linguistic and technological behaviors do appear reliant on similar cognitive mechanisms supporting social reproduction. Currently available evidence certainly does not put us in a position to associate a particular prehistoric technology with a specific level of linguistic or proto-linguistic communication and such a level of interpretation may never be possible. Nevertheless, there are important links between technology and communication in human evolution that may be expected to reward further investigation.

GENERAL CAPACITIES

One point that emerges from the earlier comparison of the neural substrates of language and tool making is that both rely on hierarchical unification functions of the inferior frontal cortex. The observed overlap in Mode I knapping is specific to manual coordination and articulatory/phonological processing; however, putative involvement of more anterior regions in more complex tool making would involve increasingly abstracted, domain-general unification processes.

This latter possibility is quite similar to the idea advanced by Gibson (1993) that distinctive human abilities across a wide range of behaviors reflect quantitatively enhanced information-processing capacities, particularly the ability to hold multiple items of information in mind simultaneously and to assemble these items into hierarchical mental constructs (Gibson 1999).

Such domain-general processing, not tied to specific sensory or motor modalities, is generally considered to be the province of association areas in the prefrontal, posterior parietal, and temporal cortex. These association areas are, in fact, among the most expanded regions of the human neocortex (Rilling 2006) for reasons that may include developmental timing, patterns of connectivity, neural design constraints, and/or specific behavioral adaptations. Involvement of these regions in complex stone tool making would not necessarily indicate a special relationship between language and technology in human evolution but would be consistent with the proposal of a more generalized human "cognitive niche" involving closely interdependent social, technological, and linguistic components (Gibson 1993). More specifically, it would provide support for the argument that archaeological traces of complex tool making can provide circumstantial evidence of comparable advances in social and linguistic behavior (Gibson 1993).

Both working memory (the ability to hold multiple items in mind) and hierarchical unification are typically associated with the prefrontal association cortex. As we have already seen, the anterior inferior frontal gyrus appears to be centrally involved in high-order unification operations across modalities (Hagoort 2005). Working memory is classically associated with more dorsal regions of the prefrontal cortex, and its behavioral expression is now thought to involve a combination of online storage in Brodmann area 8 and response selection in area 46 (Rowe et al. 2000). Along these lines, Dagher and colleagues (1999) found that dorsolateral prefrontal activation, including area 46, increased in proportion to the complexity (i.e., number of moves required) of the classic Tower of London motor-planning task.

No such prefrontal activation was observed during novice Mode I tool making, either before or after practice. This may reflect the relative simplicity of Mode I flaking or simply the fact that novice subjects never mastered elementary flake removal and were thus unable to pursue the kind of systematic and intensive reduction seen at early archaeological sites (see, e.g., Delagnes and Roche 2005; Semaw 2000). Expert Mode II tool making did result in inferior prefrontal activation (Stout et al. 2008), consistent with the greater hierarchical complexity of the action sequences involved, but again did not recruit more dorsal regions classically associated with working-memory storage.

CONCLUSIONS

A steadily growing body of evidence indicates the likelihood of important interrelationships between language and technology in human evolution on levels ranging from specific neural overlap to the broader cultural context of learning and practice. Closer study of specific, archaeologically visible technological behaviors, such as stone knapping, offers the opportunity to further specify these possible relations, to test their applicability in particular cases, and to relate these findings to the chronological and contextual information (Wynn 2002) provided by the archaeological record of human behavioral evolution.

In the particular case of novice Mode I knapping, functional imaging data indicate an overlap with phonological/articulatory processing in the left anterior PMv. This is consistent with various motor hypotheses of speech evolution (Kimura 1979; Lieberman 1991; MacNeilage 1987; Studdert-Kennedy and Goldstein 2003), as well as Greenfield's (1991) evolutionary-developmental scenario of language origins rooted in the manual combinatorial functions of the inferior frontal cortex. Together with recent evidence of functional/connectional reorganization in macaque monkeys following tool-use training (Hihara et al. 2006), these findings suggest that neural adaptations relating to tool-making skill could have provided a preadaptive foundation for the later evolution of cortical speech circuits through a process of developmental canalization (Waddington 1953).

This logic applies to both the production and comprehension of speech, capacities that appear to rely on an overlapping system of "echo-neurons" (Fadiga et al. 2002; Watkins, Strafella, and Paus 2003) comparable to the mirror-neuron system involved in visuomotor action understanding. Expansion of the response characteristics of this mirror-neuron system to include intransitive and pantomimed actions differentiates humans from macaques and may represent an important innovation in the evolution of intentional communication (Rizzolatti and Craighero 2004). Such attempts to explain the evolution of speech from mimetic precursors in the mirror-neuron system typically invoke an intervening phase of communication through referential brachiomanual gestures (Rizzolatti and Arbib 1998). However, a discrete gestural communication stage involving some form of proto–sign language may not be strictly necessary, insofar as intentional "coaching" during the acquisition of technological skills already provides a context for the association of vocalizations with referential manual gestures and pantomimes (cf. Rizzolatti and Arbib 1998). Ethnographic evidence (Stout 2002, 2005) in particular highlights the role of joint attention and intentional communication in the social reproduction of stone-knapping skills.

These capacities also play a critical role in modern human language acquisition (Bates and Dick 2002; Carpenter et al. 1998), and their elaboration during hominin evolution is likely to have been important in the emergence of novel social, technological, and linguistic behaviors. Although high-level human performance in these domains probably reflects the enhanced information-processing capacities of expanded neocortical association areas (Gibson 1993), initial adaptations may have been more affective than cognitive. In canids, for example, selection for docility and reduced emotional reactivity (i.e., domestication) is associated with enhanced social skills, including gaze following and response to referential gestures (pointing) (Hare and Tomasello 2005). Enhanced social tolerance further creates opportunities for collaborative action (see, e.g., Hare et al. 2007) and the social reproduction of skills (van Schaik and Pradhan 2003), potentially increasing the fitness benefits associated with intentional communication. In this way, distinctive human social, technological, and linguistic capacities may have their root in a form of "self-domestication" involving selection for reduced emotional reactivity to conspecifics (Hare et al. 2007). This seems particularly applicable to stone knapping, insofar as both ethnographic and experimental evidence indicate the need for relatively prolonged periods of deliberate practice in a supportive social context in order to develop the requisite perceptual-motor skills.

Functional brain imaging results from novice Mode I knappers (Stout and Chaminade 2007) shed additional light on the importance of deliberate practice and perceptual-motor learning in stone-knapping skill acquisition. Contrary to expectations from studies of skill acquisition in less challenging motor tasks, Mode I novices showed a pattern of increased activation in high-order visual association cortices following practice but no significant modulation of prefrontal activity. These findings, in conjunction with lithic evidence of a shift to controlled but noninvasive flaking following the practice period, suggest that the early stages of stone-knapping skill acquisition are devoted to exploring the perceptual-motor affordances of the task and to developing effective motor synergies for elementary flake detachment (Bril, Roux, and Dietrich 2000, Roux, Bril, and Dietrich 1995). It is only following the stabilization of these fundamental skills that it becomes possible to organize methodical and intensive core reduction of the kind seen at early Oldowan sites (Delagnes and Roche 2005; Semaw 2000) or the sequentially contingent knapping plans evident in later bifacial and prepared-core technologies. In such technologies, more anterior regions of the inferior frontal gyrus (Brodmann area 45) are in fact activated. This region of prefrontal cortex is known to be involved in syntactic and semantic levels of language processing, suggesting further possible links between language and technology in human evolution.

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NINE

Stone Tools and the Evolution of Hominin and Human Cognition

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ABSTRACT

In this chapter, I summarize some previously published work on the significance of the earliest stone tools in comparison with chimpanzee tool making and use. I then put that into the context of some theorizing about human cognition and its implications for understanding the evolution of hominin and human cognition. I then conclude with an extended discussion of the standard story of changes in stone-artifact making and use in the context of other recent theorizing about the evolution of language. I conclude that stone tools can be interpreted to give strong evidence about the evolution of cognition, but the outcomes depend on careful assessment of the theoretical basis for the argument.

RELATING COGNITIVE ABILITIES TO THE PRODUCTION OF STONE TOOLS

My present approach to stone tools and cognition was developed in 2003 during a research project titled Precursors to Culture at the Collegium Budapest led by Richard Byrne. Byrne has recorded the sequence of actions routinely engaged