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NUMBER 1

THE OLDOWAN:
Case Studies Into the Earliest Stone Age

Edited by Nicholas Toth and Kathy Schick

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CHAPTER 9

OLDOWAN TOOLMAKING AND HOMININ BRAIN EVOLUTION:

THEORY AND RESEARCH USING POSITRON EMISSION TOMOGRAPHY (PET)

BY DIETRICH STOUT

ABSTRACT

Attempts to understand the paleopsychological and neuro-evolutionary significance of early stone tools have long suffered from a scarcity of hard evidence regarding the actual neural substrates of stone toolmaking skill. The Positron Emission Tomography (PET) pilot study of Stout *et al.* (2000), together with preliminary results from ongoing follow-up research, are beginning to readdress this problem by providing a new avenue of experimental inquiry for human origins researchers. In these studies, PET was used to identify the regions of the brain that display increased activity during simple Oldowan-style (Mode I) flake production. Although results are preliminary pending further analysis, robust evidence of activation in the primary sensorimotor cortices surrounding the central sulcus, in the visual cortices of the occipital lobe, and in the cerebellum has already been observed. These activations reveal the relatively intense visuomotor demands of stone knapping and highlight those regions of the brain that would have been the most likely targets of selection on knapping skill. Somewhat less definitive evidence of superior parietal activation further suggests that higher-level visual association and spatial cognition may also be involved. Available evidence does not indicate the recruitment of prefrontal planning and problem solving regions, nor show any clear overlap between toolmaking and language processing networks. Results from the PET research, although preliminary, are already relevant to numerous hypotheses concerning the cognitive and evolutionary implications of early stone tools.

INTRODUCTION

What role might early stone tools have played in the evolution of the human mind? This is an old question, but one of enduring interest. In the past, researchers have generally approached the issue by attempting to define the cognitive demands of stone tool manufacture. This has been done in the relatively casual or “common-sense” language of archaeologists (e.g. Belfer-Cohen & Goren-Inbar, 1994; Chase, 1991; Gowlett, 1984; Isaac, 1986; Karlin & Julien, 1994; Tobias, 1979) as well as through more explicit reference to psychological theory (Mithen, 1996; Parker & Gibson, 1979; Robson Brown, 1993; Wynn, 1989). Some workers have even attempted to identify the neuroanatomical foundations for tool-behavior, usually in order to demonstrate some direct co-evolutionary connection with language abilities (Calvin, 1993; Greenfield, 1991; Wilkins & Wakefield, 1995).

Despite the quality and quantity of consideration devoted to the issue, the link between tools and cognition in human evolution remains tentative and controversial. Part of the reason is a lack of direct evidence regarding the relationship between tool-behavior and brain function. What is needed is concrete evidence regarding the actual neurophysiological underpinnings of stone toolmaking skill. The technology of Positron Emission Tomography (PET), initially suggested as a tool for the study of stone tools and cognition by Toth & Schick (1993), and applied for the first time in research (Stout *et al.*, 2000) discussed below, provides the opportunity to collect just this kind of evidence.

HOMININ “PALEOPSYCHOLOGY”

Information about the workings of the brain and mind can come from two main sources: the study of neuroanatomy/neurophysiology and the observation of behavior. This is as true in human evolutionary studies as it is in neuroscience and psychology, although the available data and degree of experimental control in the former are obviously much more limited. Direct but greatly limited evidence of protohuman neuroanatomy is provided by endocasts of hominin cranial fossils (Falk, 1980; Holloway, 1995; Tobias, 1991) while more detailed but indirect evidence comes from comparative studies of modern primate brains (Gannon *et al.*, 1998; Preuss *et al.*, 1999; Semendeferi & Damasio, 2000). Observation of modern non-human primate behavior also provides an important comparative perspective (McGrew, 1992; Savage-Rumbaugh & Lewin, 1994; Rumbaugh *et al.*, 1996; Tomasello & Call, 1997). With respect to the “observation” of pre-modern behavior, it is the reconstructive work of Paleolithic archaeologists that provides the best source of data. The use of these behavioral data to explore pre-modern mental characteristics and capacities might, for lack of a better term, be called *hominin paleopsychology*. Stone artifacts are one major source of information in this challenging undertaking.

Holloway (1981a) refers to prehistoric stone tools as “fossilized behavior”. Although far from ideal, durable stone artifacts do represent one of our best indicators of prehistoric behavior and cognition. This is due in part to practical issues of preservation and recovery, but also to the nature of chipped stone technology itself. At a theoretical level, tool-behavior rivals language as a hallmark of human cognition (Preston 1998). In fact, Schlanger (1994: 143) argues that “even if… we could actually observe a Palaeolithic band *in vivo*, it would be highly informative and rewarding to study their ubiquitous material actions and products”. Added to such theoretical considerations is what Pigeot (1990) refers to as “the privileged nature of lithic technology” - the fact that each percussive act produces a distinct physical trace. Although great care is needed to avoid over-interpretation of archaeological sites or individual artifacts, stone tools do present a unique and valuable opportunity to investigate prehistoric cognition.

The Paleopsychology of Stone Tools

Archaeologists interested in early cognition commonly hold the view, expressed by Gowlett (1992: 341), that “striking a flake from a cobble - is relatively simple. To strike a sequence of flakes, in such a way that each one helps in the removal of others, demands more ability…as in control by the brain.” This is consistent with a traditional emphasis on internal mental representation and explicit cognition as the defining characteristics of advanced, distinctly human intelligence. Correspondingly less emphasis is placed on “lower-level” processes such as perception and action.

Among human origins researchers, discussion tends to center on such concepts as the “imposition of arbitrary form” (Holloway, 1969) and the use of mental (Clark, 1996) or procedural (Gowlett, 1984) “templates” in tool production. These criteria are used to informally compare and evaluate the cognitive complexity of industrial complexes, as in the “opportunistic” Oldowan (Isaac, 1981) or the “more complicated and patterned” Acheulean (Schick & Toth, 1993). Although both informative and useful, the use of such “intuitive criteria” (Robson Brown, 1993) to evaluate lithic technologies obviously leaves many more specific questions unanswered. In order to achieve a more complete appreciation of the cognitive implications of stone tools, researchers have tended to borrow from one or another branch of psychological theory. Developmental psychology has generally been the most popular, including the constructivist developmental stages of Piaget and Inhelder (e.g. 1969) and elaborations of the nativist modularity first proposed by Fodor (1983).

Piaget

An early and influential application of Piagetian psychology to Paleolithic archaeology is that of Parker and Gibson (1979). These authors argue, not only that Piaget’s developmental stages may be used to evaluate the cognitive sophistication of early toolmakers, but that “certain projective and Euclidean preconcepts…arose as adaptations for stone-tool manufacture” (p. 375). This conclusion is presented as part of a broader, recapitulationist, model of cognitive evolution that sees sensorimotor, symbolic, intuitive and linguistic capacities as primary and secondary adaptations to intelligent tool use. The scope of the model is not such that much attention is paid to specific tool types or industries; rather the attempt is made to understand the overall pattern of human cognitive evolution.

This general model has been reworked and elaborated over the years (e.g. Gibson, 1983; Parker & Milbrath, 1993), with greater emphasis being placed on social interaction, learning, and planning. Most recently it has been presented as a three stage explanation of cognitive evolution in ancestral hominoids, *Homo erectus*, and *Homo sapiens*, through selection on extractive foraging “apprenticeship,” joint attention and declarative planning respectively (Parker & Mckinney, 1999).

In contrast to the sweeping theoretical work of Gibson, Parker and colleagues, Wynn (1989) applies Piagetian theory to a more detailed analysis of specific lithic evidence. In so doing, he expresses the view that “Selection for intelligence does not appear to have been closely tied with stone tools” (p. 98) and cautions that such tools can provide evidence only of minimum capacities. Nevertheless, he finds Piagetian theory useful in evaluating hominin intelligence, concluding that Oldowan technology displays evidence of preoperational intelligence like that of modern apes, whereas late

Acheulean hominins (c. 300,000 b.p.) had achieved fully modern operational intelligence. Early Acheulean intelligence is characterized as transitional between these.

Modularity

Of course, Piaget's developmental theory has itself been controversial. Fodor (1983) proposed that the mind is not entirely "constructed" during development, but also contains innate, domain-specific, input "modules". Although Fodor's modules were envisioned simply as input/output processors, with cognition as a kind of "black box," analogous concepts have been more generally applied by other researchers. Gardner (1983), for example, enumerated seven distinct "intelligences" in the human mind, while evolutionary psychologists (e.g. Cosmides & Tooby, 1994) see a multitude of specific cognitive adaptations. Chomsky (1972) and Pinker (1994) have taken a similarly "modular" view of language. Unlike the "domain-general" intelligence of the constructivists, it is a prediction of strict modularity that different modules should have discrete neural foundations.

Robson Brown (1993) applied this strict concept of modularity to the analysis of stone tools in much the same way as Wynn (1989) utilized Piagetian theory. Working with two Mode I assemblages from Zhoukoudian, Robson Brown inferred and evaluated aspects of a "spatial intelligence", including mental rotation, element recognition, discrimination of oblique lines, and visual attention. From her analysis, she concluded that the Zhoukoudian toolmakers "displayed a cluster of cognitive operations for which no current analogue exists" (p. 243).

Mithen (1996), on the other hand, adopted the modified modularity of Karmiloff-Smith (1992) in his recent overview of human cognitive evolution. Karmiloff-Smith integrated the ideas of Piaget and Fodor by proposing that modules are constructed developmentally and ultimately integrated through a process of "representative-redescription". Mithen argues that human evolution recapitulated these stages, progressing from domain-general cognition to the possession of cognitively isolated "intelligences" and ultimately to "cognitive fluidity" between these intelligences.

With respect to technology specifically, Mithen contends that "technical intelligence" first began to develop with the Oldowan, but was limited to "a few micro-domains". This technical intelligence blossomed in the Acheulean and Middle Paleolithic, producing impressive stone-craftsmanship, but it was still limited by isolation from other domains. In particular, isolation from "natural history intelligence" prevented flexible utilization of alternative raw materials and the manufacture of special purpose or multi-component tools. Only with modern humans was full cognitive fluidity achieved, as reflected in diverse and specialized toolkits.

Ecological Psychology

In 1979, J.J. Gibson published his classic book, *The Ecological Approach to Visual Perception*, in which he argued that perception arises directly from experience of the environment rather than indirectly via the construction of an internal mental representation. This ecological paradigm blurs or eliminates traditional boundaries between perception, action, subject and object, by defining visual perception as a dynamic activity of the unitary "organism-plus-environment" system. In this view perception is to be understood, not in terms of the information processing and representative capacities of the organism, but rather in terms of the possible relationships or "affordances" encompassed by the organism/environment system.

Together with the dynamic biomechanics of Bernstein (1967), Gibson's ecological perception theory forms the foundation of what is now known as *ecological psychology*, a theoretical approach defined by its focus on systems and dynamics rather than on organisms and structures. Although application of this perspective to the generally static and isolated evidence available to archaeologists and paleontologists can be difficult, ecological psychology has figured prominently in a number of theoretical and empirical contributions to the archaeology of human origins.

One example is the work of Roux *et al.* (1995) with modern stone-bead knappers in Khambhat, India. This "experimental field" research employed an ecological approach in order to explore the foundations of knapping skill, highlighting the importance of coordination and accuracy in the elementary percussive movement. As argued by the authors (p. 83): "This analysis suggests that the action plan depends to a large extent on the control of elementary movement. The less the control, the more difficult to organize an adequate succession of action." This view represents an interesting departure from more traditional approaches to stone tools and cognition, which tend to emphasize mental representation and planning rather than skill and execution.

Other influences of ecological psychology on human evolutionary studies have been more broadly theoretical in nature, having to do with the nature of mind and its relationship to tools, intelligence and language. Noble and Davidson (1996), for example, outline what they call the "social construct" story of the mind. In Noble and Davidson's own words (p. 105) "The 'social construct' story is that 'mental life' is an ongoing interpersonal activity. Far from 'mind' as a personal possession, it is better characterized as *socially* distributed" (emphasis original). Although these authors (p. 96-105) explicitly ground their concept of socially constructed cognition in the philosophical work of Wittgenstein, Ryle and Coulter, it nevertheless has much in common with the concept of "distributed" or "situated" cognition that has developed in cognitive and developmental psychology out of the work of Vygotsky (1976) and others (e.g. Hutchins, 1995; Lave & Wegner, 1988; Rogoff, 1984; Poon *et al.*, 1993).

The distributed cognition paradigm seeks to "move the boundary of the unit of cognitive analysis out beyond the skin of the individual" (Hutchins, 1995:287) in order to encompass the informational content and dynamics of the entire organism-plus-environment system. This includes other individuals, social contexts and artifacts. Although the philosophical stance adopted by Noble and Davidson (1996) leads them to equate "mindedness" exclusively with language (symbol use), and largely to dismiss Paleolithic stone tools as evidence of pre-modern cognition, tools figure prominently in more inclusive considerations of distributed and socially constructed cognition.

Tools may be viewed, not only as physical and perceptual extensions of the body (J.J. Gibson, 1979), but also as cognitive extensions of the mind. Hutchins (1995), for example, discusses the role of tools such as checklists and instrumentation in the distributed cognition that takes place on the bridge of a merchant-marine vessel during navigation. More mundane examples are supplied by Gatewood (1985), who describes the "spatial mnemonic" afforded fishermen by the physical organization of a salmon fishing boat, and by Graves (1994), who illustrates his theoretical discussion of tools and language with the observation that much of the information needed to acquire bike-riding skill is inherent in the design of the bicycle itself.

It is this more inclusive vision of distributed and socially constructed cognition that underlies Tomasello's (1999) theory of human cognitive origins. In contrast to Nobel & Davidson (1996), Tomasello stresses the importance of material as well as symbolic culture in establishing what he calls a "ratchet effect" in cognitive origins. Tomasello (p. 7) argues that a single "uniquely human social-cognitive adaptation" for understanding others as intentional agents forms the biological foundation for cumulative cultural evolution. It is the historical progress of this cultural evolution, rather than additional neurobiological evolution, which has produced the myriad other cognitive capacities commonly considered hallmarks of humanity. As Tomasello (p. 202) argues, "Developing children are…growing up in the midst of the very best tools and symbols their forbearers have invented…as children internalize these tools and symbols…they create in the process some powerful new forms of cognitive representation". Succeeding generations thus construct the cognitive niche in which their children develop, a niche that is saturated with distributed information and structure.

Tools and Language

In stark contrast to the ecological "social construct" views adopted by Noble & Davidson (1996) and Tomasello (1999) is the work of researchers using modular or neo-Piagetian theory to propose direct neurological and evolutionary links between tools and language (e.g. Greenfield, 1991; Calvin, 1993; Wilkins and Wakefield, 1995). As is evident from the work of Chomsky (1972), Pinker (1994) and others, the human language capacity is the single strongest candidate for characterization as an innate, biologically specified and content-rich mental module of the kind stipulated by evolutionary psychologists (e.g. Cosmides & Tooby, 1994). In addition to the universal "deep structure" of language hypothesized by Chomsky and the surprising ease with which children acquire language, the apparent localization of language function in the brain is considered to be a major piece of evidence in support of such a language module. According to the classic view, linguistic processing is localized in two areas: Broca's "motor speech" area and Wernicke's "grammatical comprehension" area. This view has engendered a number of hypotheses proposing that tool behavior spurred language evolution by contributing to the elaboration of these classic cortical language areas.

Greenfield (1991), for example, contends that a cortical region roughly equivalent to Broca's area underlies the hierarchical organization of both speech and object manipulation prior to modularization of these two capacities later in development. This leads her to "posit an evolutionary reconstruction in which tool use and manual protolanguage evolved together" (p. 547). Wilkins and Wakefield (1995) present the closely allied argument that the evolutionary emergence of Broca's area and the parieto-occipito-temporal junction corresponding to Wernicke's area occurred in order to support "motor programs dedicated to manual manipulation and throwing behavior" (p.172). Calvin (1993) on the other hand sees specialized "neural sequencing" regions in left prefrontal and premotor cortex as the common neural foundation for a range of behaviors including toolmaking, language, planning and aimed throwing.

In contrast to these modular (or neo-Piagetian in the case of Greenfield) hypotheses of language evolution is the Baldwinian argument of Deacon (1997). Citing the evolutionary theories of Mark Baldwin, Deacon proposes that the evolution of the human language capacity has actually been a process of co-evolution between language itself and the brains of those who use it. This co-evolutionary relationship arises because "learning and behavioral flexibility can play a role in amplifying and biasing natural selection because these abilities enable individuals to modify the context of natural selection that affects their future kin" (Deacon, 1997: 322). Although concerned with biological evolution rather than cultural-historical development, Deacon's "Baldwinian evolution" is very similar to the niche-constructing "ratchet effect" described by Tomasello (1999). In fact, Deacon's portrayal of language and brain evolution is complementary to that of Tomasello in many ways.

Deacon argues that the key adaptation supporting language is a generalized symbolic capacity supported by prefrontal cortex. In this view, language universals and the rapidity of language acquisition in children are thought to have more to do with the adaptation of languages to suit young minds rather than vice versa. Broca's and Wernicke's areas, instead of being anatomically distinct language centers, are simply motor and auditory association areas that present bottlenecks in information flow during language processing. These areas may have experienced evolutionary changes relating to language use and other behaviors, but they do not represent a separately evolved "language organ" in the brain. Just as Tomasello (1999) credits a generalized capacity for intersubjectivity for many of the more specific cognitive achievements of modern humans, Deacon sees an increased mnemonic and attentional capacity for learning as the fundamental adaptation supporting the specific and varied structures of human languages. This leads Deacon to view the potential evolutionary relationships between tools and language as being relatively indirect, and certainly not as involving the kind of exaptation or correlated evolution envisioned in modular and neo-Piagetian models.

Comment: Stone Tools and the Brain

Even in this brief review of literature dealing with stone tools and cognition, the diversity of everything from basic theoretical orientations to particular interpretations of empirical evidence is striking. Particular tool types might be impressive examples of planning (e.g. Gowlett, 1984) or accidental by-products (Noble & Davidson, 1996). Technical ability might be based on a terminal extension in the evolutionary recapitulation of cognitive development (Parker & McKinney, 1999), or a separately evolved mental module (Mithen, 1996) with discrete neural foundations (Robson Brown, 1993). Tools and language may be dissimilar in many ways (Chase, 1991; Wynn 1995, but might also be alternate expressions of fundamentally similar neural processes (Calvin 1993; Greenfield 1991). In the big picture, stone technology might be a mode of cultural-historic cognitive elaboration (Tomasello, 1999), a primary cause of biologically based cognitive evolution (Parker & Gibson, 1979), merely an indicator of such evolution (Wynn, 1989) or even basically irrelevant to the whole issue (Noble & Davidson, 1996).

Obviously no single research initiative will be able to resolve all of these wide ranging and deep-rooted controversies. It might, however, be argued that part of the reason for this pervasive disagreement is a lack of hard evidence regarding the relationship between tool-behavior and brain function. Exactly what demands does the manufacture of stone tools actually place on the central nervous system? Are these demands really similar to those of language processing? Is there evidence for substantial recruitment of structures associated with spatial cognition and motor imagery, as might be expected by Wynn (1989) and Robson Brown (1993)? What about planning and executive centers underlying the putative "mental templates" of Gowlett (1984) and Clark (1996), or the "neural sequencers" of Calvin (1993)? Is tool manufacture supported by an anatomically discrete module as suggested by the work of Robson Brown (1993) and Greenfield (1991) or by generalized "information processing" in neocortical association areas (Gibson, 1993)? Empirically supported answers to these questions might go a long way toward resolving some of the more long-standing and contentious issues in the study of human cognitive evolution. Used appropriately, PET offers a valuable new opportunity to pursue such answers.

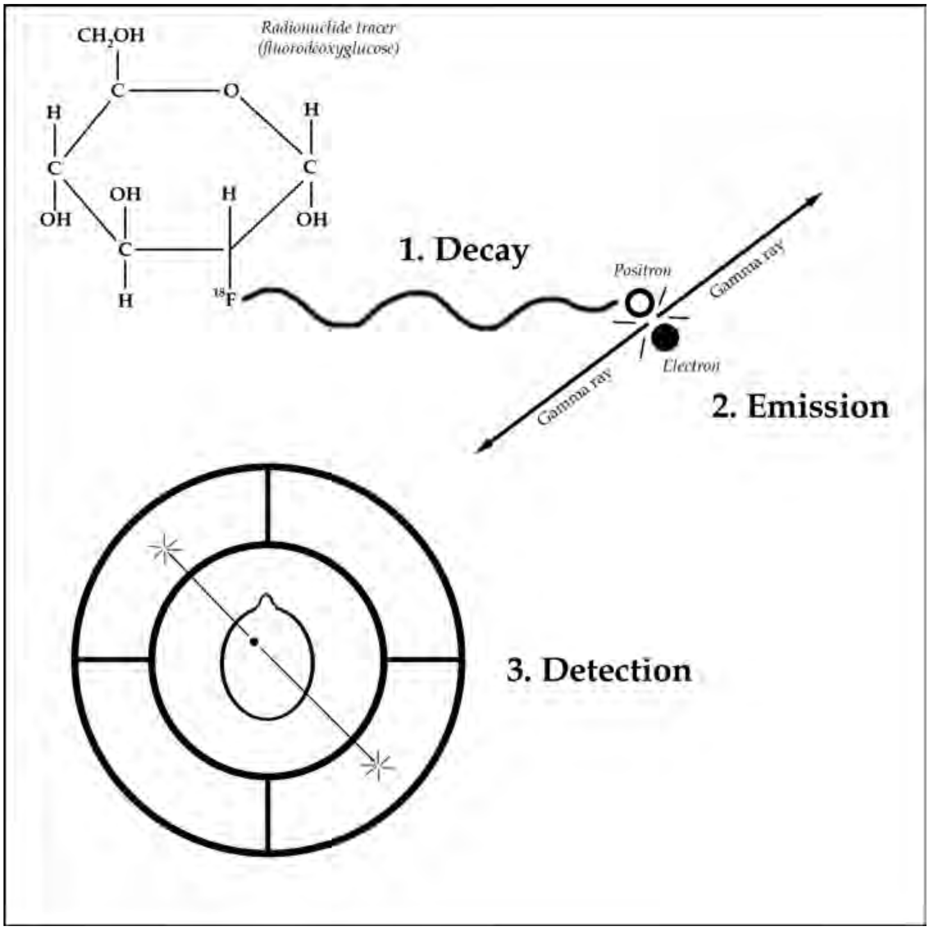
THE ROLE OF POSITRON EMMISION TOMOGRAPHY IN HUMAN EVOLUTIONARY STUDIES

Positron Emission Tomography (PET) is a radiological technique that may be used to produce images of physiological activity in the brains of living subjects (Posner & Raichle, 1994). Pioneered in the mid-70's (Ter-Pogossian *et al.*, 1975; Phelps *et al.*, 1975), PET uses the annihilation radiation produced by positron absorption to provide an image of the *in vivo* spatial distribution of a blood-born radionuclide tracer (Raichle, 1994). It is the decay of the radionuclide that makes imaging possible (Figure 1). Isotopes incorporated into the tracer molecules decay by emitting antimatter particles known as *positrons*. Each positron passes through the surrounding tissue until it encounters an electron, generally within 0.2 - 7 mm (Roland, 1993). The two particles annihilate each other, thereby generating two gamma rays traveling in exactly opposite directions. These rays are detected by a circular array of crystals surrounding the head of the subject. Data regarding the coincident arrival of gamma rays on opposite sides of this ring are used to reconstruct points of origin within the brain. Ultimately an image of the distribution of annihilation events (and thus of the tracer) within the brain is produced.

A variety of radionuclide tracers have been developed for use in PET and it is the kinetics of the particular tracer used that ultimately determine what is being imaged. One example is the radioisotope ^{15}O, which is injected in the form of $H_2{}^{15}O$ (water). During the relatively short half-life of ^{15}O, this water remains within the subject's blood vessels, and images collected reflect concentrations of blood within the brain. Because local blood flow is sensitive to the physiological action of surrounding neurons (Roland, 1993), such images may be used to identify patterns of functional activation.

In contrast, the tracer FDG (^{18}flouro-2-deoxyglucose) is a radioactively "tagged" glucose analog with a relatively long half-life. This tracer is actually absorbed by neurons, producing concentrations that reflect rates of glucose metabolism. Other tracers (*ligands*) have also been developed that have an affinity for specific receptor sites on neuronal membranes, allowing for the *in vivo* investigation of the distribution and activity of ion channels and neurotransmitter receptors (Roland, 1993).

Figure 1



1. *The mechanics of Positron Emission Tomography. 1) A radionuclide tracer injected into the bloodstream decays, producing an antimatter particle called a positron. 2) The positron collides with a nearby electron, annihilating both particles and producing two gamma rays that travel outward in opposite directions. 3) Gamma ray pairs are detected by a circular array of sensors surrounding the subject's head, and used to reconstruct points of origin within the brain.*

The Meaning of PET Data

Although it is commonly described as a "functional brain imaging" technique, PET does not really produce images of brain function. As detailed above, what PET images actually show is the distribution and concentration of a tracer within the brain. The *interpretation* of brain function on the basis of this information requires consideration of specific tracer kinetics, their relation to neuronal activation, and the further relation of such activation to brain function.

From Tracer Concentrations to Neuronal Activation

Currently available radionuclide tracers track neuronal metabolism in impressively direct and sensitive ways. The previously mentioned glucose analog, FDG, behaves in the brain in the same way as glucose. Because glucose metabolism is the only major source of energy in the brain, and because neuronal activity regulates energy metabolism (Roland, 1993), FDG concentrations provide an indication of such activity. More specifically, FDG distribution traces the activity of the Na^+ pumps in neuron membranes. Na^+ pumps function to maintain the charge differential across the neural membrane (the *resting membrane potential*) that makes action potentials possible. Each time a neuron fires, restoration of the resting membrane potential creates work for the Na^+ pumps, requiring the metabolism of intracellular ATP that can only be replaced using blood-born glucose. For this reason, FDG accumulates preferentially in brain regions where more neuronal action potentials are occurring.

Another popular tracer is $H_2{}^{15}O$, which is carried along with the blood moving through the vessels of the brain. The distribution of $H_2{}^{15}O$ in the brain thus reflects the distribution of blood. Somewhat surprisingly, this gross measure turns out to be a sensitive indicator of neuronal metabolism (and thus activity). As reviewed by Roland (1993), there is a perfect correlation between regional Cerebral Blood Flow (rCBF) and the regional Cerebral Metabolic Rate of glucose (rCMRgl) in all cerebral structures in awake rats. This coupling is sensitive enough to detect variations in rCMRgl at the microscopic level of individual functional columns of neurons. The tight coupling between rCBF and rCMRgl means that the distribution of blood revealed by $H_2{}^{15}O$ PET images indicates variation in the frequency of neuronal actions potentials across brain regions.

Although FDG and $H_2{}^{15}O$ PET may be counted on to reveal regional variation in action potential frequency, there is more than one potential cause for such variation. A major confounding factor for researchers interested in task-related variation is the influence of anatomy, and particularly of neuron density. The more neurons that are packed into a region the greater the number of synapses between them and the higher the baseline frequency of action potentials. A particularly relevant example is the primary (striate) visual cortex of the occipital lobe, which is known to have a relatively high neuron density (Blinkov & Glezer, 1968). As expected, the resting rCMR of striate cortex is higher than that observed in surrounding areas (Roland, 1993) with lesser neuronal densities.

Because regional differences in neuroanatomy can lead to differences in baseline metabolism and blood flow, functional interpretations of PET images must always be made with reference to baseline conditions. In practice, images of tracer distribution resulting from the activity of interest are compared with images from a control condition to produce a “subtraction” image. It is the statistically significant differences between control and experimental conditions revealed by this subtraction that are interpreted. This technique effectively eliminates the constant background influences of regional anatomy and reveals neuronal activation that is specific to the experimental task.

From Neuronal Activation to Brain Function

Using the subtraction method, it is possible to identify changes in neuron activation (firing) that are specifically task-related. It should be stressed that PET image subtractions do not show the absolute demands of a particular task but rather show how it differs relative to a control task. In a typical experimental design, the control task replicates the experimental task as closely as possible, excepting only those narrowly defined aspects of behavior that are under investigation. In this way, maximum experimental control and resolution is achieved.

A major problem with this approach, however, is that it ignores the possible functional importance of the resting baseline state. In a recent review of functional imaging research, Gusnard & Raichle (2001) conclude that resting brains exhibit a stable physiological baseline state that corresponds to the continual or “tonic” exercise of a particular set of mental operations. Tonically active regions are located in posterior parietal and medial prefrontal cortex, and are thought by Gusnard and Raichle to support visuospatial, emotional and cognitive aspects of a unified and continuous self-concept. Although activity in these regions is commonly attenuated during absorbing, goal-oriented tasks, it is not yet possible to say what role baseline activity may play in supporting normal human performance. It is important to remember that when we subtract task-related control activity we may also be subtracting task-independent baseline activity that is more than just random background noise.

Even accepting this caveat, there is still the question of what neuronal activation actually means in terms of brain (and mental) function. This is a difficult question from both theoretical and philosophical standpoints. Although a majority of researchers adhere to a computational model of brain function in which neuron firings represent information in much the same way as bits in the binary circuits of a digital computer, others have proposed alternative computational mechanisms (Wallace, 1995) or even suggested that the entire computational paradigm is fundamentally flawed (Penrose, 1994). Similarly, “dynamic systems” theorists have criticized conventional concepts of functional localization and representation in the brain by characterizing the brain “as a dynamic collective…[that] works in a holistic, plastic, self-organizing fashion, with structural boundaries that are less fixed than previously thought” (Thelen & Smith, 1994: 131).

Leaving aside such deep issues as the nature of consciousness and its relationship to the brain, the fact remains that systematic relationships exist between particular behaviors and coincident patterns of brain activation. These relationships are often most easily described in functional terms. For example, the fact that tasks involving motor performance invariably activate the precentral gyrus (the motor strip) to a greater degree than those not involving motor performance is most easily explained by positing that this region plays an important role in motor praxis. This is not to say that such activation necessarily indicates the presence of a “motor program” or some other such static representation, but it does help to reveal the neural systems that act as a medium for motor behavior. This kind of information about the neural substrates of specific behaviors can be of great value to researchers interested in the evolution of the human brain.

Paleopsychological and Evolutionary Interpretations of PET

There are two major ways in which PET data may be applied to human evolutionary studies: (1) as a source of insight into the psychology of archaeologically visible behaviors like stone knapping, and (2) as evidence regarding the selective pressures imposed on the evolving brain by such behaviors. Like all actualistic research, these applications are based on analogy and must be justified using uniformitarian arguments (Foley, 1992).

Paleopsychological Interpretation

The paleopsychological interpretation of PET is based on analogy between the mental demands of an experimental task and those of a similar prehistoric behavior. The basis of this analogy is the argument that similar behaviors imply similar mental processes even though the size and organization of the neural substrate may vary. At the macroscopic level revealed by PET activation images, the “basic” functional organization of the human brain appears to be highly conserved, differing little from that of chimpanzees and macaques (Passingham, 1998). However, it is still possible that evolutionary changes in microscopic organization and/or overall functional capacity have somewhat altered the composition of the neural circuits underlying knapping behavior. Whether or not this is the case, the basic informational and mental demands of the knapping task itself should remain roughly comparable in kind and magnitude.

The critical question is how accurately our interpretation of modern human data characterizes these basic mental requirements. In conventional PET methodologies, researchers use well-understood tasks to explore the functional anatomy of the brain. The application of PET to paleopsychology inverts this methodology by using existing knowledge of functional neuroanatomy to explore the mental demands of poorly understood tasks. For example, if experimental stone knapping tasks were found to activate prefrontal cortex (PFC), we might conclude that knapping is relatively demanding of the planning and problem-solving behaviors associated with PFC. In this way, brain activation patterns observed in modern humans may be loosely interpreted as reflecting task-related mental behaviors like visual perception, motor coordination or strategic planning.

As we have seen, PET subtraction methods allow researchers to identify the unique demands of an experimental task as compared with a control condition. In the current context, this method may be expected to reveal any exceptional demands of Oldowan knapping in modern humans. The two major errors that might arise in applying these results to pre-modern hominins are (1) overestimating the minimal requirements of knapping due to “extraneous” activation in modern humans, and (2) underestimating minimal requirements by failing to account for modern human baseline brain activity.

The first of these two potential errors is the more easily discounted. As long as a reasonable control condition is used, the subtraction method should eliminate extraneous or background activation not related to the experimental task. The only way in which “extraneous” activation would survive the subtraction process would be if modern human subjects uniformly employed a particular inefficient or over-elaborate strategy during knapping but not during a closely related control task.

Ironically, the effectiveness of the subtraction method in preventing the overestimation of mental demands inevitably increases the possibility of underestimation. The use of subtraction to delete “extraneous” background activity equally well removes any baseline activity that is functionally significant. Gusnard & Raichle (2001) have argued that ongoing baseline activity in the resting human brain functions to maintain a stable and unified self-concept. This may include tonic activity in dorsal medial prefrontal cortex relating to “a continuous ‘simulation of behavior’, ‘inner rehearsal’ and ‘an optimization of cognitive and behavioral serial programs’” (p. 692). Ongoing rehearsal and optimization, although not specific to any one behavior, might nevertheless provide an important functional foundation for modern human performance, including stone knapping. Subtracting this baseline brain activity could lead to underestimation of the mental demands of stone knapping in modern humans and, by extension, in early hominin toolmakers.

In strict terms, this potential for underestimation means that PET evidence should always be treated as providing only a minimum indication of mental demands. It is nevertheless worth noting that severe underestimation is relatively unlikely. As reported by Gusnard & Raichle (2001), tonic baseline activity tends to be attenuated during goal-oriented activity. This suggests that, while baseline “mental continuity” may provide an important foundation for everyday activity, it is actually subordinated to more immediately relevant processes during focused activity. It is these immediately relevant processes that are revealed by PET activations. PET may not completely characterize a subject’s mentality during task performance, but it can identify the most salient demands of a particular activity.

Evolutionary Interpretation

The second way to apply PET evidence to human evolutionary studies is by using it to identify the probable selective influences of particular prehistoric behaviors. Those areas of the brain most heavily recruited by modern humans performing a particular task are the ones most likely to have been subject to selection relating to that behavior during human evolution. Structures not recruited by modern humans may be considered much less likely to have been the direct focus of such selection. This logic is similar to that used by Marzke *et al.* (1998) in their attempt to identify skeletal indicators of habitual Oldowan toolmaking: those areas that experience the greatest physiological stress are the most likely to show adaptation.

A major challenge confronting the evolutionary interpretation of PET evidence is the fact that the basic processes through which brain evolution occurs remain poorly understood. Much research on this subject has been based upon the assumption that brain evolution occurs primarily through macrostructural changes in the absolute or relative size of the brain and its major anatomical components. More recently, however, evidence of adaptation at the microstructural level has been accumulating (Nimchinsky *et al.*, 1999; Preuss *et al.*, 1999; Buxhoeveden *et al.*, 2001). Despite this, the prevalence and importance of microstuctural adaptations in brain evolution remain unknown, as does their relationship with changes in regional brain volumes and/or overall brain size. Because it is not clearly understood how genetic inheritance, environment and developmental processes interact to produce adult brain structure on any of these levels, it is difficult to make a strong argument about the level(s) at which selection is most likely to act.

One important source of insight into macroscopic brain evolution is the study of modern brain size variation. The comparative methods of *evolutionary biology* (Harvey & Pagel, 1991) make it possible to interpret modern variation as evidence of evolutionary history. Unfortunately, students of mammalian brain evolution have been unable to agree even on the nature of modern variation, let alone on evolutionary explanations for it. In the past two years alone, four different groups of researchers have published four different characterizations of modern mammalian neuroanatomical variation, all using the same published set of brain volume data (from Stephan *et al.*, 1981).

At one extreme, Finlay *et al.* (2001) argue that the volume of major brain structures is rigidly covariant across species, showing little evidence of adaptation in individual structures or functional systems. They contend that the volumes of individual brain regions are constrained by a highly conserved order of neurogenesis, with late growing structures expanding disproportionately (but predictably) as the entire brain expands. As a result, they consider "coordinated enlargement of the entire non-olfactory brain" to be the most likely response to selection for "any behavioral ability" (Finlay & Darlington, 1995: 1578).

Barton & Harvey (2000), in contrast, see a mosaic of variation in modern mammalian brain structure, implying a similarly piecemeal history of evolutionary adaptation. These authors find evidence both of "grade shifts" in neocortex size (across insectivores, strepsirhine primates and haplorhine primates), and of independently correlated growth in specific functional systems. In direct opposition to Finlay & Darlington (1995) and Finlay *et al.* (2001), Barton & Harvey conclude (p. 1057) that "the cognitive and ecological significance of species differences in brain size should be evaluated by examining which neural systems in particular have been the target of selection."

Clark *et al.* (2001) adopt an intermediate position between these extremes, arguing that distinct, adaptive "cerebrotypes" are evident within mammals, but that these cerebrotypes are themselves conserved and "scalable" across 100-fold variations in absolute brain size. Although Clark *et al.* (2001) propose that their findings suggest a "reconciliation" between developmental (Finlay & Darlington, 1995) and adaptationist (Barton & Harvey, 2000) models, Barton (2002) has been critical of their conclusions.

Finally, there is the work of Winter & Oxnard (2001), which employs a "hypothesis-free multivariate morphometric approach" to conclude that, while mosaic brain adaptations are evident within mammalian orders, variation between orders "suggests an interplay of selection and constraints" (p. 710). Like Clark *et al.* (2001) and Barton & Harvey (2000), Winter & Oxnard (2001) thus find evidence of some degree of mosaic evolution in brain organization. However, the evidence and patterns of mosaic evolution described by each of these publications are different.

It is beyond the scope of this chapter to attempt a resolution to the ongoing debate about patterns and processes in mammalian brain evolution. A central problem is that our incomplete understanding of brain genetics, development and function provides no *a priori* reason for preferring one statistical approach or scaling method over another. Without knowing exactly how knapping-related selective pressure on particular brain regions is likely to have affected brain structure (e.g. local expansion, correlated growth, microstructural adaptation), it remains for the current investigation to clarify the nature of that selection. For the time being, results may be interpreted in terms of the multiple possible evolutionary implications suggested by competing models of mammalian brain evolution.

THE PET RESEARCH

In February of 1997 a single-subject pilot study was performed in order to more concretely assess the utility of PET to human evolutionary studies. Results from this study (Stout *et al.*, 2000) not only confirmed the practicality and value of the technique, but also suggested specific hypotheses and methodological improvements for further research. These were incorporated into a six-subject follow-up study that is now in the data analysis stage.

In the pilot study an $H_2{}^{15}O$ water tracer was used in order to examine patterns of brain activation during simple, Mode I, flake production. The subject of the study, Nicholas Toth, is an experienced Paleolithic archaeologist and experimental flintknapper with over 20 years knapping experience. Results of the study should be viewed in light of the subject's prior experience and may not reflect the brain activation that would occur in a less experienced subject performing the same tasks.

Due to the relatively short half-life of ^{15}O, all experimental tasks were performed in the PET scanner, with emission data being collected during 2 ½ minute long trials. The resulting activation images represent time-averaged emission data collected over three minutes beginning with the initiation of task performance. Images were collected during three trials for each of three task conditions in the single experimental subject.

The three task conditions employed in the pilot study were (1) a control condition, (2) "mental imagery" and (3) "knapping". The purpose and rationale of control tasks in functional PET experiments has been described above; in this experiment the control task consisted of the subject holding and viewing a spherical cobble without any attempt to imagine or carry out knapping. The "mental imagery" task consisted of the subject holding a partially reduced core with both hands while visualizing the removal of flakes from

Table 1

Location number	Centroid location	Functional attribution	Side	Talairach Coordinates (x, y, z)	Volume (mm^3)	Mean Z value
1	Superior parietal (Brodmann Area 7)	Dorsal "where" visual pathway	left	21, -49, 56	6,948	5.75
2			right	-30, -53, 61	1,948	5.16
3	Central sulcus (Brodmann Areas 1 and 4)	Primary motor and somatosensory processing	left	33, -26, 52	8,042	5.24
4	Postcentral gyrus (Brodmann Area 1)	Primary somatosensory processing	right	-39, -26, 56	5,889	5.10
5	Cerebellum (hemisphere)	Motor planning and initiation	left	10, -37, -18	1,002	5.22
6			right	-37, -51, -25	604	4.82
7	Cerebellum (vermis)	Motor Coordination	right	-3, -53, -9	1,082	5.07
8	Fusiform gyrus (Brodmann Area 37)	Ventral "what" visual pathway	right	-24, -53, -9	1,287	5.05

Table 1: Regions of differential activation observed during flake production in the pilot study (after Stout et al., 2000)

it. The "knapping" condition consisted of the subject actually striking the core with a hammerstone and removing flakes. For convenience, the subtraction data reported in Stout *et al.* (2000) from the comparison of the two experimental tasks with the control condition are re-presented here in Tables 1 and 2 and in Figures 2, 3, 5 and 6.

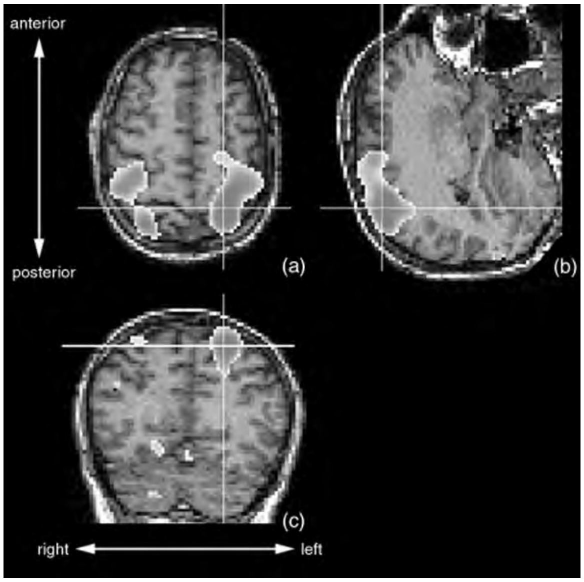
It should be stressed at the outset that the pilot study was "an heuristic, initial exploration" (Stout *et al.*, 2000) and involved only a single subject. The primary goal was to investigate the research potential of PET in human origins studies. This potential was firmly demonstrated by the collection of robust and clear-cut activation data. A secondary goal was to use the pilot study to further develop and refine research methods and hypotheses. This is best accomplished through interpretation of the results, even though definitive conclusions would be premature from a single-subject study.

As outlined in the preceding discussion, the proper interpretation of PET subtraction data requires careful consideration of the control task. In this pilot study, the control task was designed to control for visual stimulation by having the subject inspect a target very similar to the cores that would be used in the experimental conditions. The objective was to identify brain activation associated with thinking about or acting on a cobble in a purposeful, technological fashion that was absent in unmotivated perception. Numerous studies cited by Gusnard & Raichle (2001) indicate that, outside the visual cortices, passive visual inspection is associated with typical "resting" or baseline activation patterns. In addition to visual stimulation, the control condition also involved a low level of bimanual motor activity involved in holding the cobble with two hands. Motor related activity in the subtraction images may thus be interpreted as indicating demands beyond those involved in the use of the two arms as a static support system for the target.

Knapping Activations

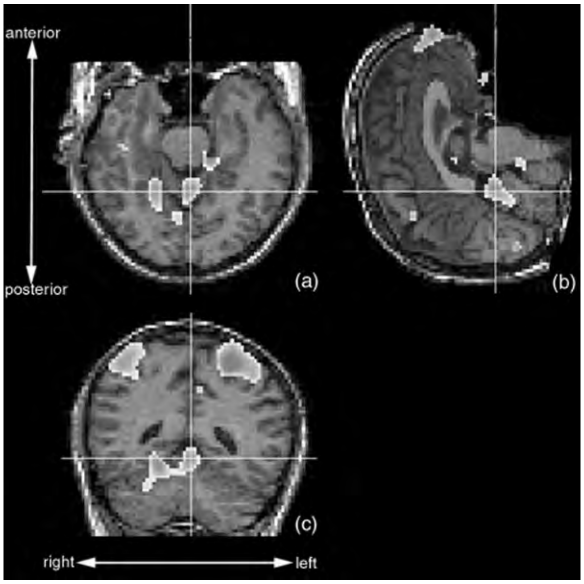
As may be seen in Table 1 and in Figures 2 & 3, the knapping task produced activation throughout broad volumes of the cerebral hemispheres and cerebellum. The most notable of these volumes is centered in the superior parietal lobule of the left cerebral hemisphere (Figure 2) and extends from the posterior parietal to the motor regions of the posterior frontal lobe, including the

Figure 2



2. ***Parietal activation during Mode 1 stone knapping*** *(after Stout et al., 2000). Crosshairs indicate activation in the superior parietal lobule of the left hemisphere, as seen in transverse (a), saggital (b) and coronal (c) section. This region is commonly associated with spatial cognition, and is part of the dorsal "position and motion" visual pathway. Contiguous activation extends into the more anterior somatosensory and motor areas surrounding the central sulcus. A small volume of activation in the fusiform gyrus of the right inferior temporal lobe is also visible in (c).*

Figure 3



3. ***Cerebellar activation during Mode 1 knapping*** *(after Stout et al., 2000). Crosshairs indicate activation of the cerebellar vermis, as seen in transverse (a), saggital (b) and coronal (c) section. This structure is associated with muscle tone and modulation of movement execution. More lateral activation of the right cerebellar hemisphere, involved in the planning and initiation of movement, is also visible in (c).*

intervening somatosensory areas of the postcentral gyrus. A similar activation pattern is visible in the right hemisphere but it is of a lesser intensity and may be distinguished into two separate volumes in the images presented. Other regions of activation include the cerebellar hemispheres and vermis, as well as the fusiform gyrus (Brodmann's area 37) of the right inferior temporal lobe.

Posterior Frontal Lobe

The posterior frontal lobe consists of three "agranular" motor areas, the premotor cortex (PM), supplementary motor area (SMA), and primary motor cortex (M1), which are anatomically distinguished from more anterior association areas by their lack of an internal granular layer (layer IV) of cortex (Roland, 1993). Without attempting to make overly fine distinctions, the activation seen in this general area (especially in the left hemisphere) may be taken to reflect the greater motor information content of active knapping as compared with simply holding a cobble.

Superior Parietal Lobe

Perhaps the most interesting result of the pilot study is the strong bilateral activation of the superior parietal lobe seen during knapping. As described in Stout *et al*. (2000: 1220) "The superior parietal lobe consists of what is referred to as 'multi-modal association cortex' and is involved in the internal construction of a cohesive model of external space from diverse visual, tactile and proprioceptive input." In particular, the superior parietal lobe is known to contain diverse functional fields involved in primary and secondary somatosensory perception, "remote" somatosensory association and higher-order visual processing (Roland, 1993).

As shown in Figure 2, knapping produced elevated activation bilaterally in the primary somatosensory cortex of the postcentral gyrus and in the classic visual association cortex of the superior parietal lobule. In the left hemisphere, increased activation of the secondary somatosensory and association areas located between these regions was also apparent.

The somatosensory areas activated during knapping have previously been shown to undergo activation during vibration of the fingers (Fox & Applegate, 1988), tactile shape discrimination (Roland, 1985) and movements in extra personal space (Roland *et al*., 1980). As with the previously discussed motor activity, the observed somatosensory activation is unsurprising in

Table 2

Location number	Centroid location	Functional attribution	Side	Talairach Coordinates (x, y, z)	Volume (mm^3)	Mean Z value
1	Superior parietal (Brodmann Area 7)	Dorsal “where” visual pathway	left	21, -53, 56	1,766	5.61
2			right	-30, -55, 58	433	4.84
3	Inferior parietal (Brodmann Area 40)	Visualization, motor imagery	left	42, -35, 43	1,572	5.67
4			right	-51, -33, 50	570	5.15
5	Precentral gyrus (Brodmann Area 4)	Primary motor processing	left	33, -19, 54	1,834	5.19
6	Occipital lobe (Brodmann Area 19)	Secondary visual processing	left	28, -78, 2	558	5.25
7			right	-30, -78, 16	1,037	5.45
8	Fusiform gyrus (Brodmann Area 37)	Ventral “what” visual pathway	right	-28, -51, -9	421	5.22
9	Cerebellum (hemisphere)	Motor planning and initiation	right	-37, -44, -20	649	4.62

Table 2: Regions of differential activation observed during "mental imagery" in the pilot study(after Stout et al., 2000).

light of the increased physical activity associated with the knapping task.

Results from the pilot study thus suggest that knapping is relatively demanding of somatosensory and motor processing, particularly with in the left hemisphere/right hand system that was involved in percussive movements by the right-handed subject of this study. It would appear that the right hemisphere/left hand system responsible for supporting and orienting the core was less heavily recruited.

Visual components appear to be very important in the perceptual-motor dynamics underlying simple stone knapping. Both hemispheres show substantially increased activation of the posterior superior parietal lobule, a visual association area belonging to what is commonly thought of as the *dorsal stream* of visual processing. The existence of two streams of visual processing (dorsal and ventral) in the primate cerebral cortex was first proposed by Ungerleider & Mishkin (1982), who localized these streams to the posterior parietal and inferior temporal cortex respectively (Figure 4). According to the classic model, the dorsal “where” stream is involved in the perception of location and motion while the ventral “what” stream is implicated in the perception of object characteristics like form and color. More recently, Milner & Goodale (1995) have suggested that the distinction between these streams is more accurately described as being between dorsal visuomotor control and ventral perceptual representation. In either case, the strong observed activation of the posterior parietal may be interpreted as reflecting the greater visual demands of active knapping as compared with passive inspection of a stationary target.

Inferior Temporal Lobe

A small but intriguing volume of activation is also visible in the fusiform gyrus on the medial aspect of posterior inferotemporal cortex (Figure 2). As noted above, the cortex of the posterior inferior temporal lobe is conventionally associated with the ventral stream of visual processing (Figure 4). Although the full extent of the inferotemporal visual association areas in humans is unknown (Roland, 1993), visual activation of the medial bank of the inferior temporal sulcus has been observed (Roland *et al.*, 1990). As reviewed by Bradshaw & Mattingley (1995), more anterior inferotemporal cortex has been linked with face recognition (Tovee & Cohen-Tovee, 1993) and with the integration of visual perception and memory in general (Miyashita, 1993).

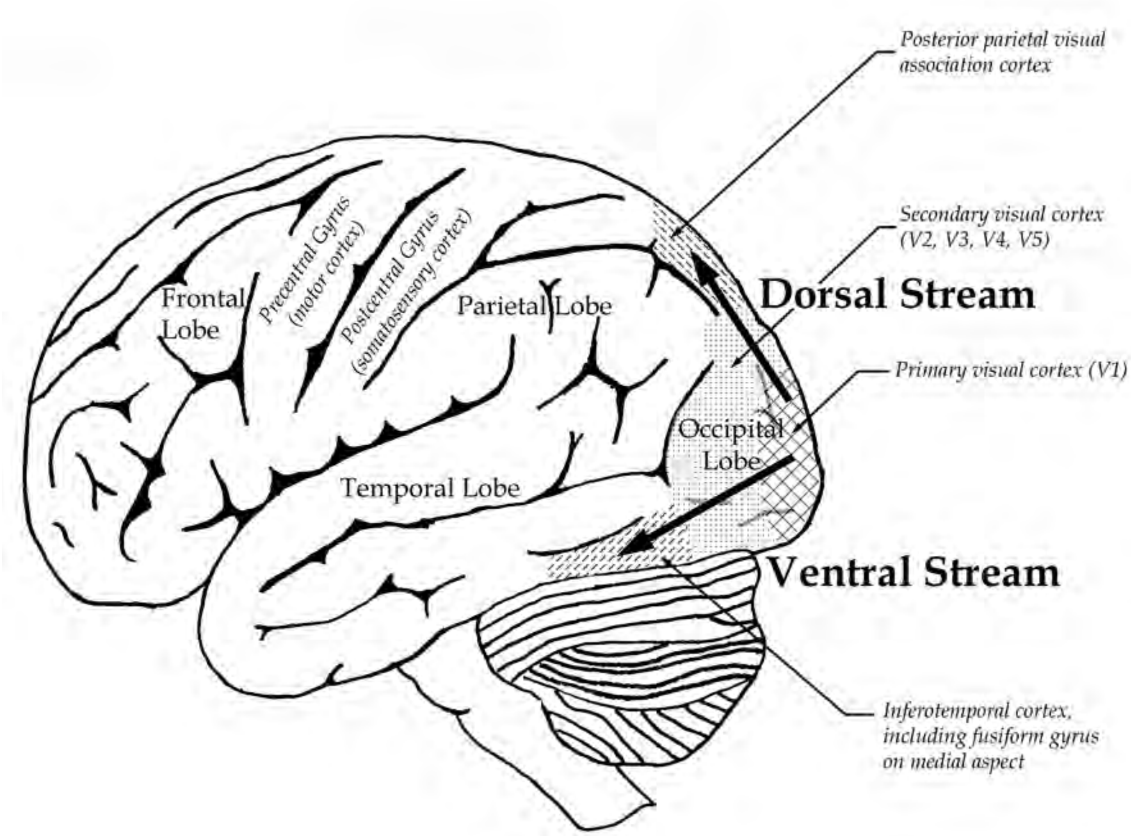
As noted in Stout *et al.* (2000), care should be taken not to over-interpret a small activation volume observed in a single subject. Nevertheless, the activation does provide a tantalizing suggestion of ventral visual processing to complement the more robustly evident activation of the dorsal stream. Following the models of Ungerleider & Mishkin (1982) and Milner & Goodale (1995), such processing would be expected to involve the perception and/or representation of object characteristics. Increased demands for such perception during knapping might arise from the visual complexity of the partially reduced core combined with greater attention to technologically relevant morphology (e.g. edges, angles, ridges, depressions). It is unclear why fusiform activation is apparent only in the right hemisphere. This may simply be a reflection of marginal significance levels in this single subject sample, or could possibly indicate preferential attention to the left visual field (the core was held in the left hand).

Cerebellum

A final region of activation observed in the knapping-minus-control subtraction is the cerebellum (Figure 3). This activation is unsurprising as the cerebellum has long been viewed as a center for the control of voluntary movement (Rolando, 1809; cited in Schmahmann, 1997b). In the current study, significant activation may be seen in both cerebellar hemispheres as well as in the medial cerebellar vermis.

The cerebellar vermis is a phylogenetically ancient structure that, together with the most medial parts of the cerebellar hemispheres, makes up the *spinocerebellum*. As summarized by Kandel *et al.* (1991), the spinocerebellum uses somatosensory, auditory, visual and vestibular feedback to control muscle tone and to help in movement execution by compensating for small variations or deviations. The observed activation of the spinocerebellum may be taken as an indication of the

Figure 4



4. ***The two streams of cortical visual processing.*** *In the conventional view, cortical visual processing may be distinguished into two different functional streams: a dorsal "position and motion" stream and a ventral "form and color" stream. A more recent re-appraisal (Milner & Goodale, 1995) has suggested that these streams are better characterized as a dorsal "visuomotor control" system and a ventral "perceptual representation" system. The PET evidence suggests that the dorsal stream in particular is heavily activated during Oldowan-style knapping.*

demands for such control imposed by the knapping task.

The more lateral cerebellar hemispheres or *cerebrocerebellum*, are generally considered to participate in the planning and initiation of movement. The cerebrocerebellum is reciprocally connected with large areas of cortex, including premotor, motor, somatosensory and posterior parietal regions, and is thought to play an important role in the precise timing of complex multi-joint movements (Kandel *et al.*, 1991). Recent perspectives on the cerebrocerebellum have also tended to emphasize its role in cognitive and sensory functions (Leiner *et al.*, 1986; papers in Schmahmann, 1997a), leading to a more general characterization of the cerebellum as a "multipurpose learning machine which assists all kinds of neural control, autonomic, motor or mental" (Ito, 1993: 449). Cerebrocerebellar activation during knapping might reflect any of these functions, but is probably most closely tied to the control of knapping movements.

Mental Imagery Activations

The mental imagery task was incorporated in the pilot study for two reasons: (1) to provide a clear example of what intrinsic brain activity (i.e. abstract thinking) related to knapping might look like, and (2) to explore the possibility of obtaining useful imaging data while avoiding the methodological difficulties posed by vigorous physical tasks. The latter objective was inspired by research (review in Kosslyn *et al.*, 2001) indicating that mental imagery tasks recruit many of the same brain regions as do conventional perceptual and motor tasks. To the extent that this is true for stone knapping, imagery tasks might be used to explore knapping behaviors that are difficult to perform within the constraints of the scanning situation. Although the use of more slowly decaying tracers in research subsequent to the pilot study (see below) has largely obviated the need for this kind of methodological contortion, the results from the imagery-minus-control subtraction remain of theoretical interest.

The concept of internal mental representation has been a particularly important one in archaeological theorizing about the cognitive implications of stone tools. Specific examples include the mental templates of Clark (1996) and Gowlett (1984), the mental rotation of Robson Brown (1993), and the abstracted spatial cognition of Wynn (1989). The mental imagery task was designed as an artificially exaggerated case of such internal representation in a simple toolmaking task.

As expected, activation in the imagery-minus-control subtraction (Table 2, Figures 5 & 6) is quite similar to that seen in the knapping-minus-control subtraction (Table 1, Figures 2 & 3), although somewhat less intense/extensive. All of the major regions recruited during knapping were significantly activated in at least one hemisphere during the imagery condition, including superior parietal, pericentral (precentral gyrus), and inferotemporal (fusiform gyrus) cortex as well as the cerebellum. This is consistent with growing evidence that visuo-motor imagery relies, at least in part, on the same neural substrates as does visuo-motor action. Turning this around, it appears that actual knapping shares many of the mechanisms involved in generating an internal representation of the knapping task.

There is, however, some activation visible in the imagery-minus-control subtraction that is not evident in the knapping-minus-control subtraction. This consists of the bilateral activation of the anterior inferior parietal lobule and secondary visual processing areas in Brodmann's area 19 of the occipital lobe. Activation of these areas indicates processing demands/mechanisms of visuo-motor imagery that are not evident in actual knapping.

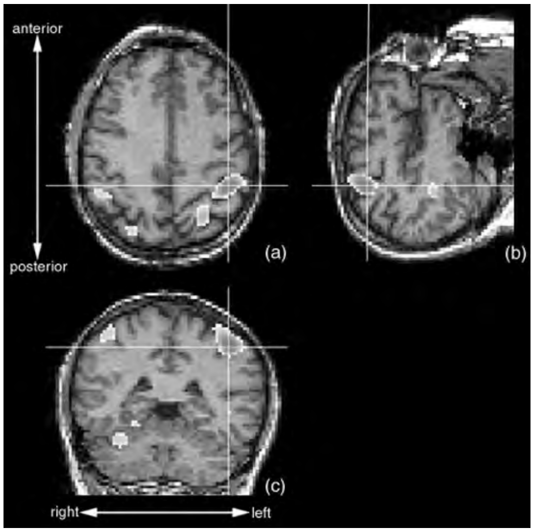
As reported in Stout *et al.* (2000), the anterior portion of the inferior parietal lobule has been described as a bi-modal visual and somatosensory association area (Roland, 1993). Siegel & Reed (1998) further describe the role of this region in integrating visual and occulomotor information to provide a "head-centered representation of space". Activation of the inferior parietal in the mental imagery condition most likely reflects a greater salience of spatial information in supporting visuo-motor imagery as compared both with visual perception in the control condition and with visuo-motor performance in the knapping condition.

Activation of secondary visual areas in the occipital lobe probably reflects a similar emphasis on visual mechanisms in supporting mental imagery. Brodmann's area 19 is made up of the visual areas V3, V4 and V5 (Kandel *et al.*, 1991). The particular volume of area 19 that is activated in this study is located near the conjunction of occipital, parietal and temporal lobes, and may correspond to V5 (also known as MT). V5/MT is an area known for its response to the direction and speed of moving visual stimuli (Maunsell & Newsome, 1987), and is part of the dorsal stream of visual processing. Activation of V5/MT in the imagery condition suggests that visualization of knapping activity not only relies upon mental processes similar to those involved in actual performance, but can actually be more demanding of these processes.

Interpreting the Pilot Study

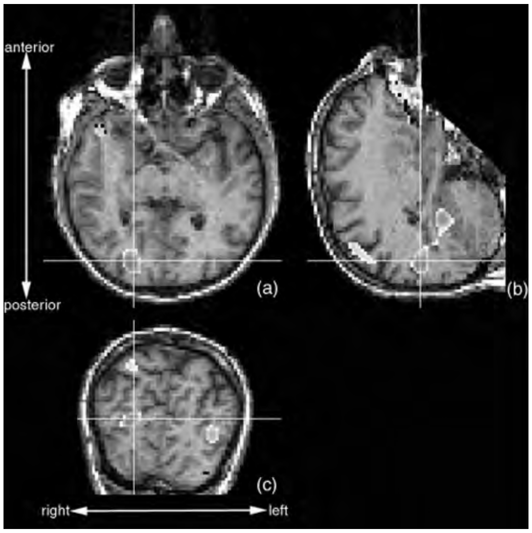
Although results from this single-subject pilot study require further corroboration, they do provide preliminary evidence regarding the system of brain structures that are recruited during Oldowan-style toolmaking by an experienced modern human knapper. The actual dynamic behavior of this distributed neural system may not visible in the static PET images collected (c.f. Segalowitz, 2000), but the time-averaged activation patterns nevertheless reveal key anatomical substrates. Together with environmental and somatic factors, it is the organization and functionality of these neural substrates that ultimately affords knapping activity.

Figure 5



5. ***Inferior Parietal activation during Mental Imagery*** *(after Stout et al., 2000). Crosshairs indicate activation of the inferior parietal lobule, as seen in transverse (a), saggital (b) and coronal (c) section. This region is particularly important in creating internal representations of space. Its activation here reflects the greater representational demands of visualizing the knapping task as compared with its actual visuo-motor execution.*

Figure 6



6. ***Occipital activation during Mental Imagery*** *(after Stout et al., 2000). Crosshairs indicate activation of secondary visual cortex in the right occipital lobe, as seen in transverse (a), saggital (b) and coronal (c) section. Corresponding activation of the left occipital is visible in (c). Secondary visual activation during mental imagery reflects the important role that even relatively low-level visual cortices can play in generating internal representations.*

As detailed above, the pericentral, posterior parietal, inferotemporal and cerebellar regions recruited during knapping are known to participate in the processing of motor, somatosensory and visual information. The co-activation of these regions during knapping supports the characterization of Oldowan toolmaking as a relatively demanding perceptual-motor activity that is heavily reliant upon visual guidance. The pilot study does not, however, provide any evidence of the recruitment of "higher order" prefrontal association cortex or classic language processing regions. Baseline activity is of course ongoing throughout the brain, but there is not yet any evidence that Oldowan knapping is particularly demanding of the cognitive processes supported by these regions. By conventional standards, Oldowan-style toolmaking does not appear to be a particularly "intellectual" pursuit.

On the other hand, it is important that the mental demands of skilled perceptual-motor performance not be underestimated. As argued by Reed & Bril (1996: 434), "the ability to construct, coordinate, and modulate movements regardless of the functional context of the organism is itself one of the most sophisticated achievements of human action systems". Artificial Intelligence (A.I.) researchers have similarly discovered the complexity of real-world perception and action. Chess-playing programs capable of competing at the highest levels have been around for decades, but A.I. researchers are still striving to produce computer programs capable of basic perceptual-motor behaviors in simulated "block worlds" consisting of nothing more than colored blocks on a table (e.g. Finney *et al.*, 2001). In the human brain itself, large regions of occipital, parietal, frontal and temporal cortex are involved in perceptual-motor activity, as are numerous subcortical structures (Figure 7). Although many of these regions are not involved exclusively in perceptual-motor processing, they nevertheless account for a large portion of total brain volume.

Recognizing that skilled perceptual-motor performance is itself a sophisticated mental achievement, the question remains as to whether the specific demands of Oldowan knapping are exceptional. Specifically, is Oldowan knapping more demanding than everyday perceptual-motor activities human ancestors may have engaged in prior to 2.5 Ma.? PET subtraction methods are ideally suited to answer this question though direct comparison of the brain activations associated with different task conditions.

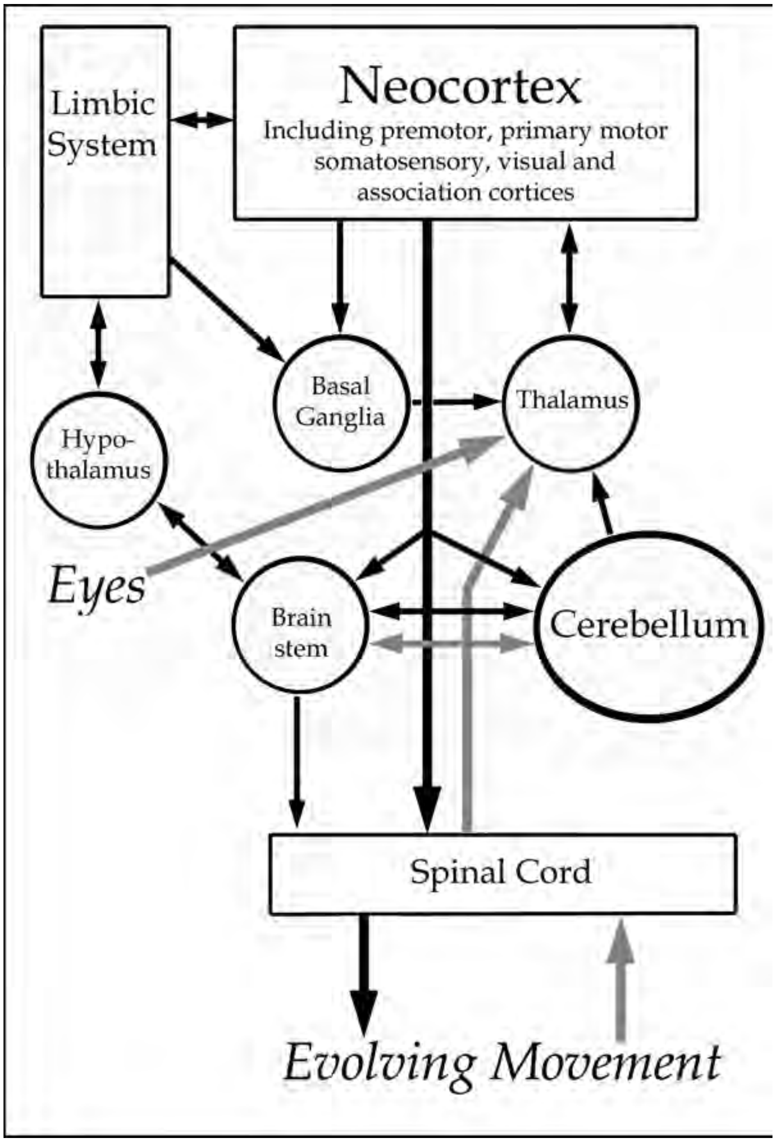
In the pilot research presented here, Oldowan-style knapping was compared with a control condition consisting of the static support and visual inspection of a stone cobble. Knapping was found to produce activations in cerebellum, primary motor and somatosensory cortex and posterior regions of superior parietal and inferotemporal cortex. This indicates that knapping exerts greater perceptual-motor demands than the control condition. Particularly interesting is the activation of posterior parietal and inferotemporal cortex. These regions, although closely tied with visual processing, are dominated by intrinsic cortico-cortical connections rather than by the extrinsic input/output connections seen in primary sensorimotor cortex. Their recruitment suggests that simple Oldowan flake removal can involve relatively high-level, intrinsic perceptual-motor processing.

It is, however, important to remember that the control condition used in this pilot study was designed to produce little beyond resting baseline activity. It remains for the follow-up research to indicate whether the demands of Oldowan knapping on visual association cortices really are exceptional when compared with other perceptual-motor activities. Even within the pilot study, it is interesting to note that the mental imagery task produced additional activation of inferior parietal and occipital cortex not seen in the knapping condition. These regions, and particularly the multi-modal association cortex of the anterior part of the inferior parietal, are important substrates for visuo-motor imagery. The fact that they are not significantly activated during actual knapping suggests that mental imagery may not be particularly important part of Oldowan toolmaking. In future research, it will be interesting to see if the neural substrates of visuo-motor imagery play a greater role in more advanced lithic technologies.

WORK IN PROGRESS

By demonstrating the utility of PET in human evolutionary research, the pilot study of Stout *et al.* (2000) set the stage for further research. At the time of this writing, data collection for two follow-up studies has been completed and analysis is ongoing. These studies include a six-subject follow-up investigation of Mode 1 toolmaking and a single-subject, exploratory study of Mode 2 handaxe manufacture (Stout *et al.*, this volume). The experimental design and hypotheses from both studies have been heavily influenced by lessons learned in the pilot study.

Figure 7



7. ***Neural structures and connections involved in visuomotor performance*** *(after Brooks, 1986). Note that nearly every part of the brain may become involved in motor performance in one way or another: from limbic motivational inputs, to retino-geniculo-cortical visual pathways and cortico-subcortical motor circuits including basal ganglia, thalamus and cerebellum. The question confronting human origins researchers is whether specifically knapping related demands on any of these structures are exceptional.*

Lessons Learned and Improvements Made

There are several important lessons to be learned from the pilot study. Most important is that it is possible to obtain clear and significant evidence of brain activation during stone tool manufacture using PET. Among other things, the strength of the results clears the way for the use of more refined control conditions.

Control Task

In the pilot study a relatively simple control task (holding and inspecting a spherical cobble) was employed. This was done in order to maximize the likelihood of obtaining significant results by maximizing the contrast between control and experimental conditions. The drawback of this approach is that it sacrifices specificity. As has been repeatedly stressed, PET subtraction data indicate relative rather than absolute neuronal activation. Results from the pilot study thus indicate that knapping is relatively more demanding than passive visual inspection (i.e. a resting baseline state) but do not provided evidence that it is more demanding than other everyday motor tasks such as reaching for or picking up an object.

In order to address this question, follow-up research employed a more active control task. This task, which consisted of striking two cobbles together without attempting to produce flakes, was designed to isolate any demands on motor accuracy, target perception, visuo-motor imagery or strategic planning that are exceptional to knapping as compared with more generic prehensile and percussive activities that human ancestors may have engaged in.

Tracer and Task Performance

Another major lesson of the pilot study was the difficulty of collecting activation data for a vigorous physical task like stone knapping. As outlined above, the relatively short half-life of ^{15}O requires that PET emission data be collected during actual task performance. This means that tasks must be performed lying prone on the scanner bed, an artificial condition that might conceivably affect numerous sensory and motor aspects of the task. In addition, the subject's head must remain motionless during imaging, which is an obvious problem when it comes to tasks like knapping that require vigorous movement. The movement problem was addressed in the pilot study by having the subject knapp using "approximately one-half normal force" (Stout *et al.*, 2000). Although flakes were nevertheless produced, this half-strength knapping task may not fully reflect the neural demands of the combined speed and accuracy employed in more naturalistic knapping.

In subsequent research (Stout, in prep.), this problem was resolved by switching to a different radionuclide tracer (^{18}flouro-2-deoxyglucose or "FDG") with a longer uptake and decay period. FDG is a glucose analog that is taken up from the blood stream by metabolically active cells (including neurons) for about 30 - 40 minutes following its injection. Tracer concentrations built up during this uptake period are subsequently stable, and may be detected using conventional PET imaging techniques. In practical terms, this means that experimental tasks may be conducted in naturalistic conditions outside the scanner. After 40 minutes of task performance, the subject is simply escorted to the scanner and images are collected. The drawbacks of using FDG are that only a single trial may be performed on a given day and that activation data reflect the average of activity over an even longer (40 minute) period than is the case with ^{15}O.

The use of FDG allowed several major improvements in experimental design. To begin with, subjects were able to perform tasks in a more natural posture: seated in a chair. This eliminates concerns about potentially anomalous visuo-motor and postural demands associated with knapping in a prone position. Even more importantly, subjects were able to engage in full force knapping, in some cases producing multiple generations of flake removals. This task condition not only captured the forceful and accurate motions of knapping, but also allowed for the unfolding of reduction sequences and any associated mental processes. As an additional benefit, artifacts produced during the knapping task were available for analysis as an independent measure of knapping skill. A final improvement allowed by the use of FDG was inclusion of raw material selection in the task (and control) condition. A cart supporting a collection of cobbles of various sizes, shapes and material compositions was placed next to the chair where subjects were seated. During the 40 minutes of task performance, subjects selected cores and hammerstones from this cart. In this way, it was possible to incorporate an additional aspect of knapping knowledge and decision-making.

Experience and Learning

The experimental subject in the pilot study was an experienced stone knapper. As outlined by Stout *et al.* (2000): "Patterns of brain activity observed in the subject were considered to represent those operative in one who has already learned the necessary skills for stone tool-making, and to provide a valuable baseline for future comparisons with less skilled or novice tool-makers." Multi-subject follow-up research has now provided the opportunity for such comparison.

Skill acquisition is thought to proceed through the streamlining or canalization of mental processing and the elimination of extraneous brain activation (Haier *et al.*, 1992). For this reason, it is reasonable to hypothesize that inexperienced knappers might display more intense and/or extensive brain activation than do experts. Such activation might be expected to reflect both the acquisition of task-specific knowledge and selection from multiple potential strategies. In fact, much of what is cognitively interesting about stone knapping is likely to occur in the process of learning rather than during expert performance.

In order to investigate learning, follow-up research was designed as a longitudinal investigation of stone knapping skill acquisition. Six subjects with no prior stone knapping experience were recruited and imaged during a novice trial in which they were asked to produce sharp stone flakes that would be "useful for cutting". Following the novice trial each subject participated in four hour-long uninstructed individual practice sessions. During these sessions, subjects were provided with a range of raw materials as well as pieces of vinyl and wood on which to test the efficacy of the flakes they produced. After completion of the practice regimen, subjects were brought back for imaging of an "experienced" trial. Although the relevant data are still being analyzed, it is hoped that this longitudinal design will help to reveal both the demands and dynamics of stone knapping skill acquisition.

Preliminary Results

Data analysis for the follow-up research described above is still ongoing, but it is nevertheless possible to present some preliminary results and interpretations. These are based on data from three subjects for the "experienced knapping"-minus-control subtraction. It is expected that more detailed analysis with the entire data set will reveal additional areas of activation, particularly in the novice condition. For the time being, only the most robust activations visible in the preliminary images will be considered.

Significant activations are visible in a number of brain regions, but at this stage may be most confidently identified in occipital and peri-central cortex and in the cerebellum. Occipital activation encompasses virtually the entire occipital lobe, certainly including the primary (striate) visual cortex (V1) surrounding the calcharine fissure and most likely extending into the secondary visual cortices (V2, V3, V4 and V5) in Brodmann's area 19. Pericentral activation is somewhat less extensive, but clearly encompasses primary motor cortex in the precentral gyrus and primary somatosensory cortex in the postcentral gyrus. Further analysis will be necessary to determine the extent to which more anterior secondary motor and more posterior sensory association cortices are activated. Observed cerebellar activation once again includes both vermis and hemispheres. It is most striking that, despite major differences in methodology (i.e. tracers, tasks, and subjects), both pilot and follow-up research implicate similar cortical and sub-cortical elements of the visuo-motor system.

The greatest apparent divergence between pilot and follow-up results is that the latter clearly show significant activation of primary visual cortex. The apparent demands of stone knapping on V1, which is generally considered to be a "low-level" visual input/output structure, are somewhat surprising given the similarity of basic visual environments in control and task conditions. Most likely this activation reflects the increased visual attention and acuity needed to guide forceful and accurate percussion. Although it is expected that further analysis of data from the follow-up study will reveal some additional activations outside primary motor and visual cortex, currently available results suggest that the most exceptional demands of Oldowan knapping are concentrated in more peripheral sensorimotor regions rather than in intrinsic association cortices.

SYNTHESIS

At the current stage of analysis, it remains most accurate to characterize Oldowan-style toolmaking as a perceptual-motor task that is particularly demanding of visual perception and guidance. No evidence has yet accrued for the exceptional involvement of the complex planning and associative capacities of prefrontal cortex, or of significant activation of Broca's and Wernicke's classic language processing regions. Nevertheless, it does appear that simple Oldowan flake production by modern humans generates increased activation in sizeable volumes of cortex, even when compared to a fairly sophisticated bimanual visuo-motor control task. This observation has important implications for both paleopsychological and evolutionary interpretations of the Oldowan Industry.

Paleopsychological Interpretation

The past twenty years have produced a growing consensus that the manufacture of Oldowan artifacts is not a cognitively demanding process. Although the various "core tools" described by Leakey (1971) were originally thought to be the intended products of early toolmakers, Toth (1982; 1985) demonstrated that the vast majority could be explained as arising from least effort flake production. Toth (1982: 328) further characterized this technology as being "quite simple to replicate once bifacial flaking is mastered". The cognitive demotion of the Oldowan Industry has been carried to an extreme by Wynn & McGrew (1989), who argue that Oldowan technology is no more demanding than the tool-use of modern chimpanzees.

Many disagree with Wynn & McGrew, particularly when such issues as raw material selectivity and transport (Schick & Toth, 1993; Gowlett, 1996; Stiles, 1998) or the probable use of stone tools to make other tools (Mithen, 1996) are taken into account. When it comes to the narrowly defined cognitive demands of Oldowan knapping, however, even the most generous commentators attribute little beyond a basic "concept of form" (Gowlett, 1996) that allows the knapper to maintain the viability of a core during sequential flake removals (Mithen, 1996; Roche *et al.*, 1999). On the other hand, these authors and others (e.g. Semaw, 2000; Ambrose, 2001; Ludwig & Harris, 1998) emphasize the motor skills needed to reliably detach useful flakes. PET research with modern humans will not reveal whether or not Oldowan toolmaking is within the capabilities of modern apes (a question better addressed in the work of Schick *et al.*, 1999 and Toth *et al.*, chapter in this volume), but it can refine our understanding of the basic mental processes involved.

To date, PET research has supported the prevailing archaeological assessment of Oldowan toolmaking: that it is a demanding visuo-motor skill but does not call upon sophisticated internal representation, planning or problem solving. The real contribution of the PET data has been to provide concrete empirical support for this intuitive assessment. The experiments described here demonstrate that effective flaking is more neurally demanding than everyday tasks like grasping or striking objects, and that these exceptional demands are concentrated in the cortical visuo-motor regions and cerebellum.

The Representational Perspective

Having identified the functional neuroanatomy underlying Oldowan knapping, it remains to provide a (paleo)psychological interpretation. As we have seen, archaeologists interested in early hominin intelligence commonly subscribe to a representational view of mind. This paradigm defines mentality as an abstract internal construction to which sensation and action are little more than peripheral input/output channels.

Spatial Cognition

In the archaeological literature, the representational paradigm is particularly well expressed in the Piagetian work of Wynn (1989). Wynn's basic assertion that "We construct the space we live in…from the coordination of internalized schemes of action" (p. 81) leads him to the ultimate conclusion that "Early artifacts are crude because early homini[n]s had not yet structured space in the way we so casually understand it…the internalized action schemes required for the manufacture of Oldowan tools were not very complex." (p. 83). Thus the sophistication of Oldowan technology is evaluated in terms of the internal mental representations required and found to be unimpressive.

Within the bounds of this interpretive paradigm, the PET evidence is broadly supportive of Wynn's conclusions. Although the pilot study did reveal increased activation of higher order visuo-motor and spatial association areas during knapping, this was in comparison with a control task involving nothing more than passive visual inspection. Preliminary results from follow-up research involving a more active and demanding control task have yet to demonstrate such activation, suggesting that spatial-cognitive "representation" may not be one of the more exceptional demands of Oldowan knapping. It is also interesting that the mental imagery task used in the pilot study evoked activation of inferior parietal spatial-cognitive association cortex that was not seen during actual knapping.

The PET research presented here, like Wynn's Piagetian analysis, fails to provide evidence of sophisticated internal representation in Oldowan knapping. However, there is some equivocal evidence suggesting involvement of the mental rotation and oblique perception capacities stressed by Robson Brown (1993) in her evaluation of Mode I artifacts from Zhoukoudian, China. Neuroimaging studies conducted over the past decade (refs. in Kosslyn *et al.*, 2001) have shown mental rotation to be associated with activation of superior parietal and right frontal lobes. Superior parietal activation was in fact observed during the pilot study, but preliminary results have yet to reveal such activation in the follow-up research. Mental rotation may not have been a particularly important operation in the simple Oldowan-style knapping observed during these experiments.

PET also provides mixed evidence regarding what Robson Brown (1993) refers to as the "significance of the oblique". It is well known (e.g. Appelle, 1972; Furmanski & Engel, 2000; Gentaz & Ballaz, 2000) that humans perceive horizontal and vertical orientations more accurately than they do oblique orientations. This also applies in the perception of motion (Loffler & Orbach, 2001). Robson Brown, following Rudel (1982), maintains that the perception and construction of oblique lines is cognitively demanding because "To differentiate opposite obliques demands holding one dual coordinate in 'mind' while comparing it with another" (p. 239). In so far as she sees evidence that obliques were "both perceived and manipulated" during the production of the Zhoukoudian artifacts, Robson Brown contends that these artifacts provide evidence of cognitive abilities "far more sophisticated than previous philosophical or psychological studies have assumed" (p. 240).

This conclusion may be evaluated on general archaeological and psychological grounds, as well as in light of the specific PET evidence presented here. To begin with, Robson Brown implicitly assumes that core forms from Zhoukoudian were the intentional end products of knapping plans rather than byproducts of flake production. This is quite possible, but in light of the experiments of Toth (1982, 1985), must be demonstrated rather than assumed. Robson Brown further assumes that the production of these core forms required that a complete internal representation be "held" in the maker's mind. Ecological psychologists would be quick to point out that much of the information needed to arrive at finished artifact forms is present in the stone being worked, and need not necessarily be represented in the mind of the maker. Altering the existing shape of a cobble through the removal of flakes is not conceptually or practically equivalent to the *de novo* construction of oblique lines on a blank sheet of paper.

In order to apply the experimental PET results presented here to the question of the "significance of the oblique", we must consider what is known about oblique perception in the brain. In a recent review, Gentaz & Ballaz (2000) concluded that the "visual oblique effect" or VOE (i.e. impaired perception of oblique orientations) is a multi-component phenomenon that occurs at different levels of processing according to the specific task at hand. At the lower end of the scale, it has been shown (Furmanski & Engel, 2000) that human primary visual cortex (V1) is more responsive to gratings with horizontal or vertical orientations rather than oblique orientations. This suggests that the VOE may result in part from V1 having a relatively smaller population of neurons tuned to the detection of oblique stimuli. The situation is complicated, however, by findings of other researchers that the VOE follows a gravitational rather than retinal reference frame (Buchanan-Smith & Heeley, 1993). In other words, the "definition" of oblique depends on an individual's perception of up and down rather than the actual orientation of their retinas. This would suggest involvement of higher-level spatial processing of the kind that occurs in the associative cortex of the parietal lobe.

It appears that, depending on the context, oblique perception may place unique demands on primary visual cortex and/or parietal association cortex. The PET research presented here provides some evidence for the involvement of both regions in Oldowan knapping. In the pilot study superior parietal and inferotemporal visual association cortex was activated, a phenomenon that might, among other things, reflect task-specific demands for the perception of oblique objects and motion. Interestingly, the pilot study was conducted with the subject prone on the scanning bed, possibly invoking higher-order processes needed to "re-define" the subject's visual frame of reference. On the other hand, follow-up research with subjects in a more natural orientation has so far only revealed primary (V1) visual activation. For the time being, the available PET evidence suggests that (naturalistic) knapping involves relatively demanding visual perceptive processes, perhaps including oblique perception, but that these processes have more to do with structuring extrinsic visual sensations than with generating sophisticated intrinsic representations.

Mental Templates

At the current stage of research, the PET data fail to provide compelling evidence of knapping-related procedural templates or instruction sets (Gowlett, 1996) more elaborate than those employed in everyday motor behaviors. Although the terms "procedural template" and "instruction set" are not commonly employed in experimental neuroscience, imaging studies have revealed that strategic planning tasks are most typically associated with prefrontal activation. One example is the *Tower of London* task (TOL) as studied by Dagher *et al.* (1999). The TOL is "a test of motor planning in which subjects must move colored balls on a computer screen to match a specified arrangement in the minimum number of moves possible." (p. 1973). Dagher *et al.* (1999) found that, although visuo-motor areas were routinely activated during TOL, activation in dorsolateral prefrontal, lateral premotor, anterior cingulate and caudate (basal ganglia) regions was correlated with the complexity of the TOL problem presented. The authors concluded that these latter regions constitute a "network for the planning of movement".

Attempts to assess the sophistication of knapping-related procedural templates and instruction sets might reasonably focus on activity in this network, and particularly in prefrontal regions thought to be involved in handling "sequential contingencies" and criterion-based pattern analysis (Roland, 1993: 344-345). In point of fact, the PET research presented here does not indicate knapping-specific activations of Dagher *et al.*'s planning network, with the possible exception of premotor cortex, although this dearth of evidence may change with further analysis and experimentation.

In evaluating these observations, it is important to consider modern human baseline brain activity, and especially the tonic activity known to exist in dorsal medial prefrontal cortex. This modern baseline activity might be sufficient to support simple, Oldowan-style knapping plans, but it is quite likely that relatively small-brained early hominin species displayed a lower level of baseline functionality. For such species, the formulation of knapping instruction sets may have required significant mental effort beyond the baseline condition. Concrete data are needed to inform such speculation, but are beyond the resolution of the experimental results presented here. Pursuit of such data should be a priority for future research.

Information Processing Capacity

Gibson (1993) has proposed that human sophistication in the superficially diverse realms of tool-use, language and social behavior shares a common foundation in the generalized information processing capacity of neocortical association areas (prefrontal, parietal and temporal). This premise leads her to conclude, among other things, that hominin intelligence has evolved in a gradual rather than punctuated fashion, that overall brain size provides a good indication of evolved intelligence, and that it would be "misleading to judge the intelligence of fossil [hominins] by the form of their tools alone" (p. 263). Instead, Gibson suggests that such judgments should be based on quantitative estimations of the "degree of information processing capacity necessary to support given sociotechnological systems" (p. 264).

The PET research presented here is focused on stone tool manufacture, and does not address broader social and environmental contexts. In this it fails to meet Gibson's criteria. Despite this, it does provide a valuable step toward the kind of quantitative evaluation that Gibson also calls for. In combination with research into the social foundations of stone toolmaking (Stout, in press), the PET evidence can enhance our ability to estimate the information processing demands of at least one archaeologically visible component of prehistoric sociotechnological systems.

Of particular importance to Gibson's hypothesis is the degree of activation observed in association cortex during toolmaking. Although a substantial volume of superior parietal association cortex was activated in the pilot study, the follow-up research has yet to reveal activation in any of the classic neocortical association cortices. For the time being, it is safest to conclude that Oldowan toolmaking does not rely upon substantial associative information processing. Since expansion of association cortex also accounts for the majority of brain enlargement in human evolution, this is consistent with the fact that the current best candidate for maker of the first stone tools, *Australopithecus garhi*, has an estimated cranial capacity of only 450 cc (Asfaw *et al.*, 1999).

The Perception-Action Perspective

Even within the prevailing representational paradigm, there are numerous different approaches to understanding hominin intelligence, and numerous different ways in which PET evidence might be interpreted. However, the overall interpretation is relatively uniform: that Oldowan toolmaking does not require sophisticated internal representation and therefore is cognitively simple. This evaluation is based largely on the fact that brain activations specific to Oldowan-style knapping currently appear to be limited to primary sensorimotor "input/output" cortex and not to include "higher-order" associative cortex.

This observation is without a doubt both meaningful and important, and the absence of major activations in associative cortex does suggest a lack of emphasis on certain kinds of mental processes. At the same time, a preoccupation with internal mental representation should not lead us to neglect the importance of knapping-specific activations in other parts of the brain. In this respect, an ecological or "perception-action" approach to understanding performance can be helpful.

As previously described, the ecological approach views performance as a dynamic property of the organism-plus-environment system, rather than as the unilateral expression by the organism of a static internal representation. While the representational view tends to privilege internal mental processing as an indication of cognitive sophistication, the ecological perspective emphasizes intelligent action as more broadly embodied in the adaptive combination of environmental *affordances* and organismal *effectivities*. Effectivities (Turvey & Shaw, 1979) are the functional units into which the neuromotor system can potentially be organized (Bongers, 2001), and are defined as much by perceptual capacities and bodily parameters as by abstract planning or representative abilities. The most valuable contribution of the ecological perspective is the realization that perception and action matter, and cannot be viewed as merely peripheral to some ideal, Platonic realm of pure cognition within the brain. As argued by Thelen & Smith (1994: 164, emphasis original): "Perception can be outside the study of concepts and categories only if mind is viewed as representing reality instead of contacting it, if knowledge exists outside of performance, and if the dynamic of knowledge acquisition is divorced from the processes of its storage and use."

In the case of stone knapping at least, knowledge does seem to be inextricably linked with performance. As observed by Roux *et al.* (1995), mastery of the forces needed for individual flake removals is the essential prerequisite for development of an effective knapping plan. Such plans are not rigid templates imposed from above, but arise flexibly from a practical understanding (*savoir-faire*) of knapping processes and potentials (Pelegrin, 1990). In the language of ecological psychology, a knapper's understanding comes not from abstract Euclidean representations but from direct experiential knowledge of flaking dynamics. These dynamics include the effectivities of the neuromotor system and the perceived affordances of the knapping materials.

The concept of an *embodied cognition* (Johnson, 1987; Varela *et al.*, 1991), although controversial in its broader application (Dennett, 1993; Kirsch, 1991; Vera & Simon, 1993), is useful in appreciating the importance of the primary visual and motor cortex activations observed during Oldowan-style knapping. To the extent that understanding is embodied in experience and performance, the fine-grained perception and manipulation supported by these sensorimotor regions is as important to "intelligence" as are more internally directed associative processes. Although Mode 1 knapping is conceptually quite simple, the PET data show that it is also a relatively demanding perceptual-motor interaction with the physical environment. The appearance of Oldowan artifacts in the archaeological record thus provides evidence for a level of behavioral sophistication beyond that evident in the everyday manipulative and percussive behaviors humans share with other primates. This ability to interact with the physical environment in increasingly complex and effective ways is as much a hallmark of hominization as are increasing social complexity and symbolic capacities.

Evolutionary Interpretation

Oldowan toolmaking, though supported by preexisting somatic (e.g. Marzke *et al.*, 1998) and neural traits, was itself a behavioral innovation. As pointed out by Deacon (1997) behavioral innovations must logically precede the biological adaptations that they foster. It is only when a useful behavior spreads through a population and begins to affect reproductive fitness that it actually leads to the changes in gene frequency that constitute biological evolution. Thus there are two questions we can ask about the evolutionary implications of Oldowan toolmaking: (1) what essential preconditions (minimal capacities) does its initial appearance imply, and (2) what selective pressures might its subsequent spread through hominin populations have created?

With respect to the first question, the PET evidence presented in this chapter is only indirectly applicable. Observed brain activations provide information only about the relative neural demands of stone knapping, not about absolute minimum requirements. It is simply impossible to equate the relative levels of activation seen in healthy, adult modern human brains to some minimum neural mass, neuron number or other such measure that would have been required of the earliest toolmakers.

In functional terms, however, the PET evidence does show Oldowan-style knapping to be a relatively demanding perceptual-motor activity. Oldowan artifacts may thus be taken as evidence of relatively greater behavioral sophistication than might otherwise be assumed. However, the absolute level of sophistication implied remains to be more concretely specified. Research with modern primates (e.g. Schick *et al.* 1999 and Toth *et al.*, chapter in this volume) and human children (e.g. Lockman, 2000; Piaget & Garcia, 1991) may ultimately prove more revealing in this respect. Functional brain imaging with tool making primates would provide a particularly interesting point of comparison if the practical difficulties attending such research could be overcome.

The activation evidence from modern humans is more directly applicable in identifying the selective pressures that Oldowan knapping might have placed on the early hominin brain. Even on this point, the evidence helps to define evolutionary possibilities and probabilities rather than certainties. For Oldowan knapping (as opposed to related aspects of tool production, transport and use) to have exerted any direct selective influence, there would have had to be variations in knapping ability that affected survivorship and reproductive fitness. We do not know if this was the case.

For one thing, we do not know how important Oldowan tools actually were to early hominin lifeways. Long tradition has of course viewed toolmaking as a defining attribute of humanity (e.g. Benjamin Franklin in Boswell, 1887; Darwin, 1871), and the developing field of paleoanthropology rather naturally came to see stone toolmaking as a kind of “prime mover” (Potts, 1993) in human evolution (e.g. Oakley, 1959; Washburn, 1960; Leakey *et al.*, 1964). This stance has more recently been bolstered by concrete evidence of the role of Oldowan tools in facilitating meat procurement (reviews in Isaac, 1984; Schick & Toth, 2001). On the other hand, hard evidence of the actual frequency with which such tool-assisted meat procurement occurred, and of its ultimate adaptive significance, is still lacking. In fact, the spatial and temporal limitations of early archaeological evidence have precluded any secure estimation of the frequency of Oldowan toolmaking and use, its prevalence within hominin groups, or its distribution across populations. We are left with the intuitively compelling yet circumstantial argument that the *potential* utility of Oldowan tools (e.g. Schick & Toth, 1993) implies an *actual* adaptive significance.

If we accept that that the use of Oldowan tools did in fact provide a significant adaptive advantage for early hominins, then there is still the question of whether meaningful variation existed in the ability to manufacture those tools. Growing appreciation of the simplicity of Oldowan tools and of the tool-using capacities of modern apes has led some to conclude that such variation did not exist. If effective Oldowan knapping was within the pre-existing capacities of the average adult, then clearly “toolmaking *per se* cannot have constituted the main ‘adaptive wedge’ driving the evolution of hands, brains and behavior in early *Homo*” (Potts 1993: 62).

Although this conclusion may ultimately turn out to be correct, it neglects the issues of skill learning and efficiency. In addition to the simple presence or absence of a behavioral capacity, the ease and reliability with which it is acquired should also be considered. For example, although modern chimpanzees are clearly capable of using stone hammers to crack open nuts, it nevertheless takes them years of learning to acquire proficiency (Boesch, 1993; Matsuzawa, 1996). Similarly, the stone flaking abilities of the bonobo Kanzi, though impressive, have developed slowly over more than a decade of experimentation (Toth *et al.*, chapter in this volume). In contrast, inexperienced modern humans are almost immediately and effortlessly able to produce near-replicas of early stone artifacts (Stout & Semaw, chapter in this volume). Although modern humans are clearly “over-qualified” to acquire Oldowan toolmaking skills, our smaller-brained ancestors quite probably found this leaning process to be more challenging. Even if nearly every healthy adult eventually acquired comparable knapping abilities, variations in learning speed and efficiency could still have provided raw material for selection.

To the extent that Oldowan knapping ability actually was important to survival, neural adaptations that facilitated its rapid and reliable acquisition would have been favored. Such adaptive facilitation would presumably have occurred through increases in the functional capacity of those neural structures most stressed during learning and performance. PET research offers a unique opportunity to identify these structures, although subsequent evolutionary interpretations are somewhat complicated by our limited understanding of the processes by which adaptive increases in functional capacity are achieved.

Mosaic Adaptation

One such process, consistent with the work of Barton & Harvey (2000) and Winter & Oxnard (2001), would be targeted increases in the size of functionally relevant brain regions. Although the relationship between size and function in brain structures is not well understood, it is commonly assumed that increases in size roughly equate to increases in neuron number and associated processing capacity. As shown by the currently available PET activation data, Oldowan-style knapping in modern humans is exceptionally demanding of neuronal activity in primary visual and motor cortices as well as in the cerebellum. Although further analysis may reveal additional areas of activation, these regions are the appropriate focus for the current discussion.

Within modern humans, performance on visual (Demb *et al.*, 1997) and motor (Grafton *et al.*, 1992; Pascual-Leone *et al.*, 1994; Karni *et al.*, 1995) tasks is positively correlated with the intensity and extent of activation in primary visual and motor cortices. Cerebellar volume is similarly correlated with the ability to learn a simple motor response (eyeblink conditioning: Woodruff-Pak *et al.*, 2001). Evolutionary increases in the size of these structures could have been one way in which the human brain became an over-qualified or "fail-safe" (Deacon, 1997) medium for the acquisition of knapping skills.

1) Primary Visual Cortex (V1)

One problem with this hypothesis is the fact that primary sensorimotor regions are actually among the least evolutionarily expanded portions of human cerebral cortex. Although concrete data regarding the size of major cortical subdivisions in humans and other primates are surprisingly hard to come by, Stephan *et al.* (1981) do report primary visual (striate) cortex volumes for 41 primate species. As a result, it is well known that the volume of human striate cortex is less than expected for a primate of its brain size (Holloway, 1979). Of course, human striate cortex is still absolutely larger than that of any other primate, including apes whose body sizes and (presumably) peripheral visual systems are quite similar to those of humans (Table 3). Thus, Deacon (1997: 216) has argued that "The human brain does not have a reduced visual cortex, but the appropriate amount of visual cortex for its retina". It may even be that human primary visual cortex is expanded relative to its retinal inputs, although any such expansion is certainly dwarfed by the much greater expansion of association cortex in the neighboring posterior parietal and elsewhere (Passingham, 1975; Holloway, 1983).

Paleoneurological evidence regarding to the evolving size of hominin striate cortex has been remarkably controversial (e.g. Holloway, 1981b; Falk, 1983), most fundamentally with respect to matters of timing. At the heart of disagreement is whether striate cortex experienced an independent reduction in *absolute* size prior to major allometric increases in hominin brain size (Holloway, 1995), or whether it merely decreased in *relative* size due to those increases (Armstrong *et al.*, 1991). In the former case, striate reduction (proposed to have occurred between 3 and 4 Ma [Holloway, 1995]) would obviously have predated any possible selective influence of Oldowan knapping, which first appears at 2.5 Ma (Semaw *et al.*, 1997). However, such reduction could have had implications for the pre-existing visual capacities of the first toolmakers.

Table 3

Species	Striate Cortex Volume (mm^3)	Body Weight (kg)
Pan troglodytes	14,691	46
Gorilla gorilla	15,185	105
Homo sapiens	22,866	65

Table 3: Primary visual (striate) cortex volume and body weight in humans and apes. Although decreased as a proportion of total cerebral volume, human striate cortex is still absolutely larger than that of any other primate. (data from Stephan et al., 1981)

2) Primary Motor Cortex (M1)

Much less is actually known about the comparative size and evolution of primary motor cortex (M1). Deacon (1997: 217) contends that this region is only 35% as large as expected for a primate brain of human size, but acknowledges that data used to make this and other estimates are "incomplete and insufficient for statistical tests". The only published data of which the author is aware are the surface area estimates of Glezer (1958; reprinted in Blinkov & Glezer, 1968), which show human M1 to be both relatively and absolutely smaller than that of chimps and orangutans (Table 4). These data indicate that, while the precentral region as a whole is of roughly the same relative size in humans and apes, a dramatic expansion of human premotor cortex at the expense of M1 has occurred within the region. This "zero-sum" relationship is highly suggestive of cortical reorganization independent of overall expansion.

It should be noted, however, that the data of Blinkov & Glezer (1968) have been questioned with respect to the small sample sizes employed and potential problems with postmortem shrinkage (Semendeferi & Damasio, 2000). Blinkov & Glezer themselves (1968: 5-10) identify numerous methodological problems in measuring the surface area of brains, including slicing deformation that may produce a 4% to 20% reduction in linear dimensions, shrinkage during preservation by up to 40% of surface area, and errors of up to 39% generated by calculating the area of a continuously curved surface from serial sections. Although generalized mathematical corrections have been developed for all of these problems, the errors produced are inevitably variable and particularly sensitive to differences in brain size and shape. This is problematic when comparing small samples across species that display dramatic differences in brain size.

In addition to the surface area work of Glezer (1958), attempts have also been made to compare the motor maps of M1 in humans and macaques. For example, Washburn (1959) concluded that the M1 hand area was relatively enlarged in humans, perhaps as an adaptation for tool use. Passingham (1973), however, used a different macaque motor map and concluded that this apparent difference was actually due to the smaller size of the foot area in humans. Unfortunately, there are no published paleoneurological observations regarding evolutionary changes in the size or morphology of hominin M1 (i.e. the precentral gyrus).

Thanks to the work of Heffner & Masterson (1975), we do know that the number of direct cortico-motoneuronal (CM) projections from motor cortex to the spinal cord is increased in humans. Interspecific variation in the number of these direct CM connections has also been found to correlate with an index of dexterity (Heffner & Masterson, 1975; Kuypers, 1981; Lemon, 1993). It is apparent from this work that human motor cortices in general have assumed a more direct and important role in controlling dexterous movements of the hands. What is less clear is how the connections and relative contributions of M1 and secondary motor cortices may have altered during this process. In humans, roughly fifty percent of CM projections arise from M1, while most of the rest originate in the more anterior secondary motor areas (Heffner & Masterson 1991). Similar data have not been reported for other species.

There is currently too little evidence to say exactly how the size of human M1 relates to that of other primates. It is at least safe to say that M1 has undergone nowhere near the degree of expansion seen in secondary motor and association cortices. In fact, M1 may even have experienced a real reduction in absolute size during human evolution. It thus seems unlikely that the apparent demands of Mode 1 knapping on M1 were a particularly influential factor in human brain-size evolution. The comparative surface area evidence instead calls attention to secondary motor cortex as a major locus of evolutionary change. At the same time, comparative CM projection data confirm a human evolutionary shift toward increasingly direct cortical control of movement. Further analysis of the PET data will provide a better indication of the degree to which secondary motor cortices are recruited during Mode 1 knapping, and help to clarify potential relationships between stone knapping and the evolution of human motor cortex.

3) Cerebellum

By this point, it should not be surprising that the role of the cerebellum in human brain evolution is also controversial. Both Deacon (1997) and Finlay & Darlington (1995) identify the cerebellum as being one the more preferentially expanded structures in the modern human brain. Clark *et al.* (2001), on the other hand, argue that the cerebellum actually constitutes an invariant fraction of total brain volume across mammals (including humans). Sultan (2002) has questioned the import of Clark *et al.*'s observation by noting that, while cerebellar white matter volume is relatively invariant, cerebellar and cerebral surface area do co-vary. Meanwhile, Barton (2002) is engaged in a disagreement

Table 4

	Precentral Region (Brodmann Areas 4 & 6)		Primary Motor Cortex (Area 4)		Premotor Cortex (Area 6)	
Species	cm^2	% of total hemisphere	cm^2	% of precentral region	cm^2	% of precentral region
Homo sapiens	62.50	8.4	7.34	12	55.1	88
Pan troglodytes	30.60	7.6	8.94	29.8	21.7	70.2
Pongo pygmaeus	41.97	7.6	13.57	33	28.4	67
Hylobates sp.	6.20	7.5	3.04	49	3.18	51
Papio sp.	8.45	6.8	4.83	58	3.63	42
Cercopithecus sp.	6.71	8.3	4.64	69	2.10	31
Callithrix sp.	1.01	5.5	0.80	79	0.21	21

Table 4: Surface areas of the "precentral region" of humans and other primates as reported by Blinkov & Glazer (1968). Note that human primary motor cortex is actually smaller than that reported for chimpanzees and orangutans, although the precentral region in general is somewhat enlarged due to a dramatic expansion of premotor cortex.

with Clark's group (Wang *et al.*, 2002) over the appropriate statistical treatment of the volume data.

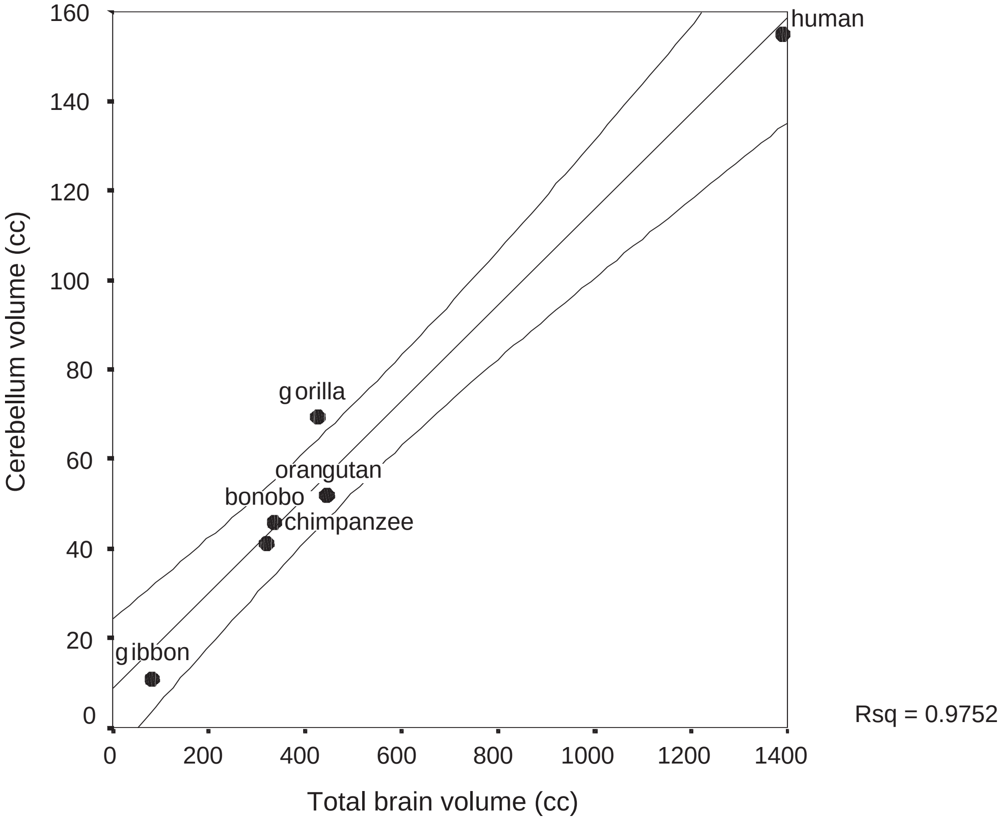
The single most important contribution that can be made toward resolution of these and other controversies regarding primate brain-size evolution is the collection and publication of new comparative data. A number of researchers (Semendeferi *et al.*, 1997; Semendeferi & Damasio, 2000; Rilling & Insel, 1998; Rilling & Insel, 1999; Rilling & Seligman, 2002) are currently making such a contribution through the pioneering use of anatomical MRI to collect *in vivo* primate brain volume data. Unfortunately, even these new data have yet to resolve the many questions surrounding primate cerebellar evolution.

Based on a study of 10 humans and 19 other hominoids, Semendeferi & Damasio (2000) conclude that the cerebellum constitutes a smaller percentage of the brain in humans than in apes. A univariate ANOVA conducted by this author on the data presented by Semendeferi & Damasio confirms that between-species differences in cerebellar proportion do exist (p = 0.005), however a subsequent post hoc (Bonferroni) test reveals that these differences arise only in comparisons involving gorillas (Table 5). It is actually the large size of the gorilla cerebellum that accounts for the difference between ape and human means reported by Semendeferi & Damasio.

Semendeferi & Damasio themselves comment on the apparently anomalous size of the cerebellum in gorillas, but caution that "The larger mean value for this species is largely due to the large cerebellum of one of the two individuals examined" (p. 329). This mean value (16.1 %) is greater than that (14.7 %) indicated by the data of Stephan *et al.* (1981), but less than the value (17.0 %) derived from the MRI data of Rilling & Insel (1998). To the extent that the data of Semendeferi & Damasio (2000) indicate any deviation from the hominoid allometric trend, it is on the part of gorillas, not humans (Figure 8).

The more phylogenetically inclusive MRI study of Rilling & Insel (1998) allows for an additional level of analysis. Comparing cerebellar and brain volumes across 44 individuals from 11 haplorhine species, Rilling & Insel observed an apparent grade-shift between cercopithecoid and hominoid primates. If humans are excluded from the regression as a presumptively divergent species, then monkey and ape trends with similar scaling relationships (slopes) but different proportions (y-intercepts) are produced (Figure 9a).

Figure 8



8. ***Allometric plot of species mean values for cerebellum and total brain volume including 95% confidence interval*** *(data from Semendeferi & Damasio, 2000). A regression using species mean values confirms the results from the post-hoc test of individual cerebellar proportions (table 5): gorillas are the only species that falls outside the mean prediction lines (95% confidence interval).*

Table 5

Comparison		Mean Difference (1-2)	Standard Error	Significance
Species 1	Species 2			
human				
	bonobo	-2.1200	.9005	.412
	chimp	-1.4200	.7064	.844
	gorilla	**-4.6200**	**1.0597**	**.003**
	orangutan	-.3450	.8093	1.000
	gibbon	-1.4200	.8093	1.000
bonobo				
	human	2.1200	.9005	.412
	chimp	.7000	.9673	1.000
	gorilla	-2.5000	1.2488	.858
	orangutan	1.7750	1.0448	1.000
	gibbon	.7000	1.0448	1.000
chimp				
	human	1.4200	.7064	.844
	bonobo	-.7000	.9673	1.000
	gorilla	-3.2000	1.1170	.131
	orangutan	1.0750	.8830	1.000
	gibbon	.0000	.8830	1.000
gorilla				
	human	**4.6200**	**1.0597**	**.003**
	bonobo	2.5000	1.2488	.858
	chimp	3.2000	1.1170	.131
	orangutan	**4.2750**	**1.1847**	**.022**
	gibbon	3.2000	1.1847	.191
orangutan				
	human	.3450	.8093	1.000
	bonobo	-1.7750	1.0448	1.000
	chimp	-1.0750	.8830	1.000
	gorilla	**-4.2750**	**1.1847**	**.022**
	gibbon	-1.0750	.9673	1.000
gibbon				
	human	1.4200	.8093	1.000
	bonobo	-.7000	1.0448	1.000
	chimp	.0000	.8830	1.000
	gorilla	-3.2000	1.1847	.191
	orangutan	1.0750	.9673	1.000

Bold indicates a significant difference in cerebellar proportion

Table 5: Post hoc (Bonferroni) test of variation in cerebellar proportion across hominoids (data from Semendeferi & Damasio, 2000). The only significant differences occur in comparisons of gorillas with humans and orangutans. Bold indicates a significant difference in cerebellar proportion

Interestingly, humans appear to be better predicted by the monkey trend. If, however, humans are included in the regression, a different (shallower) hominoid scaling relationship is produced (Figure 9b). Rilling & Insel consider several possible explanations for this pattern, and conclude that "the data can best be explained by a grade shift occurring with the evolution of hominoids, followed by a change in scaling caused by disproportionate cerebral expansion with the evolution of homini[n]s" (p. 313).

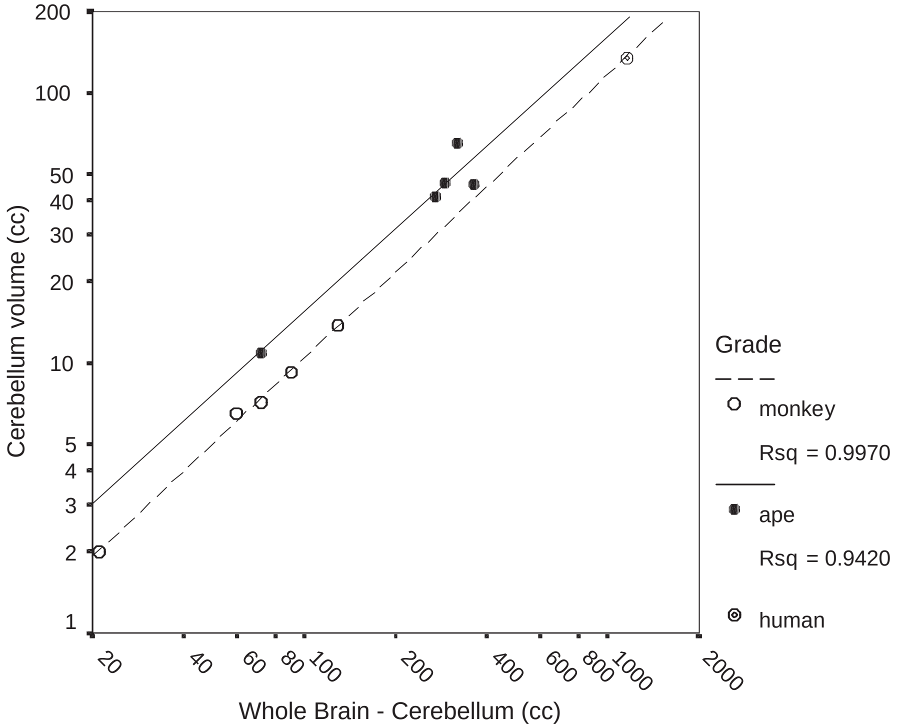
An alternative not considered by Rilling & Insel is the possibility that it is actually gorillas that are the divergent hominoid species. This possibility is suggested both by the data of Semendeferi & Damasio (2000) (Table 5) and by regression of Rilling's & Insel's own data (Figure 9b). When gorillas are excluded from the regression, a good allometric fit is observed across the remaining hominoids (Figure 9c). This suggests, not only that something very interesting has occurred in the evolution of the cerebellum in gorillas, but also that Rilling's & Insel's putative "change in scaling caused by disproportionate cerebral expansion" may characterize hominoids in general rather than hominins specifically.

Considering all available evidence, the safest conclusion appears to be that the human cerebellum has indeed undergone considerable evolutionary expansion, even if it has not quite kept pace with the rapidly ballooning neocortex. In this it appears to have conformed to a primitive hominoid allometric trend. Such proportional human cerebellar expansion is not surprising considering the close functional and anatomical connections between cerebellum and neocortex (Schmahmann & Pandya, 1997), and the involvement of cerebellum in a wide range of perceptual, motor and cognitive behaviors (Leiner *et al.*, 1993; Parsons & Fox, 1997). The coactivation the cerebellum with various cortical regions during knapping is just one example of this pervasive integration. Knapping-related demands on the cerebellum may have been one factor contributing to the rapid expansion of the cerebro-cerebellar system during human evolution.

Correlated Expansion

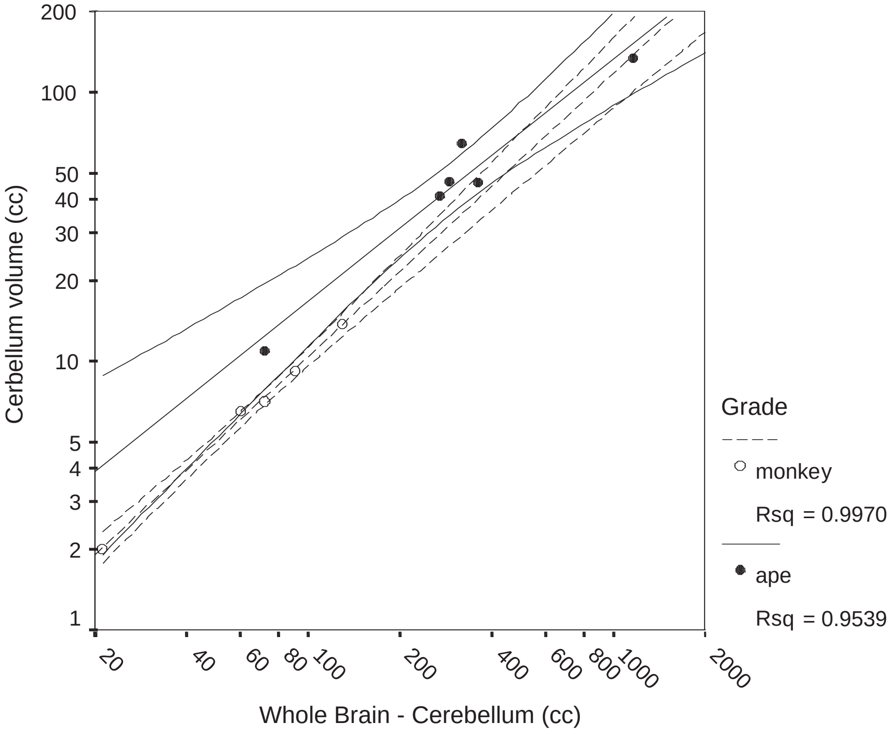
Another possibility to be considered is that selection on the primary sensorimotor cortices and cerebellum could have led to correlated expansion of the brain as a whole, as suggested by the developmental constraint hypothesis of Finlay & Darlington (1995). There is reason to be cautious in applying this hypothesis to the interpretation of the PET evidence, however. To begin with, the developmental constraint hypothesis predicts the same result (whole brain expansion) from selection on any given brain region or capacity. As Finlay & Darlington (1995: 1583) observe "theories that start from a primary behavioral trait appear to account

Figure 9A



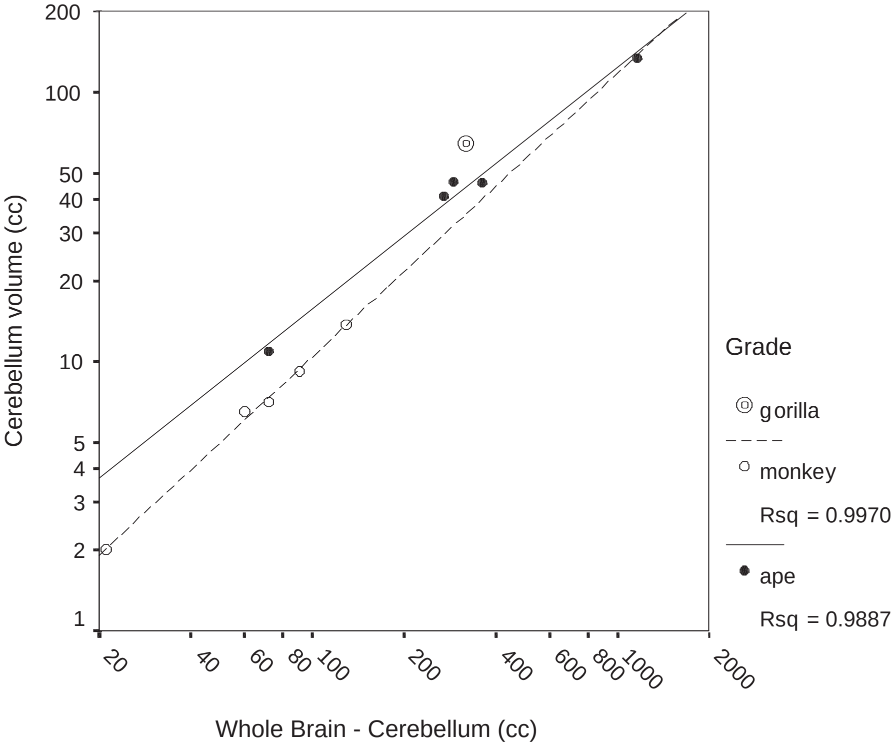
9A. ***Cerebellar scaling in monkeys and apes, excluding humans*** *(data from Rilling & Insel, 1998). When humans are excluded from the regression, it appears that apes and monkeys display similar cerebellar scaling relationships but different proportions, a classic grade shift. However, the ape trend depicted is entirely determined by the outlying gibbon value. Within the great apes, there is no significant trend (p = 0.683).*

Figure 9B



9B. ***Cerebellar scaling in monkeys and apes, including humans, with mean prediction lines (95% C.I.).*** *(data from Rilling & Insel, 1998). Inclusion of humans in the regression produces a shallower hominoid trend, but once again indicates that the only deviant hominoid value is the exceptionally large cerebellum of gorillas.*

Figure 9C



9C. ***Cerebellar scaling in monkeys and apes, excluding gorillas*** *(data from Rilling & Insel, 1998). Exclusion of the deviant gorilla value produces a very good allometric fit for the remaining hominoid species. This suggests (1) that gorillas have undergone an adaptive specialization in cerebellum size, (2) that hominoid cerebellar scaling relationships differ from those of monkeys, and (3) that humans have a cerebellum roughly the size predicted for a hominoid brain of human size.*

for human [brain] evolution many times over.” In theory, knapping-related demands on the cerebellum could have produced the overall brain enlargement seen in early *Homo*, yet the same effect might equally well have been produced by completely different demands on that or other structures. Although the PET evidence of cerebellar activation does confirm the plausibility of knapping-related contributions to overall brain expansion, the inherent equifinality of the constraint hypothesis effectively prevents any more concrete conclusions.

Unfortunately, things become even more complicated when it comes to interpreting knapping-related activations in the neocortex. This is because the constraint hypothesis was developed to explain covariance between major brain structures like neocortex and cerebellum rather than variation in the size of functional areas within neocortex. The possibility of evolution through cortical reorganization greatly complicates any hypothetical relationship between selection on any one cortical region (e.g. motor cortex) and overall neocortical or brain expansion.

As we have seen, the comparative data needed to conduct a rigorous investigation of variation within primate neocortex are simply not available. Nevertheless, it is clear that primary sensorimotor cortices have expanded far less during human evolution than have other cortical regions. The only way in which selection favoring relatively small expansions of sensorimotor cortex could have produced the much larger effects seen in association cortex would have been in the context of extremely rigid allometric constraints on cortical organization. For example, if association cortex necessarily scaled to sensorimotor cortex at an exponent of two, small increases in sensorimotor volume would produce disproportionate expansion of association cortex.

As evidence that such constraint might in fact exist, Finlay & Darlington (1995) cite the work of Nudo & Masterson (1990) indicating that the amount of cortex devoted to forelimb control across species (from “hooves to hands”) is highly predictable from total cortex volume. According to Finlay & Darlington (p. 1578), this “suggests that the amount of cortex devoted to forelimb control can increase only as the result of apparently inefficient increase in total cortex volume.” In this case, selection on primary sensorimotor cortex could hypothetically have led to more general neocortical (and correlated whole brain) expansion. Important support for this hypothesis would come from the identification of some mechanism or mechanisms accounting for such rigid constraint.

In their developmental constraint hypothesis, Finlay & Darlington (1995) propose that a highly conserved order of neurogenesis is the constraining mechanism underlying the covariation in size of major brain structures. In fact, it does seem that genetic modulation of the overall duration of neurogenesis is the most important mechanism governing the total size of the cortical sheet. There is no evidence, however, that developmental timing similarly influences the formation of functional fields (arealization) within the neocortex. Instead, cortical arealization is thought to be driven by the patterning of incoming thalamocortical projections, guided at a gross level by intrinsic gradients of cortical gene expression (Krubitzer & Huffman, 2000). Comparative evidence of sensory specializations in animals like echolocating bats and blind mole rats illustrates the way in which these mechanisms combine to produce a mammalian pattern of constrained overall cortical topography together with major adaptive variation in the size and number of cortical fields (Krubitzer & Huffman, 2000).

Evidence bearing on the development and evolution of cortical arealization comes almost exclusively from consideration of sensorimotor cortices. On the whole, these regions appear to adapt both readily and independently to changes in peripheral morphology and behavior (Krubitzer & Huffman, 2000). In primates, for example, the size of visual system structures (including striate cortex) has evolved in relative independence of other brain regions (Barton, 1998; Stout, 2001). It seems quite plausible that knapping related selective pressures on primary visual and motor cortices could have resulted in independent expansion of these regions. However, there is little evidence that it actually did.

Expansion of this kind would have been a “zero-sum” game: any expansion of primary sensorimotor cortices through cortical reorganization alone would have entailed commensurate decreases in the size of higher-order sensorimotor and associative cortices. There is no paleoneurological or comparative evidence indicating that such expansion of sensorimotor cortex at the expense of association areas occurred at any point during hominin evolution. In fact, the only proposed paleoneurological example of hominin cortical reorganization involves the exact opposite (Holloway, 1995). If, on the other hand, sensorimotor expansion were accomplished through a combination of overall expansion and adaptive arealization, then some correlated expansion of other cortical regions might possibly occur. One way this could happen would be if the total cortical expansion produced by the stochastic processes of natural selection happened to exceed the volume actually incorporated into sensorimotor cortices. Considering that each additional round of cell division during neurogenesis doubles the number of neurons ultimately produced, such an evolutionary “overshot” is not implausible.

It is also possible that cortical expansion, even if driven by selection on primary sensorimotor cortices, would favor the disproportionate growth of association cortex for functional reasons. Deacon (1997) has pointed out that, since the number of possible connections between neuron increases in geometric proportion to the number of neurons, increasingly large brains will tend to be less thoroughly integrated. As a result, Deacon argues, larger brains will need to devote increasingly more resources to integrative or “managementlike” functions, simply in order to maintain cohesion. Just as growing human organizations seem to require increasing proportions of managerial and administrative employees, cortical expansion might tend to favor disproportionate growth of intrinsic association cortex even if selective pressures were actually operating on extrinsic input/output capacity.

Microstructural Adaptation

Given the current state of knowledge in paleo- and comparative neurology, it is impossible to specify exactly how the neural demands of Oldowan knapping may have influenced hominin brain-size evolution. Even less is known about microstructural specializations in the human brain. In both cases, however, evidence from PET research directs our attention to the specific brain structures that would have been the most likely proximal targets of selection relating to Oldowan knapping.

Even at the current stage of analysis, PET evidence clearly reveals the demands placed on primary visual and motor cortices by Oldowan-style knapping. Results from the pilot study, while in need of further corroboration, also suggest involvement of neuronal fields associated with the dorsal "position and motion" stream of visual processing (Figure 3) in the superior parietal lobe. It should thus be of particular interest to human origins researchers that some of the best evidence of microstructural specialization in the human brain comes from primary visual cortex and appears to focus on the processing stream associated with motion sensitivity.

Working with the carefully sectioned and stained occipital lobes of 29 human and non-human primates, Preuss *et al.* (1999) found that humans display a unique arrangement of neurons and dendrites in layer 4A of primary visual cortex. The neurons involved are part of what is known as the "M-stream" of visual processing, a fast acting system with high contrast sensitivity (Livingstone & Hubel, 1988) that is particularly suited to motion perception. Prior to the work of Preuss and colleagues, the distribution of M-related neurons in V1 was known primarily from studies of macaques, which display a characteristic honeycomb pattern of M-tissue in layer 4A. Preuss *et al.* (1999) have now shown that, although the honeycomb pattern is shared by monkeys and apes, humans display a unique mesh-like architecture in layer 4A that results in a much greater representation of M-tissue.

Preuss and colleagues suggest that this derived characteristic of human visual cortex may represent an augmentation of the M-stream in humans, and furthermore that such augmentation would be consistent with reports indicating that humans are more sensitive to luminance contrasts than are macaques (De Valois *et al.*, 1974; Merrigan, 1980) and have M-related retinal ganglion cells with larger dendritic fields (Dacey & Petersen, 1992). Augmentation of the M-stream in human V1 would be particularly interesting in light of the PET evidence indicating the importance of this region during Oldowan-style knapping. A hominin M-stream specialization that acted to enhance motion perception could quite plausibly have contributed to the initial emergence of stone knapping or been part of an adaptive response to its later spread. If the knapping-related activation of extra-striate visual areas in the superior parietal lobe (i.e. the dorsal visual stream) is confirmed by further analysis, it will provide additional evidence of the critical role played by motion perception in Oldowan-style knapping. As noted by Preuss *et al.* (1999) specializations of primary visual cortex might be expected to have cascading effects on these higher levels of the visual system, which receive most of their input from V1.

It is remarkable that evidence of human microstructural specialization has come first from striate cortex, previously thought to be one of the best understood and most primitive regions of neocortex. This strongly suggests that further research will reveal similar specializations in other parts of the human cerebral cortex. In fact, Buxhoeveden *et al.* (2001) have already reported differences in cortical minicolumn size and morphology in the planum temporale region of human vs. non-human primates. These particular differences are not likely to be related to toolmaking in any direct fashion, but again highlight the need for further comparative research at the microstructural level.

Language

One final point to be considered is the relevance of the PET evidence to various "motor hypotheses" of language evolution (e.g. Greenfield, 1991; Calvin, 1983; Calvin, 1993; Wilkins & Wakefield, 1995). Although differing in particulars, these hypotheses generally posit that some form of neural overlap between tool behavior and language led to co-evolution of the two capacities. In the specific case of Oldowan-style knapping, however, the PET data have yet to provide convincing evidence of such overlap. More detailed consideration of the individual hypotheses offers some insight into what might be expected from further analysis and research.

The neo-Piagetian hypothesis of Greenfield (1991) focuses on the putative role of left ventral-lateral frontal cortex (i.e. Broca's area) in distributed neural circuits underlying both language and "hierarchical object combination". Greenfield posits that a Broca's area homologue present in a common ancestor of apes and humans was elaborated and differentiated during hominin evolution, producing two adjacent but functionally distinct sub-areas. It is an implication of the hypothesis that manual behaviors contributing to or enabled by this evolutionary differentiation should produce activation in the superior "manual object combination" sub-area.

Ideally, PET tests of Greenfield's hypothesis would seek to demonstrate the presence or absence of activation in this particular sub-area during various manual activities. This is made somewhat more difficult by the relatively low resolution of PET and by the fact that Greenfield does not specify the anatomical boundaries of the sub-areas she proposes. In pragmatic terms, almost any observed activation of Broca's area should probably be considered consistent with Greenfield's hypothesis. Currently available PET evidence fails to indicate such activation during Oldowan-style knapping. If these results are born out by further analysis, they will strongly suggest that Oldowan knapping did not play a major role (as cause or consequence) in the elaboration of distinct manual and language circuits within Broca's area. If additional PET research with a wider range of evolutionarily relevant tool behaviors similarly fails to produce evidence of Broca's area activation, then the hypothesis as a whole will be cast into doubt.

The "neurolinguistic preconditions" hypothesis of Wilkins & Wakefield (1995) does not lead to such concrete predictions about the recruitment of Broca's area during stone toolmaking. Unlike Greenfield's hypothesis, which envisions the evolutionary elaboration of a pre-existing Broca's area homologue, Wilkins & Wakefield propose that Broca's and Wernicke's language areas were "re-appropriated" from motor and somatosensory association cortices initially expanded in response to "selectional pressures for…the manufacture and/or use of stone tools (including throwing)" (p. 173). According to this scenario, modern patterns of activation in these re-appropriated cortices may no longer reflect their earlier evolutionary history.

Wilkins' and Wakefield's hypothesis is a specific application of the more general concept of correlated brain expansion, in which additional structure is thought to precede enhanced function (Finlay *et al.*, 2001: 277). In contrast to the developmental constraint hypothesis, however, Wilkins and Wakefield propose that correlated expansion occurred as a result of functional linkage between brain regions. This functional component makes their argument of evolutionary cause and effect at least somewhat testable using modern activation data. Strongest support for the hypothesis would come from evidence that motor and sensory association areas (especially the lateral premotor cortex bordering Broca's area and the inferior parietal cortex adjacent to Wernicke's area) are in fact activated during stone knapping. Such activation would confirm that these regions were likely targets for tool-related selective pressure, and would be consistent with the hypothesis that such selection yielded over-elaborated neural structures ripe for re-appropriation into evolving language circuits. On the other hand, compelling evidence that these regions are not recruited during stone tool behavior would falsify the proposed link. Although the PET evidence is currently equivocal regarding activation in these areas, further research and analysis should produce more concrete results.

Calvin's (1983, 1993) "neural sequencing" hypothesis of language evolution actually makes somewhat similar predictions about knapping-related activations, although for different reasons. The core of Calvin's argument is the contention that linear increases in the speed and accuracy of ballistic movements require exponential increases in the number of neurons recruited to control them. Since even the huge evolutionary increases in hominin brain size evident from the fossil record could not have kept pace with this geometric progression, the requisite neurons must be gained through "borrowing", with "the experts (probably the premotor cortex and the cerebellum) recruiting some temporary help from other brain regions" (1993: 248). Since Calvin "suspects" that such borrowing is easier in a juvenilized brain, he concludes that selection for neoteny was the driving force behind brain enlargement.

There are some important problems with Calvin's hypothesis as framed. These include the fact that the human brain is actually overdeveloped (peramorphic) rather than juvenilized (Gibson, 1991; McKinney, 2002) and that language is more meaningfully characterized as hierarchical in organization rather than sequential (Poeck & Huber, 1977). On the other hand, the basic point remains that the execution of fast and accurate movements is neurally demanding. Calvin's evolutionary scenario stresses throwing because of what he sees as its uniquely stringent neuromotor demands, yet effective stone knapping requires much the same precision. The PET evidence presented here directly confirms that Mode 1 knapping is unusually demanding of neuronal activation, although mostly within areas that might reasonably be characterized as visual or motor "specialists". There is no evidence of the more widespread neuronal "borrowing" envisioned by Calvin.

At this point, the PET evidence suggests only the most indirect of links between toolmaking and language evolution. Oldowan-style knapping is indeed associated with increased activation in large volumes of neocortex and cerebellum. It is quite possible that knapping-related pressures on these regions could have contributed to brain expansion that ultimately provided raw material for the later evolution of language circuits. This is a difficult hypothesis to test. On the other hand, there is no evidence that modern Mode 1 toolmaking and language processing rely upon similar neural substrates, a fact that argues against the existence of more direct co-evolutionary links between the two behaviors. This apparent lack of neural overlap also suggests that proposed structural similarities between language processing and tool behavior (e.g. Calvin, 1993; Greenfield, 1991; Reynolds, 1976; Wilkins & Wakefield, 1995) may be overstated (cf. Wynn, 1991; Graves, 1994).

SUMMARY AND CONCLUSIONS

Direct evidence regarding the evolution of the human brain and intelligence is notoriously difficult to come by. Brains do not fossilize, and fossil cranial endocasts can provide only limited evidence regarding brain size and macroscopic surface morphology. Archaeological evidence of behavior, though valuable, is subject to the vagaries of deposition, preservation and recovery, and requires careful interpretation. Experimental and comparative research in the modern world is thus essential in order to gain the maximum benefit from the available prehistoric evidence.

The PET evidence presented here, including results from the pilot study of Stout *et al.* (2000) and from ongoing follow-up research, is beginning to reveal the specific neural substrates of Oldowan-style stone knapping. The research was conducted with modern human subjects, but careful interpretation nevertheless yields important insights regarding pre-modern cognition and brain evolution. The ideal situation of imaging research with pre-modern hominin species will obviously remain impossible, although research with modern non-human primates may eventually provide a comparative perspective. For the time being, the modern human data provide at least one concrete reference point for the consideration of evolutionary questions.

There are two major ways in which this information may be applied in human evolutionary studies: (1) as evidence of the mental processes involved in stone knapping, and (2) as evidence of the potential targets of evolutionary selection on toolmaking skill. The former, "paleopsychological", approach is based on the assertion that similar behaviors require similar mental operations regardless of the specific cranial capacity or neural organization of the agent involved.

Paleopsychological Conclusions

Known associations between particular patterns of brain activation and particular kinds of experimental tasks make it possible to "read" activation patterns in terms of the mental task demands they reflect. As long as the issue of baseline brain function is properly considered, PET activation evidence may thus be used to provide a general psychological characterization of Mode 1 toolmaking. This leads to two major conclusions:

1. The PET evidence currently supports the prevailing archaeological view that Oldowan technology was cognitively simple. Activation evidence demonstrates the heavy recruitment of primary visual and motor areas during Mode 1 knapping, but remains equivocal regarding recruitment of secondary sensoimotor and association cortices. Final interpretation must await the completion of further analysis, but for the time being Mode 1 knapping seems best characterized as a relatively demanding visuomotor skill that is not particularly reliant upon internal representation or strategic planning.

2. The PET evidence does not indicate that Oldowan knapping was mentally trivial for its early practitioners. Ongoing baseline activity of the modern human brain may be concealing low level planning and problem solving requirements that would have been more taxing for smaller-brained Oldowan hominins. More fundamentally, the mental significance of visuo-motor skill itself should not be underestimated. Although mainstream views of cognition tend to privilege abstract internal representation as the hallmark of intelligence, ecological psychologists call our attention to the intelligence embodied in effective action. Fine-grained perception and flexible performance are as integral to human mentality as are more internally directed cognitive behaviors. Oldowan artifacts, when evaluated in light of the PET data, provide the earliest concrete evidence of intelligent behaviors more demanding than those that might be assumed in the common ancestor of humans and African apes.

Evolutionary Implications

The second major application of the PET data is in the generation of evolutionary hypotheses. The visuomotor demands of Mode 1 toolmaking are embodied in large volumes of knapping-related activation in sensorimotor cortices and the cerebellum, and these activations serve to highlight what would have been the most likely neural targets of selection acting on Oldowan toolmaking skill. Additional archaeological, paleoneurological and comparative evidence will be needed in order to determine whether neural adaptations to facilitate toolmaking skill acquisition actually occurred, but the PET evidence at least tells us where in the brain to look.

More particular evolutionary assessment of the PET evidence depends on which model of mammalian brain evolution is employed. Three such models may be considered:

1. In the case of a predominantly mosaic pattern of evolution, we might expect that those brain regions most heavily taxed by knapping activities would experience preferential expansion. There is little evidence that this has occurred. With the exception of the cerebellum, the volumes of most intense activation appear to be located in primary sensorimotor regions that have undergone relatively little expansion during human evolution. These regions, and particularly the occipital visual cortices, may have undergone some limited enlargement that was outpaced by greater expansion elsewhere, but it does not currently appear that the distributed network of structures associated with Mode 1 knapping was a major focus for mosaic brain enlargement. This preliminary conclusion may change as continuing analysis reveals additional regions of knapping-related activation, but the available evidence makes it clear that any perceived relationship between Oldowan knapping and regional brain expansion will be a relatively complex one.

2. Developmental and functional constraint models of brain evolution do suggest ways in which selection on knapping skill might have led to observed patterns of human brain expansion, but these scenarios are not currently falsifiable. According to the developmental constraint hypothesis of Finlay & Darlington (1995), selection on the size of one brain structure may be expected to produce coordinated enlargement of the whole brain. Alternatively, the information management demands attending localized sensorimotor enlargements might require disproportionate expansion of association cortex simply in order to maintain functional integration (Deacon, 1997). In either case, modest expansion of one or more of the structures supporting knapping behavior could plausibly have contributed to the broader pattern of brain enlargement seen in human evolution. In theory, such correlated expansion could also have produced neural precursors ripe for re-appropriation into evolving language circuits (Wilkins & Wakefield, 1995).

3. Finally, there is the possibility of microstructural adaptation. Although comparative research at the microstructural level is only just beginning, human specialization in primary visual cortex organization had already been documented (Preuss *et al.*, 1999). This is particularly interesting considering that some of the strongest activation observed during Oldowan-style knapping was in the primary and secondary visual cortices of the occipital lobe. The primary visual specialization reported by Preuss and colleagues specifically involves the "M-stream" of visual processing, commonly associated with motion perception and known to have strong outputs to the dorsal "position and motion" pathway in the superior parietal lobe. It will be especially interesting to see if further analysis bears out the preliminary indications of knapping-related superior parietal activation observed so far. As Preuss and colleagues point out, the microstructural reorganization of primary visual cortex is likely to have had cascading effects on such downstream visual processing areas. For the time being, it is reasonable to conjecture that M-stream adaptations in hominin primary visual cortex may have facilitated the initial invention(s) of Oldowan technology and/or been selected for in response to its later spread.

Conclusion

Although still preliminary at this stage, results from PET investigations of Mode 1 stone knapping offer tantalizing insights into the paleopsychological and neuro-evolutionary significance of the earliest stone tools. The experimental methods developed also offer exciting opportunities for the future. Research with non-human primates and investigation of more sophisticated bifacial and prepared-core technologies are two particularly interesting directions to be pursued. PET is a valuable new research tool for human origins studies and promises to add an important empirical dimension to inquiries regarding the evolution of the human brain and mind.

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