Chapter 18

Neural Foundations of Perception and Action in Stone Knapping

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Conventional archaeological, ethological and psychological approaches to understanding the origins and evolution of human tool use employ a representational perspective that emphasizes underlying cognitive mechanisms rather than overt performance. This perspective has yielded important progress in understanding the conceptual foundations of tool use and in revealing the impressive mental capacities of non-human primates, but does not address the full range of mental behaviours involved in effective action in the real world. This has led to an underestimation of the uniqueness and potential evolutionary significance of early (Oldowan) stone knapping. A perception–action approach to tool use instead emphasizes the dynamic activity of the organism-plus-environment system, investigated through the detailed empirical observation of real world behaviour. Recent (Stout et al. *2000) and ongoing experimental work using Positron Emission Tomography (PET) to examine brain activation during simple Mode I or 'Oldowan-style' stone knapping provides an excellent opportunity to explore the application of this perspective in human evolutionary studies. PET provides concrete information about task-related brain activity on an intermediate spatial and temporal scale that is useful in forging a link between dynamic behavioural processes and the (relatively) static anatomical substrates that are the medium of biological evolution. Preliminary results from this research corroborate the conceptual simplicity of Mode I knapping, but reveal the unusually demanding perceptual-motor processes involved.*

The production of knapped stone artefacts has traditionally been viewed as a uniquely hominin behaviour that exerted a major formative influence in human evolution (Oakley 1954; Washburn 1960; Leakey *et al.* 1964). More recently, however, a growing appreciation of the tool-making and tool-using capacities of modern non-human primates (Goodall 1964; Boesch & Boesch 1990; McGrew 1992; Schick *et al.* 1999), together with a reassessment of the technical sophistication of early stone tools (Toth 1985), has led many to conclude that 'toolmaking *per se* cannot have constituted the main "adaptive wedge" driving the evolution of hands, brains and behaviour in early *Homo*' (Potts 1993).

On the other hand, the intuitive conviction that stone knapping is somehow special remains hard to dismiss. After all, hominins are the only animals ever to have engaged in this behaviour in a natural setting. Can it be that this uniquely hominin behaviour is merely a 'variation on the theme' of an ape adaptive grade (Wynn & McGrew 1989, 384)? The way in which this question is answered depends quite a bit on the theoretical perspective that is adopted. This chapter explores the potential application of a *perception–action* perspective to the question of stone knapping in human evolution, especially in relation to recent functional brain-imaging research (Stout *et al.* 2000) on the subject.

The 'representational' perspective

Archaeologists and primatologists considering the psychological implications of tool behaviour commonly adopt a *representational* approach to cognition. In this view, cognition is an abstract, internal construction of the brain, much like the computation carried out by a digital computer. Actual sensation and action are seen as little more than peripheral input/output channels for the mental work carried out by the 'central processing unit'.

Informed by this representational view of mind, Palaeolithic archaeologists have commonly defined the sophistication of lithic technologies in terms of the abstract mental (Clark 1996) or procedural (Gowlett 1984) 'templates' needed to achieve the 'imposition of arbitrary form' (Holloway 1969) during tool production. Comparative investigations of primate tool use similarly focus on the issue of 'causal understanding' and the mental representation it is thought to imply (Tomasello & Call 1997). In fact, mental representation is the primary criterion used by Parker & Gibson (1977) to define 'intelligent' tool use.

The representational perspective tends to produce an essentialist view of tool behaviour. For example, McGrew (1992) uses the taxonomies of Beck (1980) and Oswalt (1976) to describe tool manufacture in terms of abstract *operational features* like *detachment*, *conjunction*, and *reduction*. Other researchers (Chevalier-Skolnikoff 1983; Poti 1996; Parker & Mckinney 1999) use (neo)Piagetian developmental stages to provide similarly abstract descriptions. In each case, the descriptive categories are intended to capture the essential cognitive (computational) operations underlying superficially variable tool-making behaviours.

From this perspective, Oldowan knapping and ape tool behaviour are quite similar. However, it might be argued that an exclusive focus on cognitive 'essence' tends to gloss over important differences in the actual performance of tool behaviours. Although valuable, the representational perspective on tool use does not exhaust the range of psychologically-meaningful comparisons to be made.

The 'perception–action' perspective

One way to more fully explore the range of such comparisons is to adopt an alternative, *perception–action* perspective on stone knapping. This perspective, which finds its origins in the ecological perception theory of Gibson (1950; 1979) and the dynamic biomechanics of Bernstein (1967; 1996), seeks to 'ground' psychological theory in real-world situations and behaviours, and views variability as a primary focus of study rather than as an undesirable source of 'noise' (Reed & Bril 1996).

In the representational paradigm, variable real-world behaviours are merely imperfect reflections of an essential world of formal cognitive operations. In contrast, the perception–action perspective sees cognition as concretely embodied in performance. In this view, perception and action are not simply peripheral input/output channels, but are themselves the stuff of which cognition is made.

The perception–action perspective has been applied to the problem of tool behaviour by a number of researchers (e.g. Smitsman 1997; Lockman 2000; Bongers 2001). In this body of work, the fundamentally-interesting property of a tool is not its representation by some kind of 'causal understanding' but rather its potential to alter the possibilities for action in an environment. What is unique about tools is that they alter environmental possibilities (*affordances*) by changing the properties of an organism's effectors (*effectivities*). Because tools allow actors to modify affordance–effectivity relationships (Bongers 2001), the foundations of tool use lie in the ability to detect the action possibilities afforded by relations between objects (Lockman 2000). What separates this ecological view from a typical representational account is that the detection of such affordances is considered to occur on the basis of environmental information that is directly perceptible rather than internally constructed.

A perception–action perspective sees tool-using capabilities and understanding as arising dynamically from experience rather than devolving from an abstract internal system of formal cognitive computations. Although the broader implications of the dynamical paradigm for cognitive science remain controversial (e.g. Bechtel 1998; Dennett 1993; van Gelder 1998) this approach has much to recommend it in the particular case of stone knapping.

Many archaeologists have noted the perceptual-motor skill evident in the earliest stone tools (Ludwig & Harris 1998; Semaw 2000; Ambrose 2001). As suggested by Bril *et al.* (this volume; Roux & David this volume) the uniqueness of Oldowan technology may be embodied more in the sophistication of the elementary knapping gestures employed than in the presence of abstract spatial and procedural representations. Work with the stone-bead knappers of Cambay (Roux *et al.* 1995; Bril *et al.* 2000) reveals that, in practice, mastery of the forces involved in individual flake removals is an essential pre-requisite for the emergence of effective knapping plans. Such plans are not abstract and inflexible templates imposed from above, but rather outgrowths from a practical understanding (*savior-faire*) of knapping processes and potentials.

This understanding arises, not from abstract Euclidean representations or formal computational procedures, but from direct experiential knowledge of flaking dynamics. In other words, it arises from the acquired ability to perceive relevant affordances.

Perception and action in human evolutionary studies

Despite the overall theoretical suitability of a perception-action approach to stone-tool making and use, there are two major difficulties to be overcome in its application to human-evolutionary studies. To begin with, there is the nature of the Palaeolithic archaeological record itself. The modified stones and bones that constitute Early Stone Age (ESA) archaeological sites present only static and isolated glimpses of behaviour. In stark contrast, the perception–action approach requires detailed, real-time observations of behaviour in its natural context.

The solution is actualistic research in the modern world. Although the complexities and pitfalls of argument by analogy must be respected, the actualistic approach provides the researcher with relevant phenomena that may be observed and manipulated in real-time. Actualistic research with stone tools promises insight into the ways in which stone knapping is situated within real-world social and cultural contexts (Stout 2002; this volume), as well as into the behavioural dynamics (Roux *et al.* 1995; Bril *et al.* 2000) and neural (Stout *et al.* 2000) and somatic (Marzke *et al.* 1998) substrates of stone-knapping skill.

The second major obstacle in applying a perception–action perspective to human-evolutionary studies arises from a perceived conflict between dynamic and structural modes of explanation. Human origins researchers are primarily concerned with understanding human 'biocultural' evolution, a process in which 'behaviour and structure form an interacting complex, with change in one affecting the other' (Washburn 1960). Those specifically interested in cognition focus on the evolutionary relationships between hominin behaviour and brain structure (especially size). In contrast, students of modern human perception and action seek dynamic explanations of behaviour and its development in individuals. The emphasis is on understanding the way in which the system changes over time and how its various states relate to each other, rather than describing the internal structure that defines any one particular state (van Gelder 1998).

The problem is that, while human-origins researchers need mechanistic, structural explanations in order to understand how behaviour relates to biological evolution, perception–action theorists operate at the more holistic level of dynamic organization. Fortunately, and despite a superficial 'appearance of tension', these two levels of explanation are actually complementary (Bechtel 1998). The trick lies in recognizing the causal relationships between levels (Fig. 18.1). Although this task is far from accomplished, Thelen & Smith (1994) advocate Edelman's (1987; 1989) Theory of Neuronal Group Selection (TNGS) as an important step in the right direction.

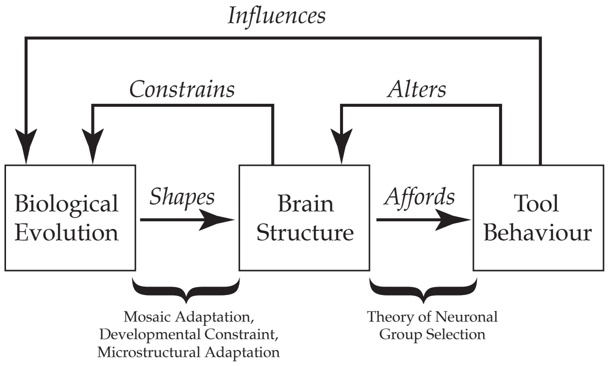

Figure 18.1. *Analytical levels and relationships in the evolution of tool behaviour (flow chart of interacting levels).*

Theoretical integration

The TNGS differs from many more conventional descriptions of brain function in its emphasis on dynamic patterns of neuronal activity rather than static, anatomically-defined neuronal networks. Nevertheless, it recognizes that neuroanatomical structure, itself a product of dynamic developmental processes, is an essential substrate:

> the brains of richly endowed organisms show a structure unique among all known physical objects … Even in biological systems such as jungles or food webs, where complex parallel dynamics occur in the exchange of signals, comparable *preexisting* structural pathways of this type cannot be found. (Edelman 1989, 64).

This preexisting structure results from the action of evolved developmental processes in a particular ontogenetic environment. Although the complexities of these evolutionary, structural and functional relationships (Fig. 18.1) can be daunting, the TNGS nevertheless points toward ways in which palaeoanthropological interest in evolving brain structure might be integrated with psychological perspectives on the dynamics of perception and action.

Positron emission tomography as a research tool in human origins

The functional brain-imaging technique of Positron Emission Tomography (PET) offers unique opportunities for human-origins researchers to examine the patterns of neuronal activity associated with evolutionarily-significant behaviours. It is exactly the kind of actualistic research tool that is needed to facilitate the application of perception–action perspectives in human-evolutionary studies. Although the temporal resolution of PET is not such that it can reveal the fine-grained dynamics of neuronal activation (Segalowitz 2000) during knapping, it can reveal global patterns. This is an important beginning in the attempt to relate structure and process in an evolutionarily meaningful way.

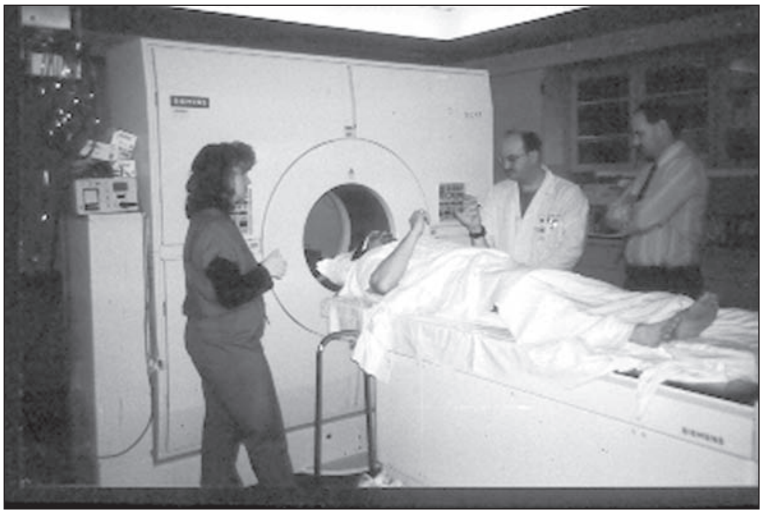

Figure 18.2. *Subject from pilot study.*

Table 18.1. *Knapping-related activations from the pilot study (Stout* et al. *2000).*

Location no.	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	6948	5.75
2			right	–30, –53, 61	1948	5.16
3	Central sulcus (Brodmann Areas 1 & 4)	Primary motor and somatosensory processing	left	33, –26, 52	8042	5.24
4	Postcentral gyrus (Brodmann Area 1)	Primary somatosensory processing	right	–39, –26, 56	5889	5.10
5	Cerebellum (hemisphere)	Motor planning and initiation	left	10, –37, –18	1002	5.22
6			right	–37, –51, –25	604	4.82
7	Cerebellum (vermis)	Motor coordination	right	–3, –53, –9	1082	5.07
8	Fusiform gyrus (Brodmann Area 37)	Ventral 'what' visual pathway	right	–24, –53, –9	1287	5.05

PET experimental design and interpretation

The immediate objective of PET research is to identify the patterns of brain activation that are associated with particular behaviours. PET images can provide this information, but must be properly interpreted in light of the effects of background or *baseline* (Gusnard & Raichle 2001) brain activity. In living subjects, neuronal activity is obviously ongoing throughout the brain at any given time. What researchers are really interested in is the way in which this pattern of activity changes during behaviour. For this reason, PET images collected during an experimental task are always compared with images collected during a control condition. It is the statistically-significant differences (*activations*) revealed by these image *subtractions* that are actually interpreted.

The meaning of brain activations thus depends as much on the nature of the control condition as it does on the experimental task itself. In a typical PET experiment, a control task is designed that replicates the experimental task as closely as possible, excepting only those narrowly-defined aspects of behaviour that are under investigation. This is done in order to isolate changes in activation patterns that are specific to the behaviour of interest.

The PET research

The pilot study

In February of 1997 a single-subject pilot study was performed in order to more concretely assess the utility of PET as a research tool in 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.

Methods

In the pilot study an $H_2^{15}O$ water tracer[1] was used in order to examine patterns of brain activation during simple (Mode I or 'Oldowan-style')

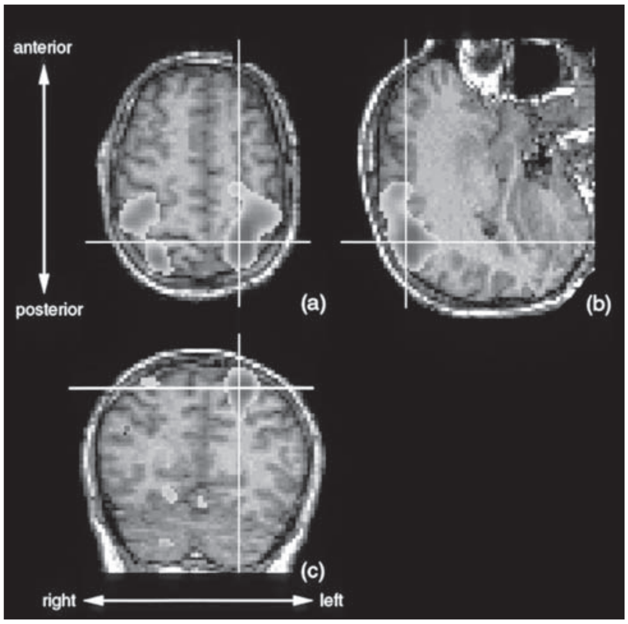

Figure 18.3. *Activation of pericentral cortex in the pilot study (Stout* et al. *2000).*

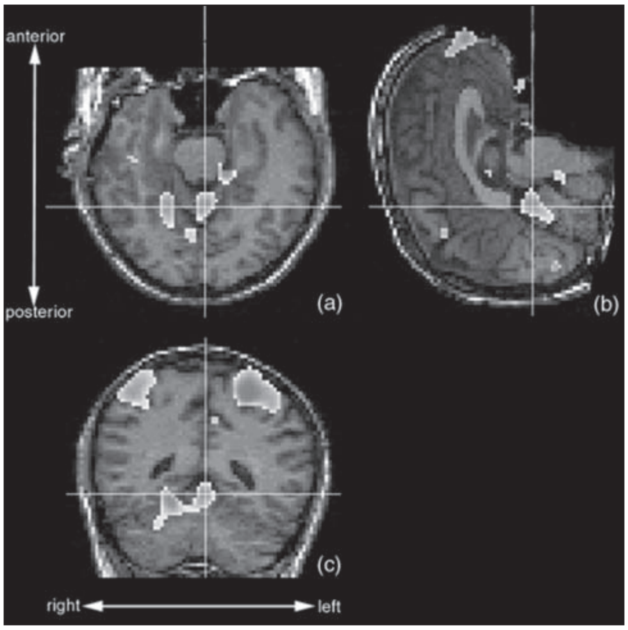

Figure 18.4. *Activation of cerebellum in the pilot study (Stout* et al. *2000).*

flake production. The subject of the study was Nicholas Toth, an experienced Palaeolithic archaeologist and experimental stone knapper with over 20 years knapping experience. Results of the pilot study should thus be viewed in light of the subject's prior experience and may not reflect the brain activation that would occur in less-experienced subjects performing the same tasks.

As described by (Stout *et al.* 2000), activation images were collected using a Siemens 951/31R whole body PET scanner. Due to the relatively short half-life of ^{15}O, all experimental tasks were performed with the subject lying prone on the scanner bed (Fig. 18.2). The control task consisted of the subject visually focusing on a roughly spherical cobble held aloft using both hands. This condition was intended to reflect a normal, baseline state of brain activation, including visual stimulation. 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. The knapping task consisted of the (right-handed) subject removing flakes from a core held in the left hand using a hammerstone held in the right hand. Because image data were being collected during actual task performance, movement of the subject's head had to be minimized. For this reason, knapping was done at approximately 'half-strength'. Despite this, flakes were removed from the core.

Pilot results

Subtraction of the control task from the knapping task revealed large volumes of significant activation during knapping. For convenience, the results of the Region of Interest (ROI) analysis reported in Stout *et al.* (2000) are re-presented here in Table 18.1. As these results show, knapping-related activations are centred in the primary motor and somatosensory cortices surrounding the central sulcus, the superior parietal lobule, the cerebellum and the fusiform gyrus of the right inferior temporal lobe.

More qualitative examination of the images reveals a large contiguous volume of activation in the left cerebral hemisphere, extending from the posterior parietal to the anterior bank of the central sulcus (Fig. 18.3). A similar pattern is visible in the right parietal, although the generally lower level of activation yields a clear separation between the anterior (peri-central) and posterior (superior parietal) volumes. In the cerebellum (Fig. 18.4), activation may be seen in the central vermis and in both hemispheres. There is a small volume of activation in the right fusiform (Fig. 18.3) but, as noted by Stout *et al.* (2000), caution is required in interpreting the more marginal results from this single subject study. With the exception of the fusiform gyrus, activation in all of these regions is of consistently greater significance/extent in the left hemisphere compared with the right. In general terms, the activations observed in the pilot study suggest that the brain structures most active during Mode I stone knapping are those associated with visuomotor performance rather than more internally-directed mental behaviours like imagery or planning.

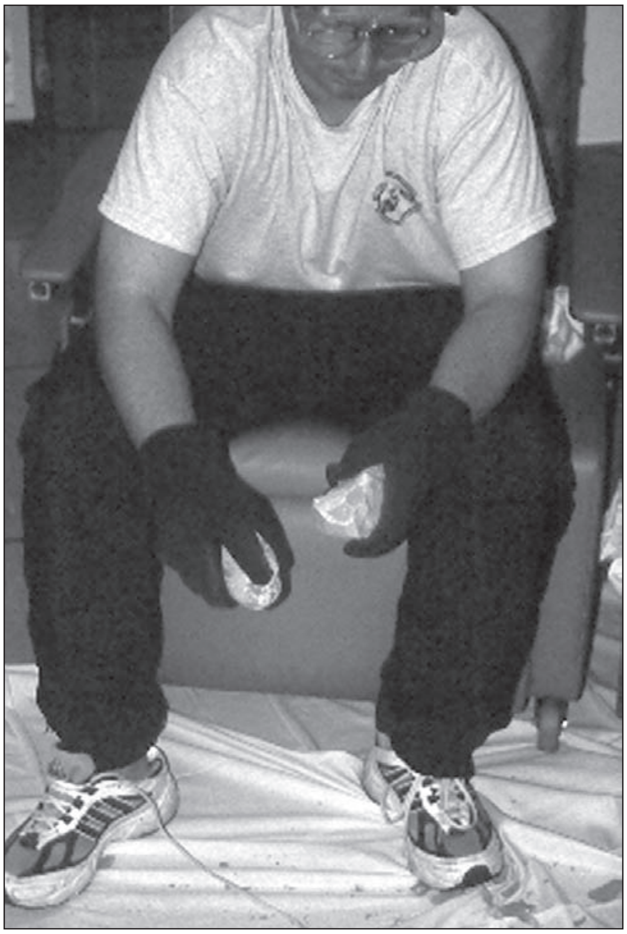

Figure 18.5. *Subject in FDG study.*

Ongoing research

Results from the pilot study may now be augmented through comparison with preliminary results from the ongoing follow-up research. This research effects an increase in sample size (*n* = 6) as well a number of other important methodological improvements. Although the image data from the follow-up research are still being analyzed, sufficient work has been done for a preliminary, qualitative assessment and comparison with the pilot study.

Methodological improvements

The major achievement of the pilot study was to demonstrate the utility and practicality of PET as a research tool in human origins. The study also provided a valuable opportunity to develop and refine research methods for use in follow-up research.

In the pilot study, a relatively 'minimalistic' control task (visual inspection) was used. Happily, the results obtained were sufficiently robust as to encourage the use of more elaborate control tasks in follow-up research. By using control tasks that more closely approximate the experimental knapping task, it should be possible to more narrowly define neural demands specific to knapping. In the ongoing follow-up research, the control task consisted of striking together two cobbles without attempting to produce flakes. This activity involved vigorous physical activity and visual guidance closely analogous, but not identical, to that involved in stone knapping.

Also important in isolating the specific neural demands of stone knapping is selection of an appropriate radionuclide tracer. The use in the pilot study of $H_2{}^{15}O$, with its relatively short half-life, required that all task be performed within confines of the scanner (Fig. 18.2). As a result, the subject was in an unnatural position (prone) and had to minimize the vigorous movements that are a natural part of knapping. Both of these factors could easily affect the neural demands of the task. Furthermore, the limited timeframe and physical constraints of the scanning situation did not allow for the unfolding of a natural knapping plan, which might (hypothetically) involve multiple generations of contingent flake removals.

In the follow-up research, the more slowly decaying glucose analog FDG (^{18}flouro-2-deoxyglucose) was employed. This tracer is taken up by metabolically active neurons over a period of 40 minutes, after which time its distribution in the brain is 'fixed' and may be imaged at any point until the isotope decays. Thus, images are collected of an activity *after* it is completed. Although the use of FDG further decreases the temporal resolution of PET to 40 minutes, it allows for much more naturalistic task conditions. Thus, experimental subjects in the follow-up research performed control and experimental knapping tasks comfortably seated in a chair (Fig. 18.5), and were able to engage in a full range of knapping actions, from core and hammerstone selection to full-force percussion and (potentially) exhaustive core reduction. The images produced indicate the time-averaged neuronal demands of sustained knapping activity in a naturalistic setting. Insofar as this experimental arrangement better reflects knapping as an everyday human activity, an additional level of ecological validity is achieved.

Preliminary results

Despite the substantial differences in experimental design outlined above, preliminary evaluation of results from the follow-up research largely corroborates the findings of the pilot study. Bilateral activation of the primary somatosensory and motor cortex surrounding the central sulcus and of the cerebellar hemispheres is clearly evident. Somewhat less intense bilateral activation of the superior parietal lobule also appears to be present, but will need to be confirmed in more thorough analysis. The follow-up research thus provides at least provisional corroboration for all of the major knapping-related activations observed in the pilot study. More conclusive evaluation of the anterior extent of activation into the secondary motor areas of the frontal lobe, as well as of possible activations elsewhere in the cerebrum, will have to await further analysis.

One striking divergence of the follow-up results from those of the pilot study is, however, readily apparent. This is the robust and extensive activation of occipital visual cortices. The activation clearly encompasses the primary (striate) visual cortex (V1) surrounding the calcharine fissure and likely extends into the secondary visual cortices (V2, V3, V4 and V5) of Brodmann's area 19. The exact reason underlying this major difference between pilot and follow-up results is not clear, but the strong activation of the occipital evident from the improved sample size and experimental conditions of the follow-up research nevertheless provides powerful evidence of its involvement in supporting knapping activity.

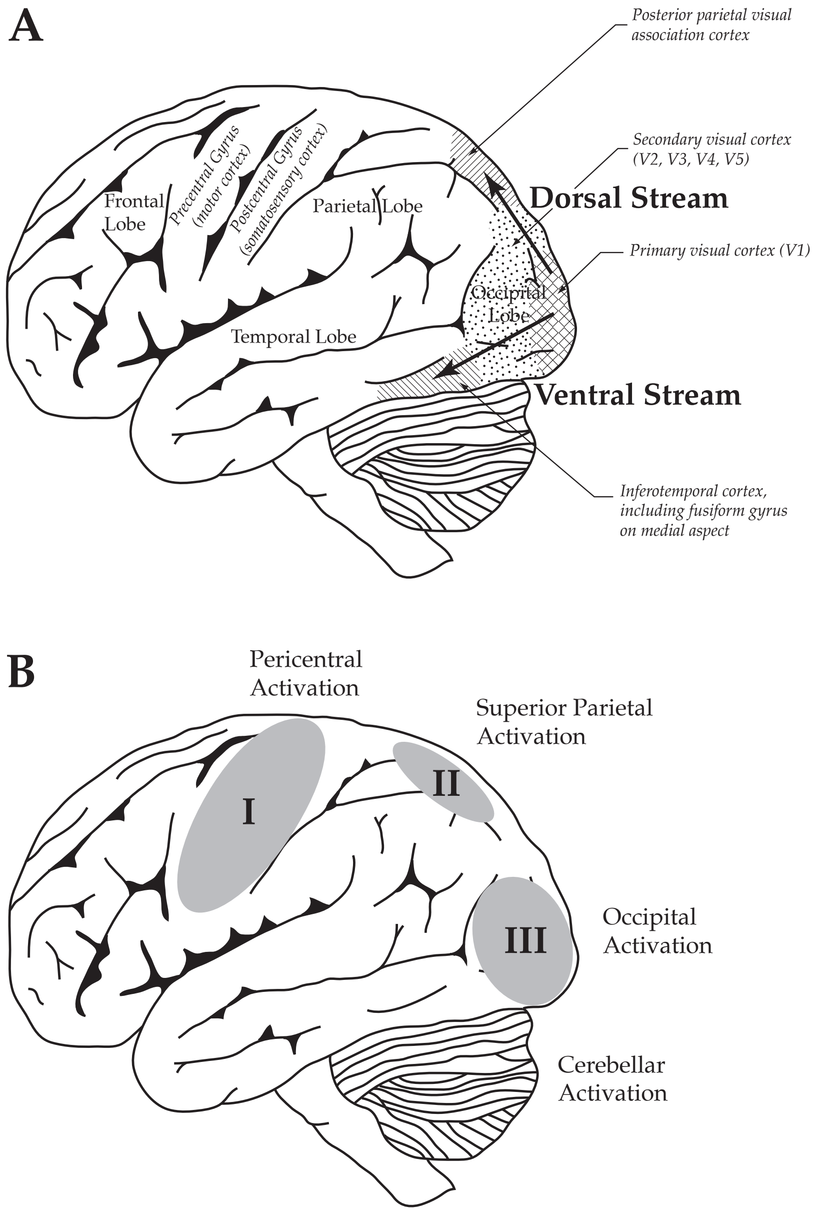

Figure 18.6. *Knapping-related activations and relevant functional neuroanatomy.*

Functional interpretation

Taken together, the pilot and preliminary follow-up results reveal those large-scale neuroanatomical structures that are exceptionally active during stone knapping. Ongoing analysis will ultimately refine this course-grained picture, and will most likely implicate additional structures. For the time being, however, it is safe to say that stone knapping involves activation of a network of structures commonly associated with visuomotor performance. This network extends in cerebral cortex from at least the primary motor cortex (M1) of the precentral gyrus, posteriorally through the primary somatosensory cortex (S1) of the postcentral gyrus and the polymodal cortex (Roland 1993) of the superior parietal lobule, to the primary and secondary visual cortices of the occipital lobe (Fig. 18.6). It also includes the sub-cortical cerebellar hemispheres and vermis. Involvement of the 'remote' visual cortex of the inferotemporal fusiform gyrus remains equivocal at present.

Dynamic cognition and functional localization

These activation data provide a static 'snapshot' view of brain activity during stone knapping. There is the danger, as Segalowitz (2000, 164) points out, that 'by focusing on average activation values, we are prone to the classic error in neuropsychology theory … of simply attributing complex cognitive processes to "centers" rather than dynamic parallel networks'. In fact, the dynamical hypothesis in cognitive science stipulates that mental behaviour is embodied in the continuous evolution of states through time rather than in 'simple transformations of static structures' (van Gelder 1998, 621). In Edelman's (1987) *Theory of Neuronal Groups Selection (TNGS)*, mental functions like categorization and memory are achieved through population-level correlations in the activity of dynamically-variable groups of neurons. They do not arise from the passage of signals along fixed neuronal networks. Nevertheless, the modal structure and organization evident in larger-scale brain regions is an essential substrate.

It is at this larger spatial and temporal scale that PET images provide insight. PET images do not explain *how* neuronal activity contributes to mental behaviour, but they do indicate *where* this activity takes place. To study behaviour using the static images of PET is not necessarily to reduce complex process to simple anatomy, it is merely to focus on a particular level of spatiotemporal organization. To put it bluntly, 'Neuropsychology is not a danger to ecological psychology' (Pickering 2001, 148). The level at which PET works may or may not be the appropriate one to address particular psychological questions, but it is well suited for use in human-evolutionary studies.

The neuropsychology of stone knapping

One way in which PET evidence may be used in human origins research is to provide a general neuropsychological characterization of stone knapping behaviour. As shown in Figure 18.6, currently available imaging evidence indicates that Mode I or Oldowan-style stone knapping is associated with activation in the four main areas: 1) pericentral cortex; 2) the superior parietal lobule; 3) the occipital lobe; and 4) the cerebellum. The first three of these are components of the *dorsal stream* of cortical visuomotor control (Milner & Goodale 1995), while the cerebellum is a classic subcortical motor structure. Considered individually, each of these regions or structures is well known for its association with perceptual-motor action.

Pericentral cortex

The 'pericentral' cortex surrounding the central sulcus includes the primary motor cortex (M1) of the precentral gyrus and the primary somatosensory cortex (S1) of the postcentral gyrus. M1 is commonly considered to be a motor 'output' structure responsible for the execution of movement. M1 receives afferent stimulation from diverse brain regions, including S1, frontal 'motor planning' areas, thalamus and cerebellum. In turn, it sends efferent impulses directly to the motoneurons of the spinal cord. In this way, neuronal activity in M1 is tightly coupled with movements of the limbs. In fact, the seminal work of Georgopoulos and colleagues (1982; 1984; Brown *et al.* 1989) has demonstrated the relationship between population-level neuronal activity in M1 and the direction of limb movements. More recent work (Pascual-Leone *et al.* 1994; Sanes & Donoghue 2000) has also begun to reveal the dynamic reorganization of somatotopic neuronal groups in M1 that occurs during motor learning. The elevated activity in M1 during knapping as compared to simple percussion likely reflects the demands of mapping the faster and more accurate actions involved.

Like M1, primary somatosensory cortex (S1) is characterized by relatively direct connections to the somatic periphery. Neurons in S1 receive afferent connections from the ventral posterior lateral (VPL) nucleus of the thalamus, a relay nucleus for impulses from the sensory receptors of the skin and joints. Thus it is not surprising to find that S1 is activated during vibration of the fingers (Fox & Applegate 1988), tactile shape discrimination (Roland 1985) and movements in extra personal space (Roland *et al.* 1980). The coactivation of S1 and M1 during knapping illustrates the general indivisibility of perception from action in *ecologically valid* (Kotchoubey 2001) behaviour, as well as the exceptional sensorimotor demands of the knapping task.

Superior parietal lobule

Activation of the superior parietal lobule is a particularly interesting result of the PET research. This region consists of *polymodal* association cortex, and supports mappings between diverse visual, somatosensory, auditory, vestibular and motivational signals. Anatomically, this region differs from primary sensorimotor regions in that it is dominated by intracortical, rather than subcortical or peripheral, connections.

The superior parietal lobule includes Brodmann's areas 5 and 7. Area 5 receives major afferent connections from neighbouring somatosensory cortex in the postcentral gyrus, as well as the vestibular (balance and orientation) system, the premotor areas of the frontal lobe, and the limbic (motivation and emotion) system (Kandel *et al.* 1991). It sends efferent connections back to the premotor cortices as well as on to the more posterior area 7. Area 7, in addition to receiving inputs from area 5, is reciprocally connected with the visual cortices of the occipital lobe and receives afferent connections from the auditory cortex of Brodmann's area 22 in the superior temporal gyrus. Area 7 sends efferent fibers to the frontal premotor cortices and to the cerebellar hemispheres. As a result of these connectional arrangements, the superior parietal lobule is a critical anatomical substrate supporting the dynamic coupling between multiple modes of sensory perception and motor action. Its heightened activation during Oldowan-style stone knapping clearly reflects on the complexity and elaboration of the polymodal mappings involved in the perception-through-action of knapping-related affordances.

Occipital lobe

The occipital lobe is composed of the primary (V1) and secondary (V2, V3, V4 & V5) visual cortices of Brodmann's areas 17, 18 and 19. V1 receives signals from the retina via the lateral geniculate nucleus and shares major reciprocal connections with the secondary visual cortices. These 'higher order' visual areas are massively interconnected both amongst themselves and with the more remote visual areas of the superior parietal and inferior temporal.

According to Edelman's (1989) Reentrant Cortical Integration (RCI) model of vision, reentrant mapping between these thoroughly interconnected regions integrates various visual attributes to produce basic perceptual phenomena like the recognition of contours. Conventional computational accounts similarly emphasize the role of the occipital cortices in creating representations of the fundamental components of visual stimuli, including colour, edges, orientation and motion. Increased occipital activity during stone knapping results from the focused visual attention required by the task (Brefczynski & DeYoe 1999), and reflects the sensitive dependence of this behaviour on details of the visual environment.

Cerebellum

The cerebellum consists of three main functional divisions, the *vestibulocerebellum*, *spinocerebellum* and *cerebrocerebellum*. Of these, the spinocerebellum and cerebrocerebellum are clearly activated during stone knapping. The centrally-located spinocerebellum receives most of its input from the spinal cord, and sends efferent fibers via two deep cerebellar nuclei (fastigial and interposed) to the descending motor pathways of the brain stem. This spino-cerebellar loop allows for detailed mapping between cerebellar activity and ongoing movement. The spinocerebellum also sends signals via the thalamus to primary motor cortex, allowing for integration at multiple levels. Activity in the spinocerebellum is thought to be linked to muscle tone and the smooth execution of movement (Kandel *et al.* 1991).

The cerebrocerebellum includes the lateral portions of the cerebellar hemispheres and is reciprocally connected with large areas of cerebral cortex, including premotor, motor, somatosensory and posterior parietal regions. It is thought to play an important role in the precise timing of complex multi-joint movements (Kandel *et al.* 1991).

Edelman (1989), on the other hand, characterizes the cerebellum as an 'organ of succession' responsible for the temporal coordination of global perceptual-motor mappings. As in more traditional views, regulation of motor timing is seen as a central function of the cerebellum. The difference is that Edelman further interprets the cerebellum as a 'modulating device' facilitating the categorization and perception of temporally defined motor synergies.

The distributed system

Considered as a whole, the brain regions activated during Oldowan-style stone knapping provide a distributed structural medium for the dynamic processes that implement behaviour. Individual regions display preexisting patterns of internal organization and external connectivity that both facilitate and constrain aspects of signal transmission and reentrant mapping. The massive interconnection of these regions supports the globally integrated, polymodal mapping of the knapping action by neuronal activity. The sustained activity observed in this distributed system, although revealed by static PET images, conforms with the expected behaviour of a system in which reentrant mapping is achieved through synchronized activity in spatially-distributed areas (Tallon-Baudry *et al.* 2001; Martinez *et al.* 2001). The fact that the level of this sustained activity exceeds that seen in an active perceptual-motor control task reflects the complexity of stone-knapping behaviour and indicates the exceptional physiological demands on the brain that are associated with it.

Implications for human origins

The PET research presented here reveals the neural substrates of Oldowan-style knapping in modern humans. In order for these actualistic results to be useful in human-evolutionary studies, some form of analogy must be made with the actual Oldowan knapping done by Plio-Pleistocene hominins. One level at which such an analogy may be made is that of the broad mental demands of the task. The basis of this analogy is the argument that similar behaviours imply similar mental processes even though the size and organization of the neural substrate may vary.

Psychological interpretation

Although it is easy to go overboard in attributing particular mental processes to discrete neural 'centres', different mental behaviours certainly are instantiated by different patterns of activity in the brain. PET reveals only the spatial dimensions of these differences, but is nevertheless capable of differentiating broad classes of mental behaviour (e.g. Roland 1993). As pointed out by Thelen & Smith (1994), thinking about an action is as much a behaviour as is performing the action, it is simply a *different* behaviour. The spatial distribution of activation during stone knapping, and particularly the absence of activation in the frontal and temporal association cortices, makes it clear that the most salient mental demands of Mode I knapping have to do with execution rather than conceptualization. PET research with modern humans cannot indicate the absolute perceptual-motor or conceptual capacities that were required of Oldowan toolmakers, but it does reveal the relative emphasis placed on these different kinds of mental behaviour.

Evolutionary interpretation

Modern PET images may also be used to identify brain regions that are relatively more likely to have been the focus of evolutionary selection relating to stone knapping ability. Those areas that experience the greatest physiological stress (i.e. activation) during knapping in modern humans are also the ones most likely to have experienced evolutionary pressure in the past. Conversely, structures not activated in modern humans may be considered much less likely to have been the direct focus of knapping-related selection. PET research with modern humans cannot directly reveal ancestral conditions, but does define at least one point along the evolutionary trajectory under investigation.

Unfortunately, interpretation of the PET evidence is hampered by our limited knowledge regarding the patterns and processes of human brain evolution. Very little is actually known about how brain structure has changed during hominin evolution, let alone about how this change came about. Adaptive processes that may have played an important role include mosaic changes in regional brain size (e.g. Holloway 1979; Armstrong 1982; Barton 1998; Dunbar 1998), coordinated overall brain expansion (Finlay & Darlington 1995; Finlay *et al.* 2001), and microstructural adaptation of neuronal organization (Nimchinsky *et al.* 1999; Preuss *et al.* 1999; Buxhoeveden *et al.* 2001). Given our limited knowledge, multiple alternatives must be entertained in interpreting the PET evidence.

Mosaic evolution

If we assume a simple process of mosaic brain evolution, we might expect that those brain regions most heavily taxed by knapping activities would have experienced preferential expansion. Although comparative data about the size of these regions is difficult to come by, this simple hypothesis does not appear to be supported. While the posterior parietal area in humans does indeed appear to have expanded (Passingham 1975; Holloway 1983), and the relative size of the cerebellum is controversial (Deacon 1997; Rilling & Insel 1999; Semendeferi & Damasio 2000), the primary visual, somatosensory and motor areas that are so heavily activated during stone knapping are actually among the least expanded portions of the human brain. It does not currently appear that the distributed network of structures associated with Mode 1 knapping was a unitary focus for mosaic brain enlargement. Although interpretations may change somewhat with further analysis, any relationship that is ultimately discerned between Oldowan knapping and mosaic brain expansion will be a relatively complex one.

Coordinated evolution

On the other hand, there is the possibility that selection on individual brain structures may have produced coordinated enlargement of the whole brain, as suggested by the developmental constraint hypothesis of Finlay & Darlington (1995). In this case, modest expansion of one or more of the structures supporting knapping behaviour could easily have contributed to the broader pattern of overall brain enlargement seen in human evolution. Unfortunately, this particular evolutionary relationship is not very testable because the constraint hypothesis predicts the same result (overall brain enlargement) from selection relating to any given behavioural capacity. The PET evidence confirms that stone knapping places relatively intense physiological demands on the brain, and so could have contributed to selection on brain size, but does not demonstrate that it actually did.

Microstructural evolution

Perhaps more interesting in light of currently-available evidence is the possible existence of microstructural adaptations relating to stone-knapping ability. As we have seen, stone knapping activates a string of structures from the occipital visual cortices through the superior parietal and into frontal motor cortex. This corresponds quite closely to what has been 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 differentiated between a dorsal 'where' stream involved in the perception of location and motion and a ventral 'what' stream implicated in the perception of object characteristics like form and colour. More recent work has stressed the role of the dorsal stream in visuomotor control (Milner & Goodale 1995) and in perception-for-action on relatively short time scales (Green 2001).

Although the anatomical segregation between visual streams does not appear to be as rigid as some (Livingstone & Hubel 1988) had hypothesized, there clearly are parallel neuronal networks that respond preferentially to stimulus components such as motion, contrast and colour. In the case of the dorsal stream, there is a loose continuity all the way from the fast acting, motion-sensitive *parasol cells* of the retina, through the *magnocellular layers* of the lateral geniculate and the *M-stream* neurons in layer 4 of V1 to the higher-order visual-processing areas of the posterior parietal cortex. The coactivation of occipital and superior parietal cortices observed during stone knapping reflects this continuity, and indicates the importance of dorsal stream activity in knapping behaviour. 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 V1, and from M-stream neurons specifically.

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 M-stream neurons and dendrites in layer 4A of primary visual cortex. 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.* have now shown that, although the honeycomb pattern is shared by monkeys and apes, humans display a unique meshlike 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. Given the level of dorsal stream activity observed during stone knapping, it is quite plausible that a hominin M-stream specialization relating to motion perception could have either contributed to the initial emergence of stone knapping or been part of an adaptive response to its later spread. Such specializations of primary visual cortex would also be expected to have cascading effects on higher levels of the visual system, which receive most of their input from V1 (Preuss *et al.* 1999).

Summary and conclusions

Over the past 75 years, research into the tool behaviour of modern apes has dramatically expanded our appreciation for the mental capacities of our closest relatives (Köhler 1925; Goodall 1964; McGrew 1992; Matsuzawa 1996). By elevating our estimations of apes, this research has also contributed to a reduction in the perceived uniqueness of the earliest knapped stone tools (e.g. Wynn & McGrew 1989). For the most part, however, students of tool behaviour in both modern apes and prehistoric hominins have focused on underlying cognitive mechanisms rather than on actual performance. This focus results from a representational perspective concerned less with what an individual does than with how the individual conceives of what he or she does (Smitsman 1997). Although the conceptual simplicity of Oldowan stone knapping has been well described (Wynn & McGrew 1989), a perception–action perspective on tool use opens the door to additional avenues of investigation.

A perception–action perspective sees tool use as the dynamic product of an integrated organisms-plus-environment system rather than as the unilateral expression of static internal concepts. This perspective is particularly useful in dealing with the issues of motor skill and practical understanding that are so important to a full description of stone-knapping behaviour. Although the application of this perspective to the evidence and questions commonly held by human origins researchers is a non-trivial undertaking, the empirical observations of functional brain structure provided by PET make it an ideal actualistic research tool.

In the preliminary research presented here, PET was used to compare brain activity during Oldowan-style (Mode I) stone knapping to that during less-elaborate control tasks. The results provide further corroboration for the view that Mode I knapping is not especially demanding in the conventional conceptual or cognitive sense. However, activations seen in motor, somatosensory, superior parietal and visual cortices and in the cerebellum indicate that it *is* an especially demanding perceptual-motor task. The mental demands of stone knapping may lie more with execution than conceptualization, but they are no less real or unique because of this.

The activations observed during stone knapping also suggest potential evolutionary relationships. Although currently available brain volume data do not reveal any simple relationship between the distributed network that supports knapping and mosaic patterns of human-brain expansion, the observed activation would be consistent with a contribution to coordinated overall brain enlargement. At the microstructural level, there is clear evidence of a uniquely human adaptation in the dorsal stream of cortical visual processing. It is a plausible hypothesis for further investigation that this adaptation may have in some way either contributed to or arisen from the development of stone knapping in human evolution.

Note

1. $H_2{}^{15}O$ is a radionuclide tracer consisting of water molecules that incorporate the radioactive oxygen isotope ^{15}O. It is carried by blood vessels in the brain and produces activation data that reflect the sensitive response of blood flow to changes in local neuronal metabolism (Roland 1993).

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