



# Stone Tool-Making and Brain Activation: Positron Emission Tomography (PET) Studies

Dietrich Stout, Nicholas Toth and Kathy Schick

*Center for Research into the Anthropological Foundations of Technology (CRAFT) and Anthropology Department, Indiana University, Bloomington, IN 47405, U.S.A.*

Julie Stout

*Department of Psychology and Program in Neural Science and Cognitive Science, Indiana University, Bloomington, IN 47405, U.S.A.*

Gary Hutchins

*Department of Radiology, School of Medicine, Indiana University, Indianapolis, IN 46202, U.S.A.*

*(Received 3 February 2000, revised manuscript accepted 19 May 2000)*

This study introduces to archaeology a new experimental technique for examining the relationship between stone tool-making and brain function. The principal focus of this exploratory study was the development of effective methods for the identification and examination of the regions of the modern human brain recruited during the manufacture of simple (Oldowan or Mode I) stone tools. The functional brain imaging technique employed, Positron Emission Tomography (PET), examines task-related brain activity by assessing changes in regional cerebral blood flow during specific tasks. The single-subject study reported here represents a heuristic, initial exploration of this subject. Results indicate that during stone tool-making there was heavy activation of cortical and subcortical regions of the brain associated with motor and somatosensory processing. Especially interesting was the high degree of activation in areas known to be involved with complex spatial cognition requiring integration of diverse sensory inputs (e.g. vision, touch, and proprioception, or sense of body position and motion). Expansion of such higher-order association areas has been particularly important during the course of human evolution. This single-subject pilot study demonstrates the application of the PET brain imaging technique to the study of early stone technologies and suggests hypotheses to be tested in more comprehensive studies in the future.

© 2000 Academic Press

**Keywords:** BRAIN, STONE TOOL-MAKING, COGNITION, HUMAN EVOLUTION, POSITRON EMISSION TOMOGRAPHY.

## Introduction

Since the time of Darwin, there has been a general appreciation of the possible role of tools and technology in the course of human evolution. In recent years, there has been a great deal of discussion and debate on the possible relationship between tools and the evolution of the hominid brain (e.g. Washburn, 1960; Parker & Gibson, 1979; Holloway, 1981; Gowlett, 1984; Toth, 1985; Isaac, 1986; Dibble, 1989; Eccles, 1989; Marshack, 1989; Wynn, 1989; Calvin, 1990; Gibson, 1990; Corballis, 1991; Greenfield, 1991; Tobias, 1991; Falk, 1992; McGrew, 1992; Gibson & Ingold, 1993; Toth & Schick, 1993; Wynn, 1993; Savage-Rumbaugh & Lewin, 1994;

Westergaard, 1995; Mithen, 1996; Noble & Davidson, 1996; Deacon, 1997). Among major issues that have emerged are questions regarding the cognitive complexity required for the production of early stone tools and the adaptive significance of technology in brain evolution. In order to address these questions, it is important to know which areas of the brain are involved in tasks related to tool-making. The current study addresses this question using imaging techniques developed during the early 1980s in the experimental neurosciences.

These advances in neurology and radiology have enabled researchers to directly examine the patterns of brain activity associated with specific tasks. In particular, the technique of Positron Emission Tomography

(PET) allows researchers to examine increased blood flow to areas of the brain involved in particular tasks, producing a three-dimensional image of areas of heightened brain activity during the execution of these tasks.

Positron Emission Tomography involves injecting a radioactive isotope (in this study,  $^{15}\text{O}$ ) “tracer” into a subject’s blood system. The technique relies upon the fact that blood flow is greater to areas of increased neuronal activity. This results in greater tracer accumulation in these areas. Detection and quantification of the distribution of tracer in the brain is allowed by the fact that each decaying  $^{15}\text{O}$  nucleus emits an antimatter particle (a positron) that rapidly collides with a nearby electron. The ensuing annihilation produces two gamma rays that travel in opposite directions from the point of collision and are detected by a circular array of sensors. Data from these sensors are then used to reconstruct points of origin within the brain. These data provide an indication of the location and intensity of activation throughout the brain during the activity under investigation.

## Historical Background to the Study

In 1990, two of the authors (NT and KS) suggested employing PET as a means of examining brain activity during stone tool-making (Toth & Schick, 1993). For the next several years, experts in this field were consulted, including Dr Marcus Raichle of the Radiology Department, School of Medicine at Washington University, and a research methodology to approach the question of stone-tool manufacture and brain activity began to develop. In 1995 GH, Director of the Division of Imaging Science, Department of Radiology, School of Medicine at Indiana University, Indianapolis, agreed to collaborate with the authors and generously made the facilities available for this pilot study. Two more of the authors (JS and DS) joined the project in 1996 and agreed to analyse and interpret the data from the PET and MRI study. This pilot study was initiated in February 1997 at the Indiana University School of Medicine.

## Methodology

### *Subject of study*

In this initial study, the experimental subject was one of the authors (NT), an experienced stone tool-maker with over 20 years background in “flint knapping”. 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. As

is the case with approximately 90% of modern humans, this subject is right-handed, a fact which can influence laterality of brain function.

### *Task conditions*

Three different experimental conditions were imaged for this study. The first was a resting or control state. As a certain level of blood flow is occurring in the brain at all times, it is necessary to subtract this “basal” flow from that observed during a specific task. This is done in order to isolate the differential blood flow directly associated with that task. In keeping with this logic, it is desirable that the control or “baseline” state mimic the task state as closely as possible, excepting only those specific aspects of greatest experimental interest.

In this study, our greatest interest was in the possible cognitive aspects of the tool-making task. As an additional perspective on such cognitive aspects, it was considered useful to compare brain activation seen during task performance to that seen while simply imagining the task (with the control state subtracted from each). Thus, the three experimental conditions investigated were:

- (1) Control (resting/baseline) state. This condition, representing the basal state of brain activity, consisted of the subject viewing a visual target (in this case, a spherical cobble) without any attempt to imagine or carry out knapping. This condition deliberately included visual stimulus so that any differences from the other two conditions would be limited to differential cognitive, motor, or somatosensory involvement.
- (2) Mental imagery. This experimental condition involved examining a partially reduced core and imagining a hammerstone striking it and removing flakes. The core was held in both hands by the subject. The subject deliberately avoided imagining himself wielding the hammerstone, in order to reduce recruitment of areas of the brain involved with motor control of the hands and arms but still retain involvement of cognitive planning areas.
- (3) Knapping. In this condition, the subject actually struck the core with the hammerstone in a manner to remove flakes. In practice, it was found that full force knapping caused too much motion in the head for accurate imaging; flaking was conducted at approximately one-half normal force in order to reduce vibration but still retain the gross motor and cognitive activities. During this experimentation, flakes were actually removed from the core.

### *Data collection*

Task performance began 30 s before tracer injection and continued for 2 min. All images were collected using a Siemens 951/31R whole body PET scanner located at the Radiology Department of the Indiana

Table 1. Regions of differential activation in the knapping-control subtraction

Location number	Centroid location	Functional attribution	Laterality	Talairach coordinates (x,y,z)			Area (mm <sup>3</sup> )	Mean z value
1	Superior parietal (Brodmann Area 7)	Spatial cognition	Left	21	-49	56	6948	5.75
2	Superior parietal (Brodmann Area 7)	Spatial cognition	Right	-30	-53	61	1948	5.16
3	Central sulcus (Brodmann Areas 1 and 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 coordination	Left	10	-37	-18	1002	5.22
6	Cerebellum (hemisphere)	Motor coordination	Right	-37	-51	-25	604	4.82
7	Cerebellum (vermis)	Postural control	Right	-3	-53	-9	1082	5.07
8	Fusiform gyrus (Brodmann Area 37)	Visual association	Right	-24	-53	-9	1287	5.05

University Medical Center in Indianapolis, Indiana. This machine has an intrinsic resolution of 6 mm Full Width Half Maximum (FWHM) and an in-plane axial resolution of 5 mm.

The subject fasted for 4 h prior to image collection, and was injected with a 50 millicurie (mCi) bolus of radioactive <sup>15</sup>O water for each of nine separate trials (three control, three imagery and three knapping). This constituted the maximum recommended experimental dose of radiation for a 1-year period. The tracer was injected intravenously into the leg of the subject in order to avoid possible confounding stimulation and/or restriction of the motion of the subject's arms during the knapping task.

Task performance was initiated 30 s before tracer injection and continued for approximately 2 min following tracer injection. Annihilation photon data were collected from the time the task was initiated and continued for a period of 3 min. The PET data were collected using a dynamic imaging sequence consisting of 9 × 5 s frames, 5 × 15 s frames, and 2 × 30 s frames. During image collection, the subject was lying prone on the scanner bed and the gantry was inclined. An inflatable Dermafoam<sup>®</sup> pillow and restraining strap were used in order to minimize head movement.

#### Image processing

The acquired data were reconstructed to an approximate 8 mm FWHM resolution using conventional filtered back projection and a Hanning smoothing filter. The temporal sequence of PET images was then integrated from the time of arrival of the tracer in the brain (defined as the point at which the influx of tracer reached 75% of the peak brain uptake level) over a period of 90 s.

#### Image analysis

Processed images were analysed using the University of Michigan Statistical Analysis for PET Activation Software, Version 3.0. Changes in regional cerebral blood flow (rCBF) associated with each task state were estimated from the difference between mean pixel

counts in task versus control states (i.e. imagery-control and knapping-control). *T*-tests were performed for each individual pixel in order to determine the significance of these differences, and used to create z-map image subtractions. Image volumes for each task condition were linearly transformed in Talairach stereotactic space (Talairach & Tournoux, 1988). For subsequent Region of Interest (ROI) analysis the z-image threshold was set at 4.0, so that only activation differing by four or more standard deviations from the control state was visible. ROIs were then created by using a computer to visually trace the outlines of the 17 most salient non-overlapping activation areas (eight for knapping-control, nine for imagery-control) in these z-images. The coordinates for the centre of each selected region (the centroid) as well as the total volume of the region and its mean z-value were then calculated. Anatomical locations were attributed to these centroid points using the *Co-Planar Stereotaxic Atlas of the Human Brain* developed by Talairach & Tournoux (1988) and double-checked visually by superimposing the PET images on an anatomical magnetic resonance image (MRI) of the subject.

#### MRI superposition

To enhance visual interpretation and presentation of the PET activation images, a whole brain proton density weighted magnetic resonance image (MRI) of the subject's head was collected in axial plane. This was co-registered with the PET images using an iterative procedure minimizing the least squared differences between MRI and PET images.

## Results

The results of ROI analysis are presented in Tables 1 (knapping-control) and 2 (imagery-control). In each case, large volumes of highly significant activation were observed. For the most part, the same regions were active on both sides of the brain, although left hemisphere activity was greater in extent and intensity. Holding threshold significance level roughly equal, left

Table 2. Regions of differential activation in the imagery-control subtraction

Location number	Centroid location	Functional attribution	Laterality	Talairach coordinates (x,y,z)			Area (mm <sup>3</sup> )	Mean z value
1	Superior parietal (Brodmann area 7)	Spatial cognition	Left	21	-53	56	1766	5.61
2	Superior parietal (Brodmann area 7)	Spatial cognition	Right	-30	-55	58	433	4.84
3	Inferior parietal (Brodmann area 40)	Visualization, motor imagery	Left	42	-35	43	1572	5.67
4	Inferior parietal (Brodmann area 40)	Visualization, motor imagery	Right	-51	-33	50	570	5.15
5	Precentral gyrus (Brodmann area 4)	Primary motor processing	Left	33	-19	54	1834	5.19
6	Occipital lobe (Brodmann area 19)	Secondary visual processing	Left	28	-78	2	558	5.25
7	Occipital lobe (Brodmann area 19)	Secondary visual processing	Right	-30	-78	16	1037	5.45
8	Fusiform gyrus (Brodmann area 37)	Visual association	Right	-28	-51	-9	421	5.22
9	Cerebellum (hemisphere)	Motor coordination	Right	-37	-44	-20	649	4.62

hemisphere activity occupied volumes between 1.5 and 3.5 times that observed in the right hemisphere. This difference is almost certainly due to the preferential right-handedness of the subject and the laterality of the task (percussion was performed with the right hand, core manipulation with the left).

In the knapping-control subtraction (Table 1), significant activation was observed in the superior parietal lobe (locations 1 and 2), the pre- and post-central gyri surrounding the central sulcus (locations 3 and 4), in left and right cerebellar hemispheres (locations 5 and 6) as well as the medially located cerebellar vermis (location 7) and the right fusiform gyrus of the inferior temporal lobe (location 8). Figure 1 provides a broad overview of the relevant neuroanatomy while Figure 2(a), (b) shows the actual pattern of activation in selected slices. Both primary motor and sensory (pre- and post-central gyri: see Figure 2(a)) as well as "higher-order" association regions (superior parietal: see Figure 2(a)) of the neocortex were active, as well as a subcortical structure (cerebellum: see Figure 2(b)) associated with motor learning and control. A somewhat lower level of confidence should be placed in the attribution of activity to the fusiform gyrus (location 8 on Table 1), as the observed centroid was very close to the point of contact between this gyrus and cerebellum. The fusiform gyrus is generally considered to be a "remote" visual association region involved in the ventral "object-identification" visual processing pathway (as opposed to the dorsal "location" pathway).

A very similar pattern of activation was observed in the imagery-control subtraction (Table 2), although the areas of significantly different blood flow were only about 25% the size of those seen in the knapping-control subtraction. Once again, superior parietal (locations 1 and 2), peri-central (location 5), fusiform (location 8) and cerebellar (location 9) activity were observed. In addition, significant activation occurred in the anterior portion of the inferior parietal lobules (locations 3 and 4) and in the secondary visual cortex (locations 6 and 7: Brodmann area 19 of the occipital lobe) of both hemispheres.

The inferior parietal lobule is a phylogenetically recent and functionally heterogeneous area (Roland, 1993). Many researchers have placed Wernicke's language processing area within this region, which is more generally associated with the manipulation, integration and interpretation of a wide variety of sensory inputs. Inferior parietal lobe activity is illustrated in Figure 2(c) while occipital and cerebellar activity are shown in Figure 2(d).

## Discussion

The most important achievement of this study is that it has developed a viable method for exploring the neuronal activity associated with stone tool technology. The high significance levels obtained with a single subject clearly show that this activity is accessible to the researcher using existing PET technology. Due to the known variability between individuals in patterns of task-related brain activation, the results of the single subject study reported here provide plausible hypotheses and predictions for further research rather than definitive conclusions at this time.

Keeping this in mind, it may be observed that the pattern of activation seen in the knapping-control subtraction is essentially that which would be expected for a complex motor task requiring hand-eye coordination and conducted in extra-personal space (that is, with reference to external objects and locations). Primary motor and somatosensory areas surrounding the central sulcus are very strongly activated (Figure 2(a)). These areas may be characterized as relatively basic input/output structures and are fairly directly connected to peripheral sensory receptors and muscular effectors. Although these activation fields are concentrated around the central sulcus, it is likely that their anterior boundaries encompass portions of the secondary motor-planning regions of the frontal lobe.

The presence of cerebellar activity (Figure 2(b)) is also as expected for a motor task. The cerebellum in general acts to indirectly regulate movement and



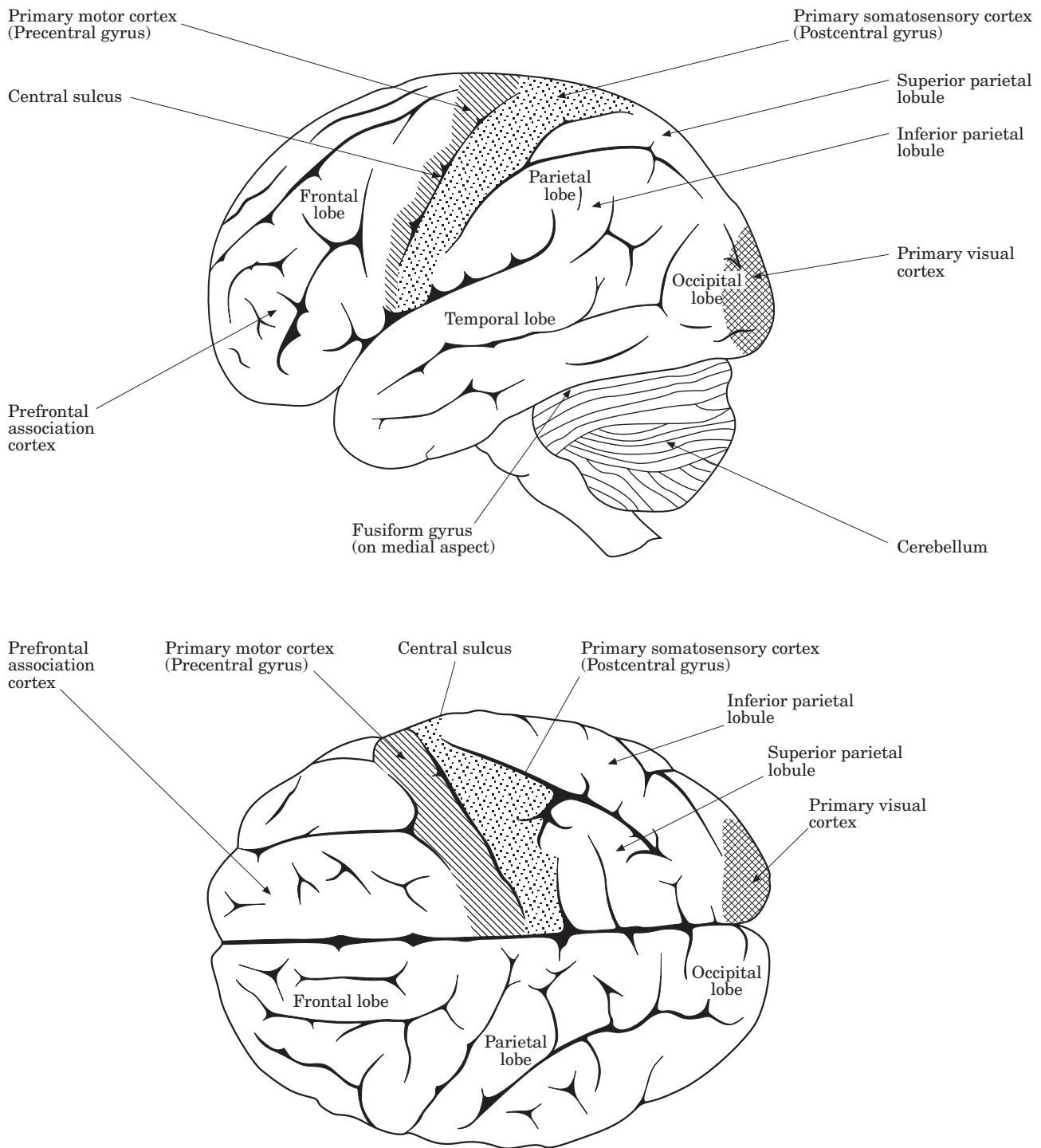


Figure 1. Surface anatomy of the human brain, with cortical lobar divisions and primary motor and sensory areas indicated (after Gray, 1977; Kandel *et al.*, 1991).

posture by integrating internal (motor) and external (sensory) feedback (Kandel *et al.*, 1991). The cerebellum is also closely involved in motor learning. In the knapping-control, subtraction activity is seen in both hemispheres, which are involved in movements of the limbs, and in the central vermis, a phylogenetically

ancient structure involved in regulating posture. Neither this cerebellar activity nor the previously discussed activity around the central sulcus provide evidence for the presence of a cognitive component in the manufacture of simple stone tools by an experienced knapper.

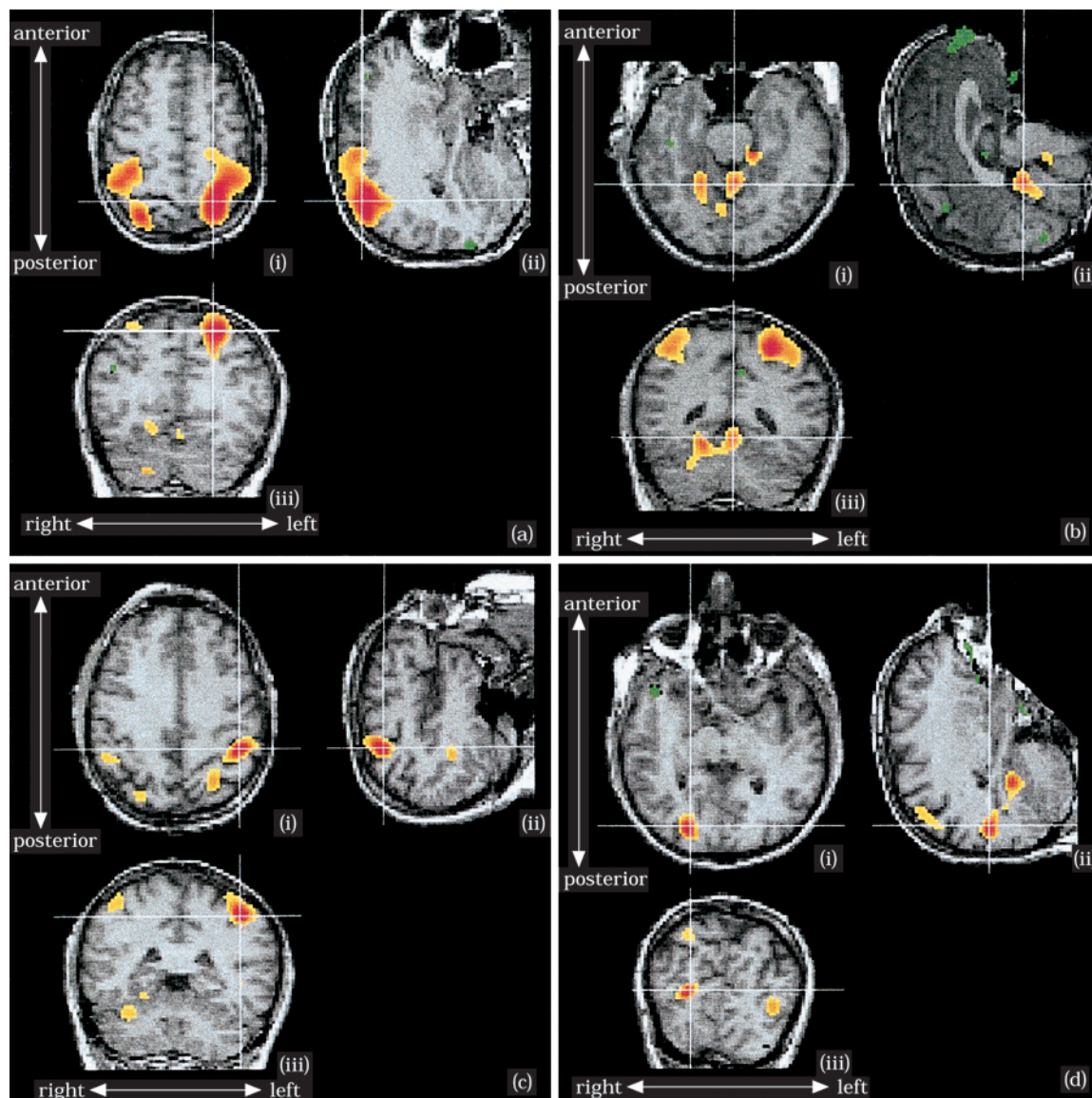


Figure 2. Axial (i), sagittal (ii) and coronal (iii) views of differential activity in the knapping-control [(a) and (b)] and imagery-control [(c) and (d)]. Red indicates areas of greatest blood-flow increase relative to control while green indicates a relative reduction in blood flow. Only differences by four or more standard deviations ( $z \geq 4.00$ ) are depicted. All images are in standard orientation, which is intended to reflect the position of the subject in the scanner. Left and right are thus mirrored, and the anterior–posterior axis is vertical. (a) Cortical activation in the knapping-control subtraction. Crosshairs indicate superior parietal activity associated with spatial cognition. Primary motor and somatosensory activity around the central sulcus may be seen as a contiguous anterior extension of this region in (i) and (ii). (b) Cerebellar activation in the knapping-control subtraction. Crosshairs indicate activity in the cerebellar vermis, which is associated with postural control. Activity in the right cerebellar hemisphere (motor learning and control) may be seen to the anatomical right of the crosshairs in (i) and (iii). Cortical activity may be seen in (iii). (c) Cortical activity in the imagery-control subtraction. Crosshairs indicate inferior parietal activation most likely associated with the use of mental imagery. Superior parietal (spatial cognitive) activity may be seen posterior to this in (i). (d) Cerebellar and occipital activation in the imagery-control subtraction. Crosshairs indicate activity in the secondary visual processing areas of the right occipital lobe. Similar activity in the left occipital is visible in (iii) while activity of the right cerebellar hemisphere may be seen in (ii).

A cognitive component is implied, however by the observed activity in the superior parietal lobes (Figure 2(a)). 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. Damage to the superior parietal lobe of the right hemisphere in particular tends to

produce a characteristic disorder of spatial cognition known as “unilateral neglect” in which patients fail to recognize the existence of the entire left side of their spatial environment, despite unimpaired perception (Bradshaw & Mattingley, 1995). Unlike the primary sensorimotor and cerebellar structures discussed above, the superior parietal cortex is closely involved in the cognitive processes of representation and attention.

Its activation in the current study suggests that relatively sophisticated cognitive information processing can occur in association with simple flake production by an experienced modern human knapper. An interesting question for future research is whether less experienced or novice flint knappers might display even greater cognitive involvement related to the demands of skill learning as opposed to simple execution.

Patterns of differential activation similar to those discussed above were also seen in the imagery-control subtraction and are subject to similar interpretations. Although there was no active knapping in this task-condition, it seems likely that activation of the primary motor cortex of the left precentral gyrus, as well as of the right hemisphere of the cerebellum, resulted from the fact that the subject was holding the core during the task. Superior parietal activity once again indicates ongoing spatial cognition, probably related to the internal representation of the objects and spaces involved in the imagined knapping task. Interestingly, this activation was less intense in the imagine-control subtraction, perhaps due to the absence of activity-related changes in spatial locations and relationships of the core and hammerstone.

On the other hand, activity not present in the knapping-control subtraction was seen in visual processing areas as well as the inferior parietal. Brodmann area 19 of the occipital lobe is involved in secondary visual processing and has been characterized as an intermediate relay for the three major visual pathways (motion, form, colour) that originate in the primary visual cortex (Kandel *et al.*, 1991). It seems likely that the explicit emphasis placed on visual inspection of the core in this task state as compared to the active knapping task accounts for the differential activation of this secondary visual region.

Inferior parietal activation in the imagery-control subtraction is particularly interesting due to the sophisticated nature of the associative information processing which occurs in this general region (the parieto-occipital-temporal junction) as well as to previous speculation regarding the region's evolutionary significance (e.g. Wilkins & Wakefield, 1995). As has already been observed, this region is held to be phylogenetically recent, and perhaps even without a true homologue in non-human primates (Roland, 1993). In some individuals, Wernike's "grammatical" language area may intrude upon the posterior-inferior parietal lobule, and left hemisphere parietal damage is often associated with language deficits (aphasia) (Kandel *et al.*, 1991). However, it should be noted that in the current study activation appears to be concentrated in the more anterior portion of the inferior parietal lobule, perhaps including the parietal operculum. The anterior inferior parietal lobule has been characterized as a bi-modal visual and somatosensory association area (Roland, 1993), while more recent work has linked the parietal lobe in general with motor imagery (Crammond, 1997 and references therein). In the current study, differen-

tial inferior parietal lobe activation is most likely related to the somewhat artificial emphasis on visualization in the imagery task itself since such activation is absent in the more "naturalistic" active knapping task.

The results of this pilot study suggest that Mode I flake production might best be characterized as a complex sensorimotor task with a spatial-cognitive component. This represents a hypothesis to be tested by further multi-subject research. Based on current results, the *a priori* predictions which might be used to test this hypothesis include activation of the: (1) pre- and post-central gyri; (2) cerebellar hemispheres; and (3) superior parietal lobes. It is interesting to note that prefrontal activation was not observed in this study, but with a sample of 1 it would be premature to interpret this absence of evidence as evidence of absence. Similarly, although the study fails to provide any evidence of a distinct, shared neuroanatomical substrate for stone-tool manufacture and language (as possibility suggested by the work of Lieberman, 1985; Greenfield, 1991; Calvin, 1993; and others), it cannot be viewed as falsification of such a hypothetical link.

### Possible Evolutionary Significance

The research presented here has been aimed at establishing viable research methods and proposing testable hypotheses for the investigation of modern human brain activity during simple stone-tool production. Although this subject is interesting in itself, the ultimate objective of the research programme is to provide insight into human brain evolution. What can modern imaging studies tell us about the evolutionary past?

On the basis of the results obtained in this study, it is most reasonable to hypothesize that simple flake production by an experienced modern human knapper is a complex motor task with a strong spatial-cognitive component. This is indicated by robust patterns of activation in neocortical sensorimotor and association regions, as well as in the cerebellar hemispheres.

Of course it cannot be simply concluded that the same neuronal fields and populations activated by modern humans would *necessarily* have been recruited in pre-modern hominid knappers performing a similar task. However, it could be argued that the particular regions of observed activation were at least *sufficient* for the flint knapping task. In fact, the most parsimonious conclusion would be that the production of simple flakes by pre-modern knappers would have been mediated by these structures or by a smaller subset of them.

It follows that, *if* the cerebral demands associated with the habitual manufacture of simple (i.e. Oldowan or Mode I) stone tools actually did exert selective pressure on the early hominid brain, this pressure would most likely have acted directly on some or all of the structures recruited by modern humans, and only



indirectly on other brain regions. Obviously, brain activation studies offer no direct evidence of the presence or absence of such selective pressure, but observed patterns of activation may nevertheless be used to test evolutionary hypotheses.

For example, it is interesting to note that the broad divisions of the brain recruited by an experienced modern knapper (neocortex and cerebellum) in the current study are exactly those that have undergone the greatest expansion in hominid evolution (Deacon, 1997). The more particular recruitment of superior parietal association cortex is further suggestive, as the association cortex in general (i.e. prefrontal, parieto-occipital-temporal and limbic; Kandel *et al.*, 1991) is allometrically expanded in humans relative to the remainder of the neocortex (Passingham, 1975). If these putative activation patterns are verified by further research, they will represent corroboration of the hypothesis that early stone tool technology played an important selective role in hominid brain evolution.

## Summary and Conclusion

This exploratory investigation has demonstrated the effectiveness of Positron Emission Tomography (PET) in examining brain activity during Oldowan (Mode 1) stone tool-making. In addition, the results obtained have provided plausible and testable hypotheses for further research. These results include highly significant activation in areas of the brain associated with complex spatial cognition integrating different sensory inputs, such as vision, proprioception (sensing of body position and movement), and touch. Neuroanatomical regions of high activity included the superior parietal lobes (locations 1 and 2 in Table 1), primary motor and somatosensory regions surrounding the central sulcus (locations 3 and 4 in Table 1), and the cerebellum (locations 5 and 6 in Table 1). Observed superior parietal lobe activity suggests the presence of complex spatial cognition, while activation around the central sulcus reflects basic sensorimotor processing, and cerebellar activity represents the integration and control of motor activity. Further research with multiple subjects will be needed to test the validity of these putative activation patterns.

On the basis of current results, it is hypothesized that the habitual manufacture of early stone tools can call upon areas in the superior parietal lobe of the brain typically involved in the cognitive representation of the external world (here, the demands of the tool-making task), and the integration of multiple modes of sensory input. The hypothesized involvement of parietal association cortex in the making of simple stone tools suggests constructive mental processes going beyond simple direct perception and execution. Although we cannot assume that because particular regions are activated in a modern human that they would be required in a non-human or protohuman performing

the same task, we may conclude that they are sufficient for the task. Further research should help to more fully resolve this relationship. Until this is accomplished, it remains interesting to note that those areas of the brain that have shown the greatest enlargement in hominid evolution, i.e. association cortex and cerebellum, are the same ones implicated in this exploratory study of stone tool-making.

The use of brain-imaging techniques opens new avenues of investigation for addressing a range of problems related to human evolution. Current research, incorporating multiple subjects, is addressing potential differences in brain activation during the acquisition of stone tool-making skills, between different modes of tool production (e.g. Oldowan, Acheulean, Levallois, or blade tools), and among preferentially right-handed versus left-handed tool-makers. These investigations will also make use of alternative procedures such as functional magnetic resonance imaging (fMRI) to improve spatial and temporal resolution, and employ slower-decaying isotopes in order to allow tasks to be performed outside the scanner. This research should provide a firmer empirical foundation for investigations of the relationship between cognitive and technological change in hominid evolution.

## Acknowledgements

We would like to thank Terrence Deacon (Harvard University and Boston University), Ralph Holloway (Columbia University), and Dean Falk (SUNY Albany) for advice, and Rich Fain (I.U. Medical Center) and Eric Peters (I.U. Bloomington) for technical assistance. Any shortcomings in the research presented here are, however, ours alone. Funding for this research was provided by the Center for Research into the Anthropological Foundations of Technology (CRAFT), at Indiana University, the office of Research and the University Graduate School at Indiana University, and the Indiana University School of Medicine.

## References

- Barton, R. A. (1996). Neocortex size and behavioral ecology in primates. *Proceedings of the Royal Society of London B* **263**, 173–177.
- Bradshaw, J. L. & Mattingley, J. B. (1995). *Clinical Neuropsychology*. New York: Academic Press.
- Calvin, W. H. (1993). The unitary hypothesis: A common neural circuitry for novel manipulations, language, plan-ahead and throwing? In (K. Gibson & T. Ingold, Eds) *Tools, Language and Cognition in Human Evolution*. Cambridge: Cambridge University Press, pp. 251–270.
- Calvin, W. H. (1990). *The Ascent of Mind*. New York: Bantam.
- Corballis, M. C. (1991). *The Lopsided Ape*. New York: Oxford University Press.
- Crammond, D. J. (1997). Motor imagery: never in your wildest dream. *Trends in Neurosciences* **20**(2), 54–57.
- Deacon, T. W. (1997). *The Symbolic Species: the Co-Evolution of Language and the Brain*. New York: Norton.



- Dibble, H. L. (1989). The implications of stone tool types for the presence of language during the Lower and Middle Palaeolithic. In (P. Mellars & C. Stringer, Eds) *The Human Revolution*. Edinburgh: Edinburgh University Press, pp. 415–432.
- Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology* **6**(5), 178–190.
- Eccles, J. C. (1989). *Evolution of the Brain: Creation of the Self*. London: Routledge.
- Falk, D. (1992). *Brain Dance: New Discoveries about Human Origins and Brain Evolution*. New York: Henry Holt and Company.
- Gibson, K. R. (1990). New perspectives on instincts and intelligence: brain size and the emergence of hierarchical construction skills. In (S. T. Parker & K. R. Gibson, Eds) *'Language' and Intelligence in Monkeys and Apes*. Cambridge: Cambridge University Press, pp. 97–128.
- Gibson, K. R. & Ingold, T. (Eds) (1993). *Tools, Language and Cognition in Human Evolution*. Cambridge: Cambridge University Press.
- Gowlett, J. A. J. (1984). Mental abilities of early man: A look at some hard evidence. In (R. Foley, Ed.) *Hominid Evolution and Community Ecology*. London: Academic Press, pp. 167–192.
- Gray, H. (1977). *Gray's Anatomy: Classic Collector's Edition*. New York: Bounty Books.
- Greenfield, P. M. (1991). Language, tools and brain: the ontogeny and phylogeny of hierarchically organized sequential behavior. *Behavioral and Brain Sciences* **14**, 531–595.
- Holloway, R. L. (1981). Culture, symbols and human brain evolution: a synthesis. *Dialectical Anthropology* **5**, 287–303.
- Isaac, G. (1986). Foundation stones: early artefacts as indicators of activities and abilities. In (G. N. Bailey & P. Callow, Eds) *Stone Age Prehistory*. Cambridge: Cambridge University Press, pp. 221–241.
- Kandel, E. R., Schwartz, J. H. & Jessell, T. M. (1991). *The Principles of Neural Science*. Norwalk, Connecticut: Appleton and Lange.
- Lieberman, P. (1985). On the evolution of human syntactic ability. Its pre-adaptive bases – motor control and speech. *Journal of Human Evolution* **14**(7), 657–668.
- Marshack, A. (1989). Evolution of the human capacity: the symbolic evidence. *Yearbook of Physical Anthropology* **32**, 1–34.
- McGrew, W. C. (1992). *Chimpanzee Material Culture*. Cambridge: Cambridge University Press.
- Mithen, S. (1996). *The Prehistory of the Mind*. New York: Thames and Hudson.
- Noble, W. & Davidson, I. (1996). *Human Evolution, Language and Mind*. Cambridge: Cambridge University Press.
- Parker, S. T. & Gibson, K. R. (1979). A developmental model of the evolution of language and intelligence in early hominids. *Behavioral and Brain Sciences* **3**, 367–408.
- Passingham, R. E. (1975). Changes in the size and organization of the brain in Man and his ancestors. *Brain and Behavioral Evolution* **11**, 73–90.
- Posner, M. I. & Raichle, M. E. (1994). *Images of Mind*. New York: Scientific American Library.
- Roland, P. E. (1993). *Brain Activation*. New York: Wiley-Liss.
- Savage-Rumbaugh, S. & Lewin, R. (1994). *Kanzi: The Ape at the Brink of the Human Mind*. New York: John Wiley and Sons.
- Schick, K. D., Toth, N., Garufi, G., Savage-Rumbaugh, E. S., Rumbaugh, D. & Sevcik, R. (1999). Continuing investigations into the stone tool-making and tool-using capabilities of a Bonobo (*Pan paniscus*). *Journal of Archaeological Science* **26**, 821–832.
- Talairach, J. & Touroux, P. (1988). *Co-Planar Stereotaxic Atlas of the Human Brain* (trans. M. Rayport). New York: Thieme Medical Publishers.
- Tobias, P. V. (1991). *Olduvai Gorge*, Vol. 4b. *The Skulls, Endocrasts and Teeth of Homo habilis*. Cambridge: Cambridge University Press.
- Toth, N. (1985). The Oldowan reassessed: a close look at early stone artefacts. *Journal of Archaeological Science* **12**, 101–120.
- Toth, N. & Schick, K. D. (1993). Early stone industries and inferences regarding language and cognition. In (K. R. Gibson & T. Ingold, Eds) *Tools, Language and Cognition in Human Evolution*. Cambridge: Cambridge University Press, pp. 346–362.
- Washburn, S. (1960). Tools and human evolution. *Scientific American* **203**, 63–75.
- Westergaard, G. C. (1995). The stone tool technology of capuchin monkeys: possible implications for the evolution of symbolic communication in hominids. *World Archaeology* **27**, 1–24.
- Wilkins, W. & Wakefield, J. (1995). Brain evolution and neurolinguistic preconditions. *Behavioral and Brain Sciences* **18**, 161–226.
- Wynn, T. (1989). *The Evolution of Spatial Competence*. Urbana: University of Illinois Press.
- Wynn, T. (1993). Layers of thinking in tool behavior. In (K. R. Gibson & T. Ingold, Eds) *Tools, Language and Cognition in Human Evolution*. Cambridge: Cambridge University Press, pp. 389–406.