
ACTIONS SPEAK LOUDER THAN FUNCTIONS

THE IMPORTANCE OF MANIPULABILITY & ACTION IN TOOL REPRESENTATION

Marion L. Kellenbach, Matthew Brett & Karalyn Patterson

MRC Cognition and Brain Sciences Unit, Cambridge, U.K.

Acknowledgements

We are grateful for the skilled assistance from the staff at the Wolfson Brain Imaging Centre, particularly Gloria Gee, Ruth Bisbrown-Chippendale, Tim Donovan, Vicky Liversidge and Nahal Mavaddat. We are also grateful to Ian Nimmo-Smith for statistical advice and to Rhodri Cusack for writing the program for scrambling the photographs.

Running heading: Action and function attributes in object representation

Corresponding author:

Marion Kellenbach
MRC Cognition and Brain Sciences Unit,
15 Chaucer Road,
Cambridge CB2 2EF
U.K.

Tel: +44 1223 355294 ext. 273

Fax: +44 1223 359062

Email: marion.kellenbach@mrc-cbu.cam.ac.uk

ABSTRACT

PET was used to investigate the neural correlates of action knowledge in object representations, particularly the left lateralised network of activations previously implicated in the processing of tools and their associated actions: ventral premotor cortex (VPMCx), posterior middle temporal gyrus (PMTG) and intraparietal sulcus (IPS). Judgements were made about the actions and functions associated with manipulable man-made objects (e.g. *hammer*); this enabled us to measure activations in response to both explicit and implicit retrieval of knowledge about actions associated with manipulable tools. Function judgements were also made about non-manipulable artifacts (e.g. *traffic light*) providing a direct comparison for manipulable objects. Although neither the left VPMCx nor the left PMTG were *selective* for tool stimuli (non-manipulable objects also activated these areas relative to a visual control condition), both regions responded more strongly to manipulable objects, suggesting a role for these cortical areas in the processing of knowledge associated with tools. Furthermore, these activations were insensitive to retrieval task, suggesting that visually presented tools automatically recruit both left VPMCx and left PMTG in response to action features which are inherent in tool representations. In contrast, the IPS showed clear selectivity for explicit retrieval of action information about manipulable objects. No regions of cortex were more activated by function relative to action judgements about artifacts. These results are consistent with the brain's preferential responsiveness to how we interact with objects, rather than what they are used for.

INTRODUCTION

Following on from an extensive cognitive neuropsychological literature, a growing number of functional neuroimaging studies have investigated the distinctiveness of the neural substrates associated with category-specific object recognition. In line with some of the most robust and intriguing cognitive neuropsychological dissociations, a large proportion of these imaging studies have focused on comparisons between man-made objects, natural kinds (animals), and faces. Although some consistent category-specific activations have been reported, there have been relatively few systematic attempts to investigate processing differences which might account for these category-specific effects. This is despite a widespread (although not unanimous) view that object category delineations may be better defined in terms of differential weightings on a range of perceptual and functional/motor features than in terms of category membership *per se* (e.g. Allport, 1985; Martin & Chao, 2001; Saffran & Sholl, 2000; Warrington & Shallice, 1984).

The handful of functional neuroimaging studies which have examined a more feature-based processing account of category-specific differences have addressed the hypothesis that recognition of natural objects depends more on differentiating visual features than the recognition of man-made artifacts, which depends more critically on distinguishing functional/sensorimotor features (Gerlach, Law, Gade, & Paulson, 1999; Moore & Price, 1999). The outcome of at least some of these studies does indeed suggest that the differential processing of visual structure can usefully account for the unique activation patterns associated with natural kinds. The complementary extension of this hypothesis is that, relative to natural objects, man-made object representations are more crucially defined by ‘functional’ features which reflect how an object is used and/or what it is used for (e.g. Warrington & Shallice, 1984). Rather surprisingly, although there have been numerous studies probing the specificity of activations elicited by man-made objects, none of these to date has directly investigated whether the proposed ‘functional’ features can account for the observed activations.

One of the difficulties with addressing the issue of ‘functional’ feature representations associated with man-made objects is that such features tend to be under defined. For example, information about what an object is used for (its function), and how it is held, manipulated and moved, can all be described as ‘functional’ features. Knowledge about the function of man-made objects in contrast to how they are manipulated can, however, doubly dissociate in neuropsychological disorders, with some patients showing a pattern of impaired knowledge about tool function while manipulation knowledge remains relatively intact (Buxbaum, Schwartz, & Carew, 1997; Magnie, Ferreira, Giusiano, & Poncet, 1999; Sirigu, Duhamel, & Poncet, 1991), and other patients showing the reverse pattern (Buxbaum, Veramonti, & Schwartz, 2000). This double dissociation has led to the recent proposal that these two knowledge types are distinct and neuroanatomically discrete (Buxbaum et al., 2000). Furthermore, there are neuropsychological data suggesting that knowledge of manipulability or action, rather than function, may be particularly critical in the semantic representations of tools. First, there have been reports of patients with a relative deficit for tools compared to animals, who exhibit quite intact knowledge about object function in the face of degraded visual information (Lambon-Ralph, Howard, Nightingale, & Ellis, 1998: manipulation knowledge was not tested in this patient) or degraded information about how to manipulate the tool (Buxbaum et al., 2000). Second, selective preservation of knowledge about large man-made objects (e.g. buildings, vehicles) relative to small manipulable man-made objects has been reported (Warrington & McCarthy, 1983; Warrington & McCarthy, 1987; Yamadori & Albert, 1973). Finally, selective impairment of body part knowledge tends to co-occur with deficits for artifacts, suggesting a common substrate for actions and movements associated with body parts and man-made objects (Sacchett & Humphreys, 1992; Warrington & McCarthy, 1987).

Recent studies investigating the cortical regions involved in the identification of tools (or artifacts) have interpreted most of the observed activations in terms of representations specialised for actions or motor programs, and have implicated a network of cortical areas which overlaps with that

suggested by the neuropsychological studies.¹ Three cortical areas have been implicated in the representation of man-made objects/tools: left ventral precentral gyrus in the frontal lobe (ventral premotor cortex: VPMCx), left posterior parietal cortex in the region of the intraparietal sulcus (IPS), and posterior middle temporal gyrus (PMTG) either on the left or bilaterally (Cappa et al., 1998; Chao, Haxby, & Martin, 1999; Chao & Martin, 2000; Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Grabowski, Damasio, & Damasio, 1998; Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Martin, Wiggs, Ungerleider, & Haxby, 1996; Moore & Price, 1999; Mummery, Patterson, Hodges, & Price, 1998; Mummery, Patterson, Hodges, & Wise, 1996; Perani et al., 1999; Beauchamp, Lee, Haxby, & Martin, 2002). The majority of these studies have, however, restricted the comparison of tools to natural object categories (e.g. faces, animals). This approach makes it difficult to determine whether the observed patterns of activity reflect processing of features specifically related to the manipulability of the tools, or rather index the activation of other more associative aspects of ‘functional’ knowledge related to the purpose of the objects, or indeed any of the other dimensions along which natural and manmade domains might differ (e.g. visual complexity, emotional valence, structural similarity). A contrast between tools and other categories of man-made objects, holding other factors relatively constant, is necessary to isolate processes and representations uniquely associated with objects which are manipulated. Only two functional neuroimaging studies have compared tools to another category of man-made objects (houses) (Chao et al., 1999; Chao & Martin, 2000). These two studies used identical stimuli (object photographs) and tasks (naming, viewing) but examined different cortical regions: temporal cortex in the study by Chao, Haxby and Martin (Chao et al., 1999); fronto-parietal regions in the experiment by Chao and Martin (Chao & Martin, 2000). Interestingly, this pair of studies identified essentially the same network of cortical regions associated with tools as has been reported for man-made objects

¹ While many studies describe their stimuli as ‘tools’, it is not always clear that this refers exclusively to the category of manipulable manmade objects. For example, Cappa and colleagues refer to one of their object categories as tools, but cite *piano* and *couch* as examples of these (Cappa, Perani, Schnur, Tettamanti, & Fazio, 1998). Other studies do not explicitly define or provide examples of what they include as tool stimuli.

compared to ‘natural’ objects (see above). We will briefly consider the potential relevance of each of these cortical areas to manipulable object processing.

Looking at or naming tools relative to houses elicited significantly more activity in the left (or bilateral) PMTG (Chao et al., 1999), suggesting that this region of the temporal lobe supports some aspect of processing specific to manipulable objects rather than artifacts more generally. Primarily based on its proximity to the visual movement perception area V5/MT, and also evidence that a similar activation is observed during generation of names of actions associated with objects (e.g. Damasio et al., 2001; Fiez, Raichle, Balota, Tallal, & Petersen, 1996; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Warburton, Wise, Price, Weiller, & et al., 1996; Wise et al., 1991; see also Grezes & Decety, 2001b), Chao and colleagues have argued that this region stores information about visual motion associated with object use or so-called non-biological motion (Chao et al., 1999; Martin & Chao, 2001; Martin et al., 1996). More recently, however, Martin and colleagues (Beauchamp et al., 2002) have directly demonstrated that the PMTG responds more to video clips of moving tools than to either static images of tools or human forms, be they moving or static.

The second study demonstrated that areas of left VPMCx and left posterior parietal cortex (including the IPS) were selectively activated by viewing and naming manipulable tools relative to houses (Chao & Martin, 2000). It has been proposed that the left VPMCx stores movement representations and supports the retrieval of motor information about tool use, as this cortical region has been activated during motor imagery, observation of movement, copying of movements, and real and imagined pantomime of tool use (Buccino et al., 2001; Decety et al., 1994; Grafton, Fagg, Woods, & Arbib, 1996; Moll et al., 2000), as well as during verb generation tasks (Grafton et al., 1997; Martin et al., 1995; Petersen, Fox, Posner, Mintun, & Raichle, 1988). Furthermore, parallels have been drawn between activation of this cortical region in humans and neurones in the VPMCx of the monkey (area F5) which respond both to visually presented graspable objects, even when no subsequent movement is required, and during compatible grasping actions (Murata et al., 1997;

Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Rizzolatti et al., 1988; Sakata & Taira, 1994; Sakata, Taira, Murata, & Mine, 1995; Taira, Mine, Georgopoulos, Murata, & Sakata, 1990).

Chao and Martin speculated that the left posterior parietal activation reflected the retrieval of tool-specific grasp information, as this region has been implicated in the tactile manipulation of (meaningless) objects (Binkofski, Buccino, Posse et al., 1999; Binkofski, Buccino, Stephan et al., 1999). Consistent with this hypothesis, Grezes and Decety recently reported left posterior parietal activation associated with perception of photographs of tools across a range of tasks (Grezes & Decety, 2001a), while another recent study using line drawing of tools reported a similar activation (Okada et al., 2000). This region has also been activated by the observation of object-directed actions (but not hand actions in the absence of tools: Buccino et al., 2001), visually guided grasping (Binkofski et al., 1998; Faillenot, Toni, Decety, Gregoire, & Jeannerod, 1997), and by real and imagined pantomimes of tool-use (left hemisphere regardless of hand used: Moll et al., 2000). It is puzzling why this cortical area was not activated in previous functional imaging studies of tool representation (e.g. Damasio et al., 1996; Martin et al., 1996) which also used a picture naming task and compared tools to animals. It has also been suggested that this area may be the human homologue of the anterior IPS area in the monkey, where neurophysiological recordings have identified neurones which respond to both visual and motor aspects of grasping, as well as being selective for particular shapes of graspable objects (Murata et al., 1997; Murata et al., 2000; Rizzolatti et al., 1988; Sakata & Taira, 1994; Sakata et al., 1995; Taira et al., 1990; see also Binkofski, Buccino, Posse et al., 1999; Binkofski, Buccino, Stephan et al., 1999; Binkofski et al., 1998; Chao & Martin, 2000; Culham & Kanwisher, 2001). These findings have led to the proposal that the anterior IPS plays a critical role in the pragmatic description of objects for action (Jeannerod, 1994; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995). Finally, human lesion data suggest a role for posterior parietal cortex in finger movement coordination associated with object grasping and manipulation (Binkofski et al., 1998; Pause, Kunesch, Binkofski, & Freund, 1989), while the importance of left posterior parietal cortex in retrieving object-appropriate actions is

indicated by reports of ideational apraxia (impaired tool-use) in association with focal lesions to this region (Heilman, Maher, Greenwald, & Rothi, 1997).

In summary, the recent studies of Chao and colleagues comparing tools to another artifact category have implicated a network of three cortical areas in supporting the recognition of tools. This network has been interpreted as reflecting the representation of action and motion knowledge pertaining to the use of tools, primarily on the basis of converging evidence from functional neuroimaging studies of action naming, execution, observation, pantomime and imagery, as well evidence from neurophysiological studies of non-human primate grasping and object viewing. Furthermore, the data from the studies of Chao and Martin were argued to indicate that the observed cortical network associated with tools reflects activation of stored knowledge about motor-based properties of the tools which feature prominently in their semantic representations. This implies that these aspects of representation are accessed *automatically* during the processing resulting in object recognition, just as has been argued for the neurophysiological data demonstrating that neurones in regions of VPMCx and the IPS of the monkey respond simply to viewing graspable objects.

Despite these proposals, the precise roles and processing properties of the individual cortical regions in tool representation remain underspecified. This is in part because these studies which have compared manipulable and non-manipulable artifacts have not directly demonstrated that it is the retrieval of action knowledge which accounts for the observed activations. Even if action is the critical factor, questions remain about the aspects of action knowledge which might be implicated, and about the role of goal-directed attention. Furthermore, previous investigations have only compared tools to the single non-manipulable object category of ‘houses’, which seem a more visually and semantically homogeneous category of objects than tools. Conversely, the studies of action retrieval and execution which have provided critical converging data have restricted their investigations to tools, and therefore do not establish that the activations are specific to this object category.

The current study aimed to provide a first step in addressing some of these issues by explicitly investigating the hypothesis that the network of activations associated with tools reflects the retrieval of components of action knowledge. We have chosen to approach this issue of the specificity of the observed activations in two main ways. First, the experiment was designed to investigate the relationship between the activations previously observed to tools and the explicit retrieval of action versus function knowledge pertaining to manipulable objects; neuropsychological data suggest that these two types of knowledge may have distinct neural substrates. This goal was implemented by asking participants to make judgments about the actions or functions of objects. Although we expect that relevant aspects of semantic knowledge outside the focus of the task are implicitly activated (e.g. action knowledge when functional information is retrieved about manipulable objects; see below), we assume that directing attention to a particular aspect of semantic knowledge (e.g. action or function) will result in a relative enhancement of activity in those cortical areas supporting that knowledge. As the critical comparison here is between the same stimuli (manipulable objects) with two different tasks, we assume that any implicit knowledge activation will be the same for the two conditions. Second, the experiment was designed to examine the neural substrates associated with intrinsic manipulability, by comparing manipulable with non-manipulable artifacts when retrieval of action knowledge is not the focus of attention (i.e. during judgements about function). A central difference between these two questions lies in the automaticity of the action knowledge being explored. This contrast permits questions about differences in activation when explicit knowledge about a tool's action is activated/retrieved according to the goal-directed attention of the subject, and when similar features might be automatically activated by the presence of a manipulable object, regardless of the subject's goal.

RESULTS

Behavioural data

Reaction time: Reaction times (RT) differed between the four conditions [$F(3,24)=6.23$, $p=0.003$] (Table 1), which reflected the significantly faster responses to make function decisions about non-manipulable objects relative to both the action and function decisions for manipulable objects [Bonferroni corrected $\alpha = 0.008$: $t(1,8)=4.849$, $p=0.001$, $t(1,8)=9.191$, $p<0.001$ respectively]. The control condition RTs did not differ significantly from any of the experimental condition RTs at this conservative statistical threshold.

----- Insert Table 1 about here -----

Accuracy: Percentage of errors (either ‘no’ to a target or ‘yes’ to a non-target) did not differ between the four conditions [$F(3,24)=0.39$, $p=0.762$] (Table 1). The number of misses (failures to respond within the allotted time for the stimulus) did differ (just) reliably between the four conditions [$F(3,24)=2.96$, $p=0.052$], although no two pairs of conditions differed significantly from each other [Bonferroni corrected $\alpha = 0.008$: $t(1,8)=0.426-2.857$, all $p>0.02$] (Table 1). Note that the miss rate is probably somewhat inflated by the instruction ‘Do not respond if you do not recognise the object’. Accuracy of responses in this paradigm is desirable but not essential as long as the participants were accessing information germane to the experimental question.

PET data

REGIONS OF INTEREST ANALYSES

Left ventral premotor cortex (Brodmann’s area 6(44): Table 2, Figure 1): Activation in the region of left VPMCx was observed in all three experimental conditions relative to the control condition. Furthermore, both types of judgement regarding manipulable objects resulted in significantly larger activations in this area than did responses to non-manipulable objects. Action and function judgements about manipulable objects did not differ significantly from each other in this region. The activation foci for the comparisons involving action decisions about manipulable objects (precentral gyrus) were, however, somewhat more posterior to those elicited by the

comparisons involving function decisions (most posterior region of the inferior frontal gyrus). Nonetheless, inspection of the parameter estimate plots reveals that the pattern of activations across conditions is comparable for these two locations and, taken in conjunction with the overlapping nature of the two activations and the spatial resolution of PET, it seems likely that they reflect the same neural system in left VPMCx.

----- Insert Table 2 and Figure 1 about here -----

Left Posterior middle temporal gyrus (Brodmann's area 21: Table 3, Figure 1): Activation in the left PMTG was higher for both of the judgements regarding manipulable objects relative to non-manipulable objects. Relative to the control condition, all of the object conditions yielded activation in this region, although the activation foci identified by the ROI analysis fell within a large swathe of activation which encompassed most of the inferior temporal lobe, from the occipito-temporal junction to the temporal pole.

----- Insert Table 3 about here -----

Left posterior parietal cortex: intraparietal sulcus (Brodmann's area 7/40: Table 4, Figure 2): Left posterior parietal cortex in the region of the IPS was selectively activated by the explicit action judgements, relative to both of the functional judgement conditions (for both manipulable and non-manipulable objects) and to the control condition.

----- Insert Table 4 and Figure 2 about here -----

ACTIVATIONS OUTSIDE THE ROIs (WHOLE-BRAIN ANALYSES)

Left inferior parietal lobule (Brodmann's area 40: Table 5, Figures 1 & 2): An additional parietal activation focus was observed in the left inferior parietal lobule associated with action judgements to manipulable objects in comparison to non-manipulable objects and the control condition, and there was also evidence for a similar activation (although not achieving corrected significance) relative to the manipulable objects when a function judgement was made.

----- Insert Table 5 about here -----

Additional frontal activations (Table 6): While none of the ROIs was more activated by function judgements relative to the action condition, or by the non-manipulable objects relative to either of the judgements about manipulable objects, there were two regions of frontal cortex which approached whole-brain corrected statistical significance or which appeared in more than one comparison, suggesting some robustness: a region of right (and left) orbital frontal gyrus when function decisions regarding manipulable objects were compared to function decisions about non-manipulable objects, and an area of right inferior frontal gyrus when both manipulable and non-manipulable objects requiring function judgements were compared to the action condition.

----- Insert Table 6 about here -----

Activations of object judgement conditions compared to control (Appendix 1): When each of the experimental conditions was contrasted with the control condition, very similar left lateralised regions of inferior temporal and inferior frontal cortex were activated (see Appendix 1, Figures 1 & 2). While this pattern confirms what has been reported previously when semantic retrieval conditions are compared to a lower level control condition, activation outside the ROIs in these contrasts are not of explanatory value to the questions under investigation and therefore will not be discussed further.

DISCUSSION

Significant activations were observed in all three left hemisphere regions previously implicated in the processing of manipulable objects and the actions performed with them: left VPMCx, left PMTG and left posterior parietal cortex (in the region of the IPS). Most importantly, however, these ROIs were subject to differential patterns of activation across the experimental conditions, suggesting that these cortical regions probably play distinct processing roles in relation to man-made objects.

Left ventral premotor cortex and left posterior middle temporal gyrus: These two cortical areas will be discussed together because the patterns of results observed in these locations were

remarkably similar and therefore have comparable implications for interpretation. Both left VPMCx and left PMTG were activated by all the object conditions relative to the control condition, but also more activated by manipulable objects (irrespective of task) than by the non-manipulable objects.

The activations common to all real object types, including non-manipulable objects, were unexpected as both of these cortical regions have been argued to be selectively activated by tool stimuli and to reflect the defining nature of action- and motion-related attributes in the representation of these objects. Indeed, previous studies which have compared various object categories to non-objects and/or scrambled pictures have not reported enhanced activations of either left VPMCx or PMTG associated with any object category other than tools. One difficulty with interpreting the weaker activation elicited by non-manipulable objects is that only a small selection of object categories were examined within the present paradigm, so we cannot determine whether other categories, such as animals or cars would have also elicited activation in these cortical regions. Perhaps most relevant to the current results, the building stimuli used by Chao and Martin and colleagues did not elicit left VPMCx or PMTG activity relative to a scrambled object control condition, whereas tools did (Chao et al., 1999; Chao & Martin, 2000). This may indicate that our non-manipulable objects are somehow more similar to tools than buildings are, although it is not clear what dimension of similarity would elicit activation of left VPMCx and PMTG. The main hypotheses to date regarding the functional correlates of the left VPMCx and PMTG in tool processing are that they store information about motor movements and non-biological motion, respectively (Chao et al., 1999; Chao & Martin, 2000; Martin, 2001; Martin & Chao, 2001; Martin, Ungerleider, & Haxby, 2000; Martin et al., 1996; Beauchamp et al., 2002). These accounts are not, however, easily reconciled with the activation of these regions by non-manipulable objects (relative to the control condition), as objects like shelves have little or no motor movement or motion associated with their use.² Alternatively, the response of these regions to non-manipulable objects

² Although buildings and faces did not elicit more activity than the baseline task in left VPMCx or left PMTG in the studies by Martin and colleagues (Chao et al., 1999; Chao & Martin, 2000: personal communication), the cortical

may not be informative about the representation of this category of objects, but may simply reflect non-specific processes in response to object forms (e.g. increased attention) relative to the scrambled control. It is not possible to distinguish between these possibilities on the basis of the current data.

Nonetheless, the fact that activation of both left VPMCx and PMTG was greatest in response to manipulable objects suggests that these regions do play a role in representing information which is retrieved whenever a manipulable object is viewed; the insensitivity of these activations to the retrieval demands of the task further suggests that these regions are engaged by manipulable objects regardless of attention or intention. These enhanced activations are compatible with the hypothesis that they reflect the automatic retrieval of action and motion representations associated with manipulable objects. As proposed by Chao and Martin (2000), these properties of tools seem to be automatically activated when people encounter and recognise such objects.

The data therefore suggest that although left VPMCx and PMTG are not exclusively involved in representing knowledge associated with manipulable man-made objects, these regions are more sensitive to objects that can be manipulated. Why non-manipulable objects recruited these cortical regions in the current study remains to be explained, although the use of unusually engaging judgement tasks may be a pertinent factor.

Finally, it is important to note that although the left VPMCx and PMTG activations have been discussed together here, these activations do not always co-occur in studies of tool representation or action naming, with left PMTG activations more consistently reported than those in left VPMCx. Martin has suggested that the relatively less prominent response of left VPMCx may reflect the masking of activations in this region by tasks which recruit adjoining prefrontal regions (e.g. those with verbal output: Martin, 2001). Although the consistency of the activation in left PMTG suggests a particularly critical role for this region in the representation of tools, we note that it was

regions analysed for between-condition effects were determined on the basis of sensitivity to all object types relative to baseline (i.e. object main effect).

the least robust of the observed activations in the present study (both in terms of extent and statistical significance).

Left posterior parietal cortex (IPS) and inferior parietal lobule: Previous reports of activation of the left posterior parietal cortex from studies examining tool representations have been extremely sporadic and, even when present, the activations have not been particularly large or robust (Chao & Martin, 2000; Okada et al., 2000), particularly in comparison to the other two members of this triadic network discussed above. It is also interesting to note that while both left PMTG and VPMCx regions have also been activated by action naming paradigms, the IPS has not (Damasio et al., 2001; Fiez et al., 1996; Martin et al., 1995; Wise et al., 1991) see also (Grezes & Decety, 2001b). Given these discrepancies, it is perhaps not surprising that the activation of left posterior parietal cortex observed in the present study exhibited a quite different pattern from that seen in the left VPMCx and PMTG. A large and highly significant activation was elicited in left posterior parietal cortex (in the region of the IPS) by explicit judgements about the type of movement engaged during the use of manipulable objects. This cortical area was not activated by either of the function judgements even relative to the control condition, suggesting that this structure is *selectively* activated by retrieval of knowledge concerning action, rather than simply relatively more activated in this condition. The fact that the left intraparietal sulcus was not also activated by function judgements about manipulable objects suggests that this structure is not activated *automatically* by either visuomotor affordances or by knowledge about the manipulability of the objects, as these would be equivalent for the two manipulable object conditions (which had identical stimuli across subjects). The specificity of this activation to action judgements is, however, consistent with a role for this cortical region in the *intentional* retrieval of information about hand and finger movements associated with tool use, and also with claims that what might be the monkey homologue of this region (IPS) plays a critical role in the pragmatic description of objects for action (Binkofski, Buccino, Posse et al., 1999; Binkofski, Buccino, Stephan et al., 1999; Binkofski et al., 1998; Jeannerod, 1994; Jeannerod et al., 1995). Curiously, however, the neurones

in monkey IPS respond simply to viewing graspable objects. In light of the present evidence suggesting that activation of human IPS requires attentional processing, this might suggest either a lack of functional equivalence between the human and monkey IPS, or that monkeys explicitly plan grasping actions even when simply viewing graspable objects.

How might one interpret activation of left IPS in the few previous experiments which have reported it but which simply required naming or observation of tools (Chao & Martin, 2000; Grezes & Decety, 2001a; Okada et al., 2000)? Although these tasks do not explicitly require access to knowledge about hand movements, the rather undemanding nature of the primary task would almost certainly have allowed active consideration of the way in which the tools are utilised. This highlights a possible drawback of using tasks which do not specifically control for the type of knowledge attended to and/or retrieved. The lack of control for such task factors may at least partially account for the activations observed in this cortical region in previous studies of tool representations.

An additional activation focus in the left inferior parietal lobule, and therefore ventral and adjacent to the IPS, was also associated with the action retrieval condition relative to function judgments about non-manipulable objects, although a similar (but not quite statistically significant) activation was also evident in the comparison between action and function judgements about manipulable objects. This suggests a gradation of activation in this region, with manipulable objects eliciting the most activation when a decision was made about the hand movements associated with their use, and non-manipulable objects eliciting the least activation.

Both the left IPS region and adjacent left inferior parietal lobule have recently been shown to play a critical role in (covert) motor attention in relation to limbs, regardless of whether a subsequent movement is made (Deiber et al., 1998; Krams, Rushworth, Deiber, Frackowiak, & Passingham, 1998; Rushworth, Krams, & Passingham, 2001; see also Crammond, 1997).³ The evidence from the present study that both these regions are activated when the task requires explicit retrieval of

motor-based knowledge about tool use is clearly entirely consistent with these findings relating to motor attention processes. Interestingly, a similar region of IPS was more activated during an episodic retrieval task involving noun-verb word pairs when encoding was associated with overt action than covert action (Nyberg et al., 2001), again suggesting that attention to action elicits activation in this region.

Further consistent with the hypothesis that the IPS supports the (active) description of objects for action (Jeannerod, 1994; Jeannerod et al., 1995), activation of this region has been observed across a wide range of both explicit and implicit ‘motor’ tasks, as reviewed in the Introduction. It should be noted, however, that activation of the IPS has also been reported in studies of motion (attentive movement tracking (Culham et al., 1998), motion processing (Braddick et al., 2001; Bremmer et al., 2001) and motion imagery (Binkofski et al., 2000)), as well as a number of other more diverse experimental manipulations, such as numeric processing (Kazui, Kitagaki, & Mori, 2000; Pesenti, Thioux, Seron, & De Volder, 2000), visuospatial detection tasks (Haxby et al., 1994), visual working memory (Belger et al., 1998; Klingberg, O’Sullivan, & Roland, 1997; Manoach et al., 1997), surface orientation discrimination (Shikata et al., 2001), and a range of visual attention tasks (Wojciulik & Kanwisher, 1999). Thus, although implicated in the processing of knowledge about tool use, the left IPS is clearly not uniquely involved in such processing and is recruited across a range of motor and non-motor tasks, leaving open the possibility that this region supports a more general cognitive function involved in visuomotor attention. In this context it is perhaps worth noting that, as the action condition did not elicit longer RTs or higher error rates in the present experiment, it appears unlikely that IPS activation simply indexes ‘task difficulty’ (to the extent that these behavioural measures index ‘difficulty’).⁴ Further investigation of both the lateralisation and possible fractionation of the IPS into distinct regions (e.g. anterior/posterior) is necessary to determine whether the many paradigms which activate the IPS do so uniformly or whether there are

³ Although Rushworth and colleagues (Rushworth et al., 2001) localised their activation to the left supramarginal gyrus rather than the left inferior parietal lobule, the Talairach and Tournoux (1988) coordinates obtained in their study and in the present study are very similar.

⁴ RTs were included as a covariate in the PET data analyses

distinct neuroanatomical substrates which underlie different functional processes. The lateralisation of the posterior parietal activations to the left hemisphere in both this and previous studies involving tool stimuli is interesting in light of the fact that ideational apraxia has been associated with damage to this left-lateralised region. Functional dissociations between left and right IPS on the basis of visually guided hand movements for the former and perception for the latter, have also been suggested by both functional neuroimaging (Faillenot et al., 1997; Taira, Kawashima, Inoue, & Fukuda, 1998) and clinical (Goodale et al., 1994; Perenin & Vighetto, 1988) data. It is also worth noting that although we used only right-handed volunteers in the present study, it appears less likely that the left hemisphere parietal activations reflect aspects of action processing which are induced by imagined hand movements associated with the contralateral hand since Moll and colleagues reported left lateralised activations irrespective of which hand was employed in a tool-use pantomime paradigm (Moll et al., 2000).

So, where's the functional knowledge? Rather surprisingly, no regions of cortex were selectively more activated by the retrieval of knowledge relevant to the functions of objects relative to their actions. While there was some suggestion that an area of right inferior frontal gyrus responded to function judgements, this effect did not reach statistical significance. Nonetheless, it is notable that the only region even hinting at being specialised for function knowledge was frontal, rather than in the temporal cortical regions which have been suggested as critical on the basis of neuropsychological data (e.g. Buxbaum et al., 2000; Sirigu et al., 1991).

A region of right (and perhaps bilateral) orbital frontal gyrus also approached significance when function decisions were made about manipulable objects compared to similar judgements regarding non-manipulable objects. Interpretation of this effect must be treated cautiously given the lack of statistical significance, but this activation is interesting in the light of evidence that orbito-frontal cortex may play a role in inhibiting motor actions (Marshall, Halligan, Fink, Wade, & Frackowiak, 1997).

The lack of activations specific to the retrieval of function knowledge about manmade objects, in contrast to the multiple robust activations associated with action and manipulability knowledge, is consistent with neuropsychological evidence that knowledge pertaining to aspects of action, rather than knowledge about function, is central in the semantic representations of tools (Buxbaum et al., 2000; Lambon-Ralph et al., 1998; Sacchett & Humphreys, 1992; Warrington & McCarthy, 1983; Warrington & McCarthy, 1987; Yamadori & Albert, 1973): hence our title, actions speak louder than functions. Of course brain networks must incorporate knowledge of what man-made objects are used for, but they seem more egocentrically responsive to how we interact with such objects.

METHOD

Participants

Nine males (mean age 27 years, range 23-33 years) who were right-handed, had English as their first language, and had normal or corrected-to-normal vision were paid for their participation. All were screened for medical and other exclusion criteria and provided informed consent prior to scanning.

Design and Materials

Three experimental conditions were designed to require access to knowledge regarding the action or function of familiar man-made objects. Action knowledge was probed for manipulable objects (tools) only, while functional knowledge was probed for both manipulable and non-manipulable objects. Participants used binary button-press responses to respond ‘yes’ or ‘no’ to questions which probed these two types of knowledge (see Table 7). Three questions were used for each condition, one for each scan. The participants’ understanding of the tasks was consolidated by using examples and practice trials prior to the commencement of scanning.

----- Insert Table 7 about here -----

Three sets of seventy-two colour photographs of manmade objects on a white background were selected for each of the three experimental conditions, with 50% chosen to elicit a positive response

and 50% to elicit a negative response. The objects in the photographs were sized to reach a roughly constant distance from the edges of the background, with the result that both large and small objects were depicted as a similar size. Two of the sets of photographs comprised manipulable objects (all manipulated by the hand), while the third set comprised non-manipulable objects.⁵ Each of the two manipulable object sets contained both action and function targets, and half the subjects saw Set 1 in the action knowledge condition and Set 2 in the function knowledge condition, while the other half of the subjects saw the reverse combination. This ensured that the same stimuli were seen in the manipulable object action and function conditions across subjects, and all stimulus characteristics were thereby controlled across these two conditions. For each condition, three subsets of 24 stimuli were created which corresponded to each of the three questions relevant to that condition (Table 7). The objects were matched for familiarity across conditions, and the two manipulable object stimulus sets were matched for high ‘manipulability’, while the non-manipulable objects were confirmed to be of low ‘manipulability’ (see below: Table 8). Finally, the consistency with which the actions and functions were associated with the target (‘yes’ response) objects was tested and matched across all stimulus sets.

----- Insert Table 8 about here -----

Familiarity and manipulability ratings for 187 objects were obtained from 13 paid volunteers (all male, mean age 30 years, range 21-40 years). Volunteers rated photographs of the objects on a white background (which were later used as stimuli in the experiment). In addition, volunteers indicated the name of each object (identification), whether each object was used for each the functions probed in the experiment (see Table 7), and whether its use involved the movements/actions probed in the experiment. For the manipulability rating, volunteers were asked to rate ‘how strongly you associate manipulation with each of the objects’ on a 3-point scale. Examples with a range of responses were used to indicate what was meant by this. Familiarity was

⁵ ‘Manipulable’ objects is used to refer to objects which are manipulated by hand during their use. In contrast, ‘non-manipulable’ objects are defined as objects which are not usually manipulated (although it may be possible to physically interact with them: e.g. it is possible to pick up/move a speaker, but this action is not intrinsic to the function of the object nor carried out in a way specific to this object rather than any other of a similar size/shape).

rated on a 5-point scale and, following Snodgrass & Vanderwart (1980), volunteers were asked to rate ‘the degree to which you *come into contact with* or *think about* each of the objects’. Participants were reminded to rate their familiarity with the type of object depicted rather than the exact exemplar used, and were given three examples with a range of responses.

A control condition was constructed which was visually similar to the experimental conditions while having no semantic or cohesive structural (3D object) content. This condition comprised scrambled photographs of objects not used in the experimental conditions. For each photograph, pairs of blocks (each 32 pixels square) were randomly swapped 200 times to create a scrambled image. A white border comparable to that surrounding the object photographs was also maintained. Half of the scrambled photographs contained a solid black circle, while the other half did not. For this condition the question posed was ‘Is there a black circle?’.

Procedure

Participants were instructed and given examples of the tasks before being positioned in the PET scanner. Once in the scanner they were also given a short practice for each condition to familiarise them with both the tasks and the scanner set-up. The stimuli were presented on a monitor suspended over the scanner, which was 100 cm from the participant’s eyes and positioned so that he had an unobstructed view. Behavioural responses were recorded via a two-button mouse, and responses were made with the middle (‘no’) and index (‘yes’) fingers of the left hand. Speed and accuracy of responses were given equal weighting in the instructions.

Each participant was scanned 12 times, with three scans for each of the four conditions (three experimental, one control), and a different set of 24 stimuli presented during each condition repetition. The scan order of the conditions was counterbalanced across participants, while within each scan the order of the stimuli was randomised for each participant.

Prior to image acquisition, condition and response instructions were displayed for ten seconds, and one unique lead-in item appropriate to the condition was presented. Onset of the experimental stimuli coincided with the onset of image acquisition. Stimulus photographs were presented for

2000 ms each, with an ISI of 2000 ms. After the presentation of the experimental stimuli (56 sec), participants viewed a fixation point (colon) for the remainder of the scanning period (34 sec). This technique of switching from the task of interest shortly after the count rate reaches its peak has been used to improve the signal-to-noise ratio by reducing isotope washout from activated regions (e.g. Cherry, Woods, Doshi, Banerjee, & Mazziotta, 1995; see also Gerlach et al., 1999; Kanwisher, Woods, Iacoboni, & Mazziotta, 1997; Simons, Graham, Owen, Patterson, & Hodges, 2001).

PET scanning and data analysis

A GE Advance scanner was used to obtain 12 scans for each participant, each comprising 35 image slices at an intrinsic resolution of approximately 4.0 x 5.0 x 4.5 mm. Each participant received twelve 20 sec intravenous bolus injections of 300 MBq ml⁻¹ H₂¹⁵O, at a flow rate of 10 ml min⁻¹, through a forearm cannula. This method results in images of rCBF integrated over a 90 sec period from the time the tracer enters cerebral circulation. Head movements were restricted by foam padding.

We used SPM99 software for image analysis (Wellcome Department of Cognitive Neurology, London, UK). The twelve scans for each subject were first realigned using the first scan as a reference. Inspection of the realignment parameters indicated that none of the nine participants had head movements exceeding 3mm. For each subject, the mean of the PET images was spatially normalised to a template matching the Montreal Neurological Institute (MNI) standard template. Each of the individual realigned PET images was then resliced using the same transformations to give 12 scans per subject matched to the MNI brain. These images were smoothed with a 16mm FWHM isotropic Gaussian kernel to increase signal relative to noise. As is standard for SPM99, the effect of global signal in each scan was removed with subject-specific global signal covariates in the statistical analysis. Reaction time was entered as a covariate of interest. We included reaction time as a covariate in order to remove the components of the task differences that could be explained by differences in reaction times. With this covariate in the model, contrasts between conditions will reveal differences that cannot be explained by a simple linear relationship to

reaction time. The results therefore can be thought of as reflecting differences between conditions after any task effects reflected in reaction time have been adjusted for. In fact, analysis with and without reaction time included as a covariate were extremely similar and, importantly, all of the results reported as significant here were also significant in the analysis without reaction time as a covariate. Task related differences in rCBF were estimated for each voxel using SPM99; time (scan order) and head movement (three planes of rotation, three dimensions of translation) were set as confounding factors in the analysis (Brett, Bloomfield, Brooks, Stein, & Grasby, 1999). Peak activations outside specified regions of interest (ROIs) were thresholded with the conservative criterion of $p < .05$ corrected for multiple comparisons across the entire brain volume. In addition, in line with our *a priori* hypotheses, significance thresholds for three brain regions were adjusted using ROIs. Each of the ROIs were defined by taking a sphere of 10mm radius centred on co-ordinates derived by averaging the peak voxel co-ordinates reported for the relevant cortical area in previous studies of tool representation (Chao et al., 1999; Chao & Martin, 2000):

- Left ventral premotor: -46 05 24
- Left posterior parietal (intraparietal sulcus): -31 -43 45
- Left posterior middle temporal gyrus: -46 -54 3

Results are presented in tables giving coordinates with statistics and in figures showing brain slices through the regions of interest. The tables give results abstracted from the SPM results output, and coordinates are in terms of the MNI brain to which the data have been spatially normalised. To estimate the Brodmann areas of each activation focus, we have used the Talairach atlas (Talairach & Tournoux, 1988). The brain in this atlas is not the same shape or size as the MNI brain, so a simple transform of the MNI coordinates (<http://www.mrc-cbu.cam.ac.uk/Imaging/mnispac.html>) was used to estimate their locations in the Talairach atlas. For the ROI analyses, only local maxima co-ordinates which fall within the cortical region of interest are reported. Figure 1 uses colour intensity overlaid on the MNI brain template to show activation in various key regions. The colour intensity represents the size of effect at each voxel, in terms of estimated ml/min/dl blood flow

change. The outlined areas in Figure 1 and the activations shown in Figure 2 show where activity is significant at the threshold determined for the 10mm radius sphere ROIs ($t \geq 2.94$, d.f.=78, $\alpha=.05$), and therefore where the t statistic (which is the size of effect divided by an estimate of its standard error) is above the threshold given by random field theory (Worsley et al., 1996).

TABLES

Table 1

	Action decision manipulable objects	Functional decision manipulable objects	Functional decision non-manipulable objects	Control condition (circle detection)
RT	1228 (189)	1254 (211)	1107 (177)	1084 (218)
% Errors	3.4 (3.2)	4.5 (3.6)	3.7 (2.8)	3.7 (5.5)
% Misses	5.3 (6.7)	5.0 (7.7)	3.7 (4.2)	3.2 (6.3)

Mean reaction times, standard deviations, error rates, and miss rates for each condition.

Table 2

Comparison	Coordinates			T	Uncorr	ROI corr
	x	y	z			
<i>Action - NonManipulable Function</i>	-50	-02	26	3.65	<.001	.009
<i>Manipulable Function - NonManipulable Function</i>	-54	10	28	3.72	<.001	.007
<i>Action - Control</i>	-46	04	20	6.90	<.001	<.001
<i>Manipulable Function - Control</i>	-50	14	22	8.33	<.001	<.001
<i>NonManipulable Function - Control</i>	-46	16	24	6.24	<.001	<.001

Activations in left ventral premotor cortex. Anatomical localisation of maximal t-values are in stereotaxic coordinates in mm. Activation peaks ≥ 6 mm apart per cluster were identified. T=t-value, uncorr=uncorrected p-values, ROI corr=p-values corrected for 10mm radius spherical ROI (see text).

Table 3

Comparison	Coordinates			T	Uncorr	ROI corr
	x	y	z			
<i>Action - NonManipulable Function</i>	-48	-62	00	3.89	<.001	.004
<i>Manipulable Function - NonManipulable Function</i>	-52	-52	00	3.21	.001	.026
<i>Action - Control</i>	-46	-60	-04	7.48	<.001	<.001
<i>Manipulable Function - Control</i>	-52	-50	-02	7.54	<.001	<.001
<i>NonManipulable Function - Control</i>	-52	-48	-00	5.30	<.001	<.001
	-42	-50	-04	5.17	<.001	<.001
	-46	-60	-04	4.58	<.001	.001
	-38	-58	08	3.25	.001	.024

Activations in left posterior middle temporal gyrus. Anatomical localisation of maximal t-values are in stereotaxic coordinates in mm. Activation peaks ≥ 6 mm apart per cluster were identified. T=t-value, uncorr=uncorrected p-values, ROI corr=p-values corrected for 10mm radius spherical ROI (see text).

Table 4

Comparison	Coordinates			T	Uncorr	ROI corr
	x	y	z			
<i>Action - Manipulable Function</i>	-38	-44	48	4.34	<.001	.001
<i>Action - NonManipulable Function</i>	-38	-44	42	5.30	<.001	<.001
<i>Action - Control</i>	-38	-44	44	5.90	<.001	<.001

Activations in left posterior parietal cortex (intraparietal sulcus). Anatomical localisation of maximal t-values are in stereotaxic coordinates in mm. Activation peaks ≥ 6 mm apart per cluster were identified. T=t-value, uncorr=uncorrected p-values, ROI corr=p-values corrected for 10mm radius spherical ROI (see text).

Table 5

Comparison	Coordinates			T	Uncorr	Whole Brain Corrected
	x	y	z			
<i>Action - Manipulable Function</i>	-62	-42	26	4.04	<.001	.466
	-52	-30	24	3.98	<.001	.518
	-70	-24	08	3.63	<.001	.848
<i>Action - NonManipulable Function</i>	-58	-36	36	5.20	<.001	.016
	-52	-38	30	5.11	<.001	.022
<i>Action - Control</i>	-56	-44	20	5.27	<.001	.012

Activations in left inferior parietal lobule. Anatomical localisation of maximal t-values are in stereotaxic coordinates in mm. Activations in bold type indicate region maxima, and peaks are ≥ 8 mm apart per cluster. T=t-value, uncorr=uncorrected p-values, whole brain corrected=p-values corrected for entire brain volume.

Table 6

Comparison	Coordinates			T	Uncorr	Whole Brain
Cortical area (Brodmann's area)	x	y	z			Corrected
<i>Manipulable Function - NonManipulable Function</i>						
Left orbital frontal gyrus (BA 11)	-20	62	-14	4.45	<.001	.065
Right orbital frontal gyrus (BA 11)	26	64	-14	4.26	<.001	.131
<i>Manipulable Function - Action</i>						
Right inferior frontal gyrus (BA 47)	48	28	-20	4.78	<.001	.063
<i>NonManipulable Function - Action</i>						
Right inferior frontal gyrus (BA 47)	50	28	-22	4.09	<.001	.419

Activations in the frontal lobe outside the ROIs. Anatomical localisation of maximal t-values are in stereotaxic coordinates in mm (R=right, L=left). Activations in bold type indicate region maxima, and peaks are ≥ 8 mm apart per cluster. T=t-value, uncorr=uncorrected p-values, whole brain corrected=p-values corrected for entire brain volume.

Table 7

Knowledge type probed	Questions	Example of a 'yes' response object	Example of a 'no' response object
Action (manipulable objects)	<i>Does using the object involve...</i>		
	A twisting or turning action?	<i>Key</i>	<i>Stapler</i>
	A squeezing or pinching action?	<i>Clothes peg</i>	<i>Lipstick</i>
	A back-and-forth action?	<i>Saw</i>	<i>Scissors</i>
Function (manipulable objects)	<i>Is the object used to...</i>		
	Attach or hold objects together?	<i>Stapler</i>	<i>Saw</i>
	Alter the shape or size of another object?	<i>Scissors</i>	<i>Key</i>
	Put a substance on another object?	<i>Lipstick</i>	<i>Clothes peg</i>
Function (non-manipulable objects)	<i>Is the object used to...</i>		
	Put other objects in or on?	<i>Shelves</i>	<i>Stop sign</i>
	Make light or noise?	<i>Speaker</i>	<i>Hinge</i>
	Increase safety or protection?	<i>Traffic light</i>	<i>Ceiling fan</i>

Questions used to probe action and function knowledge, and examples of 'yes' and 'no' response items for each question.

Table 8

	Familiarity (5-point scale)	Manipulability (3-point scale)	% agreement on Action	% agreement on Function
Manipulable objects (Set 1)	3.3 (1.1)	2.6 (0.5)	96 (5)	91 (9)
Manipulable objects (Set 2)	3.5 (1.0)	2.5 (0.5)	94 (8)	90 (8)
Non-manipulable objects	3.2 (1.2)	1.2 (0.4)	-	89 (8)

Means and standard deviations (in parentheses) for ratings of familiarity and manipulability, and the degree of agreement (in %) as to the actions and functions associated with the objects.

APPENDIX 1

Comparison	Brodmann's Area	Coordinates x y z	T	Uncorr	Whole Brain Corrected
<i>Action - Control</i>					
L. Inferior temporal gyrus	37	-46 -62 -12	9.02	<.001	<.001
L. Fusiform gyrus	20	-42 -26 -26	7.70	<.001	<.001
L. Middle temporal gyrus	21	-46 04 20	6.90	<.001	<.001
L. Inferior frontal gyrus	47	-36 34 -16	7.43	<.001	<.001
L. Inferior frontal gyrus	47	-42 38 -02	6.72	<.001	<.001
L. Postcentral gyrus	1/2	-56 -18 24	5.57	<.001	.004
L. Intraparietal sulcus	7/40	-38 -44 44	5.90	<.001	.001
L. Inferior parietal lobule	40	-56 -44 20	5.27	<.001	.012
R. Cerebellum		26 -82 -42	5.50	<.001	.006
<i>Manipulable Function - Control</i>					
L. Inferior temporal gyrus	37	-50 -48 -20	9.12	<.001	<.001
L. Inferior frontal gyrus	47	-38 34 -14	8.71	<.001	<.001
L. Inferior frontal gyrus	45	-50 18 22	8.53	<.001	<.001
L. Fusiform/occipital gyrus	19	-44 -74 -12	7.80	<.001	<.001
L. Inferior temporal/fusiform gyrus	20	-44 -14 -38	5.91	<.001	.001
R. Middle occipital gyrus	19	34 -76 -48	7.36	<.001	<.001
R. Cerebellum		26 -82 -38	7.01	<.001	<.001
R. Superior parietal lobule	7	50 -74 -22	5.25	<.001	.013
L. Superior parietal lobule	7/19	-40 -74 38	5.05	<.001	.026
<i>NonManipulable Function - Control</i>					
L. Fusiform gyrus	36/37	-36 -38 -18	8.07	<.001	<.001
L. Inferior temporal gyrus	37	-40 -54 -16	7.98	<.001	<.001
L. Inferior temporal gyrus	37	-48 -48 -20	7.73	<.001	<.001
L. Inferior frontal gyrus	47	-36 34 -14	7.48	<.001	<.001
L. Fusiform gyrus	20	-38 -24 -30	7.22	<.001	<.001
L. Superior temporal gyrus (pole)	38	-50 18 22	6.41	<.001	<.001
L. Inferior frontal gyrus	45/47	-48 28 02	5.75	<.001	.002
L. Superior temporal gyrus (pole)	38	-44 14 -30	5.73	<.001	.002
L. Superior parietal lobule	7/19	-40 -74 30	5.31	<.001	.011
R. Inferior/middle occipital gyrus	18/19	54 -78 -14	5.75	<.001	.002
R. Cerebellum		28 -82 -44	5.30	<.001	.011
R. Hippocampus		20 -10 -22	5.28	<.001	.012

Brain regions activated by each of the object judgement conditions compared to the control condition. Anatomical localisation of maximal t-values are in stereotaxic coordinates in mm (R=right, L=left). Activations in bold type indicate region maxima, and peaks are ≥ 8 mm apart per cluster. T=t-value, uncorr=uncorrected p-values, whole brain corrected=p-values corrected for entire brain volume.

REFERENCES

- Allport, A. (1985). Distributed memory, modular subsystems and dysphasia. In S. K. a. E. Newman, R. (Ed.), *Current perspectives in dysphasia*. (pp. 32-60). Edinburgh: Churchill Livingstone.
- Beauchamp, M. S., Lee, K. E., Haxby, J. V., & Martin, A. (2002). Parallel visual motion processing streams for manipulable objects and human movements. *Neuron*, 34, 1-20.
- Belger, A., Puce, A., Krystal, J. H., Gore, J. C., Goldman Rakic, P., & McCarthy, G. (1998). Dissociation of mnemonic and perceptual processes during spatial and nonspatial working memory using fMRI. *Hum Brain Mapp*, 6, 14-32.
- Binkofski, F., Amunts, K., Stephan, K. M., Posse, S., Schormann, T., Freund, H. J., Zilles, K., & Seitz, R. J. (2000). Broca's region subserves imagery of motion: a combined cytoarchitectonic and fMRI study. *Hum Brain Mapp*, 11, 273-285.
- Binkofski, F., Buccino, G., Posse, S., Seitz, R. J., Rizzolatti, G., & Freund, H. (1999). A fronto-parietal circuit for object manipulation in man: evidence from an fMRI-study. *Eur J Neurosci*, 11, 3276-3286.
- Binkofski, F., Buccino, G., Stephan, K. M., Rizzolatti, G., Seitz, R. J., & Freund, H. J. (1999). A parieto-premotor network for object manipulation: evidence from neuroimaging. *Exp Brain Res*, 128, 210-213.
- Binkofski, F., Dohle, C., Posse, S., Stephan, K. M., Hefter, H., Seitz, R. J., & Freund, H. J. (1998). Human anterior intraparietal area subserves prehension: a combined lesion and functional MRI activation study. *Neurology*, 50, 1253-1259.
- Braddick, O. J., O'Brien, J. M., Wattam Bell, J., Atkinson, J., Hartley, T., & Turner, R. (2001). Brain areas sensitive to coherent visual motion. *Perception*, 30, 61-72.
- Bremmer, F., Schlack, A., Shah, N. J., Zafiris, O., Kubischik, M., Hoffmann, K., Zilles, K., & Fink, G. R. (2001). Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron*, 29, 287-296.
- Brett, M., Bloomfield, P., Brooks, D., Stein, J., & Grasby, P. M. (1999). Scan order effects in PET activation studies are caused by motion artefact. *Neuroimage*, 9, S56.
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R. J., Zilles, K., Rizzolatti, G., & Freund, H. J. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur J Neurosci*, 13, 400-404.

- Buxbaum, L. J., Schwartz, M. F., & Carew, T. G. (1997). The role of semantic memory in object use. *Cognitive Neuropsychology*, 14, 219-254.
- Buxbaum, L. J., Veramonti, T., & Schwartz, M. F. (2000). Function and manipulation tool knowledge in apraxia: Knowing 'what for' but not 'how.' *Neurocase*, 6, 83-97.
- Cappa, S. F., Perani, D., Schnur, T., Tettamanti, M., & Fazio, F. (1998). The effects of semantic category and knowledge type on lexical-semantic access: a PET study. *Neuroimage*, 8, 350-359.
- Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nat Neurosci*, 2, 913-919.
- Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *Neuroimage*, 12, 478-484.
- Cherry, S. R., Woods, R. P., Doshi, N. K., Banerjee, P. K., & Mazziotta, J. C. (1995). Improved signal-to-noise in PET activation studies using switched paradigms. *J Nucl Med*, 36, 307-314.
- Crammond, D. J. (1997). Motor imagery: never in your wildest dream. *Trends Neurosci*, 20, 54-57.
- Culham, J. C., Brandt, S. A., Cavanagh, P., Kanwisher, N. G., Dale, A. M., & Tootell, R. B. (1998). Cortical fMRI activation produced by attentive tracking of moving targets. *J Neurophysiol*, 80, 2657-2670.
- Culham, J. C., & Kanwisher, N. G. (2001). Neuroimaging of cognitive functions in human parietal cortex. *Curr Opin Neurobiol*, 11, 157-163.
- Damasio, H., Grabowski, T. J., Tranel, D., Hichwa, R. D., & Damasio, A. R. (1996). A neural basis for lexical retrieval. *Nature*, 380, 499-505.
- Damasio, H., Grabowski, T. J., Tranel, D., Ponto, L. L., Hichwa, R. D., & Damasio, A. R. (2001). Neural correlates of naming actions and of naming spatial relations. *Neuroimage*, 13, 1053-1064.
- Decety, J., & Grezes, J. (1999). Neural mechanisms subserving the perception of human actions. *Trends in Cognitive Sciences*, 3, 172-179.
- Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., Mazziotta, J. C., & Fazio, F. (1994). Mapping motor representations with positron emission tomography. *Nature*, 371, 600-602.
- Deiber, M. P., Ibanez, V., Honda, M., Sadato, N., Raman, R., & Hallett, M. (1998). Cerebral processes related to visuomotor imagery and generation of simple finger movements studied with positron emission tomography. *Neuroimage*, 7, 73-85.

- Faillenot, I., Toni, I., Decety, J., Gregoire, M. C., & Jeannerod, M. (1997). Visual pathways for object-oriented action and object recognition: functional anatomy with PET. *Cereb Cortex*, 7, 77-85.
- Fiez, J. A., Raichle, M. E., Balota, D. A., Tallal, P., & Petersen, S. E. (1996). PET activation of posterior temporal regions during auditory word presentation and verb generation. *Cereb Cortex*, 6, 1-10.
- Gerlach, C., Law, I., Gade, A., & Paulson, O. B. (1999). Perceptual differentiation and category effects in normal object recognition: a PET study. *Brain*, 122, 2159-2170.
- Goodale, M. A., Meenan, J. P., Bulthoff, H. H., Nicolle, D. A., Murphy, K. J., & Racicot, C. I. (1994). Separate neural pathways for the visual analysis of object shape in perception and prehension. *Curr Biol*, 4, 604-610.
- Grabowski, T. J., Damasio, H., & Damasio, A. R. (1998). Premotor and prefrontal correlates of category-related lexical retrieval. *Neuroimage*, 7, 232-243.
- Grafton, S. T., Fadiga, L., Arbib, M. A., & Rizzolatti, G. (1997). Premotor cortex activation during observation and naming of familiar tools. *Neuroimage*, 6, 231-236.
- Grafton, S. T., Fagg, A. H., Woods, R. P., & Arbib, M. A. (1996). Functional anatomy of pointing and grasping in humans.
- Grafton, S. T., Mazziotta, J. C., Woods, R. P., & Phelps, M. E. (1992). Human functional anatomy of visually guided finger movements. *Brain*, 115, 565-587.
- Grezes, J., & Decety, J. (2001a). Does visual perception of objects afford action? Evidence from a neuroimaging study. *Neuropsychologia*.
- Grezes, J., & Decety, J. (2001b). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human Brain Mapping*, 12, 1-19.
- Haxby, J. V., Horwitz, B., Ungerleider, L. G., Maisog, J. M., Pietrini, P., & Grady, C. L. (1994). The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. *J Neurosci*, 14, 6336-6353.
- Heilman, K. M., Maher, L. M., Greenwald, M. L., & Rothi, L. J. (1997). Conceptual apraxia from lateralized lesions. *Neurology*, 49, 457-464.
- Jancke, L., Kleinschmidt, A., Mirzazade, S., Shah, N. J., & Freund, H. J. (2001). The role of the inferior parietal cortex in linking the tactile perception and manual construction of object shapes. *Cereb Cortex*, 11, 114-121.

- Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences*, 17, 187-245.
- Jeannerod, M., Arbib, M. A., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends Neurosci*, 18, 314-320.
- Kanwisher, N., Woods, R. P., Iacoboni, M., & Mazziotta, J. C. (1997). A locus in human extrastriate cortex for visual shape analysis. *Journal of Cognitive Neuroscience*, 9, 133-142.
- Kazui, H., Kitagaki, H., & Mori, E. (2000). Cortical activation during retrieval of arithmetical facts and actual calculation: a functional magnetic resonance imaging study. *Psychiatry Clin Neurosci*, 54, 479-485.
- Klingberg, T., O'Sullivan, B. T., & Roland, P. E. (1997). Bilateral activation of fronto-parietal networks by incrementing demand in a working memory task. *Cereb Cortex*, 7, 465-471.
- Krams, M., Rushworth, M. F., Deiber, M. P., Frackowiak, R. S., & Passingham, R. E. (1998). The preparation, execution and suppression of copied movements in the human brain. *Exp Brain Res*, 120, 386-398.
- Lacquaniti, F., Perani, D., Guigon, E., Bettinardi, V., Carrozzo, M., Grassi, F., Rossetti, Y., & Fazio, F. (1997). Visuomotor transformations for reaching to memorized targets: a PET study. *Neuroimage*, 5, 129-146.
- Lambon-Ralph, M. A., Howard, D., Nightingale, G., & Ellis, A. W. (1998). Are living and non-living category-specific deficits causally linked to impaired perceptual or associative knowledge? Evidence from a category-specific double dissociation. *Neurocase*, 4, 311-338.
- Magnie, M. N., Ferreira, C. T., Giusiano, B., & Poncet, M. (1999). Category specificity in object agnosia: preservation of sensorimotor experiences related to objects. *Neuropsychologia*, 37, 67-74.
- Manoach, D. S., Schlaug, G., Siewert, B., Darby, D. G., Bly, B. M., Benfield, A., Edelman, R. R., & Warach, S. (1997). Prefrontal cortex fMRI signal changes are correlated with working memory load. *Neuroreport*, 8, 545-549.
- Marshall, J. C., Halligan, P. W., Fink, G. R., Wade, D. T., & Frackowiak, R. S. (1997). The functional anatomy of hysterical paralysis. *Cognition*, 64, 1-8.
- Martin, A. (2001). Functional neuroimaging of semantic memory, Cabeza, R. and Kingstone, A. (Eds). *Handbook of functional neuroimaging of cognition*. Cambridge, MA, US: The MIT Press.

- Martin, A., & Chao, L. L. (2001). Semantic memory and the brain: Structure and processes. *Current Opinion in Neurobiology*, 11, 194-201.
- Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science*, 270, 102-105.
- Martin, A., Ungerleider, L. G., & Haxby, J. V. (2000). Category specificity and the brain: The sensory/motor model of semantic representations of objects, *Gazzaniga, Michael S. (Ed). The new cognitive neurosciences (2nd ed.)*. Cambridge, MA, US: The MIT Press. xiv, 1419 pp.
- Martin, A., Wiggs, C. L., Ungerleider, L. G., & Haxby, J. V. (1996). Neural correlates of category-specific knowledge. *Nature*, 379, 649-652.
- Moll, J., de Oliveira Souza, R., Passman, L. J., Cunha, F. C., Souza Lima, F., & Andreiuolo, P. A. (2000). Functional MRI correlates of real and imagined tool-use pantomimes. *Neurology*, 54, 1331-1336.
- Moore, C. J., & Price, C. J. (1999). A functional neuroimaging study of the variables that generate category-specific object processing differences. *Brain*, 122, 943-962.
- Mummary, C. J., Patterson, K., Hodges, J. R., & Price, C. J. (1998). Functional neuroanatomy of the semantic system: divisible by what? *J Cogn Neurosci*, 10, 766-777.
- Mummary, C. J., Patterson, K., Hodges, J. R., & Wise, R. J. (1996). Generating 'tiger' as an animal name or a word beginning with T: differences in brain activation. *Proc R Soc Lond B Biol Sci*, 263, 989-995.
- Murata, A., Fadiga, L., Fogassi, L., Gallese, V., Raos, V., & Rizzolatti, G. (1997). Object representation in the ventral premotor cortex (area F5) of the monkey. *J Neurophysiol*, 78, 2226-2230.
- Murata, A., Gallese, V., Luppino, G., Kaseda, M., & Sakata, H. (2000). Selectivity for the shape, size and orientation of objects for grasping in neurons of monkey parietal area AIP. *Journal of Neurophysiology*, 83, 2580-2601.
- Nyberg, L., Petersson, K. M., Nilsson, L. G., Sandblom, J., Aberg, C., & Ingvar, M. (2001). Reactivation of motor brain areas during explicit memory for actions. *Neuroimage*, 14, 521-528.
- Okada, T., Tanaka, S., Nakai, T., Nishizawa, S., Inui, T., Sadato, N., Yonekura, Y., & Konishi, J. (2000). Naming of animals and tools: a functional magnetic resonance imaging study of categorical differences in the human brain areas commonly used for naming visually presented objects. *Neurosci Lett*, 296, 33-36.

- Pause, M., Kunesch, E., Binkofski, F., & Freund, H. J. (1989). Sensorimotor disturbances in patients with lesions of the parietal cortex. *Brain*, *112*, 1599-1625.
- Perani, D., Schnur, T., Tettamanti, M., Gorno Tempini, M., Cappa, S. F., & Fazio, F. (1999). Word and picture matching: a PET study of semantic category effects. *Neuropsychologia*, *37*, 293-306.
- Perenin, M. T., & Vighetto, A. (1988). Optic ataxia: a specific disruption in visuomotor mechanisms. I. Different aspects of the deficit in reaching for objects. *Brain*, *111*, 643-674.
- Pesenti, M., Thioux, M., Seron, X., & De Volder, A. (2000). Neuroanatomical substrates of arabic number processing, numerical comparison, and simple addition: a PET study. *J Cogn Neurosci*, *12*, 461-479.
- Petersen, S. E., Fox, P. T., Posner, M. I., Mintun, M., & Raichle, M. E. (1988). Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature*, *331*, 585-589.
- Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Exp Brain Res*, *71*, 491-507.
- Rushworth, M. F., Krams, M., & Passingham, R. E. (2001). The attentional role of the left parietal cortex: The distinct lateralization and localization of motor attention in the human brain. *Journal of Cognitive Neuroscience*, *13*, 698-710.
- Sacchett, C., & Humphreys, G. W. (1992). Calling a squirrel a squirrel but a canoe a wigwam: A category-specific deficit for artefactual objects and body parts. *Cognitive Neuropsychology*, *9*, 73-86.
- Saffran, E. M., & Sholl, A. (2000). Clues to the functional and neural architecture of word meaning. In C. a. H. Brown, P. (Ed.), *Neurocognition of Language*. Oxford: Oxford University Press.
- Sakata, H., & Taira, M. (1994). Parietal control of hand action. *Curr Opin Neurobiol*, *4*, 847-856.
- Sakata, H., Taira, M., Murata, A., & Mine, S. (1995). Neural mechanisms of visual guidance of hand action in the parietal cortex of the monkey. *Cereb Cortex*, *5*, 429-438.
- Seitz, R. J., Canavan, A. G., Yaguez, L., Herzog, H., Tellmann, L., Knorr, U., Huang, Y., & Homberg, V. (1994). Successive roles of the cerebellum and premotor cortices in trajectorial learning. *Neuroreport*, *5*, 2541-2544.
- Shikata, E., Hamzei, F., Glauche, V., Knab, R., Dettmers, C., Weiller, C., & Buchel, C. (2001). Surface orientation discrimination activates caudal and anterior intraparietal sulcus in humans: an event-related fMRI study. *J Neurophysiol*, *85*, 1309-1314.

- Simons, J. S., Graham, K. S., Owen, A. M., Patterson, K., & Hodges, J. R. (2001). Perceptual and semantic components of memory for objects and faces: A PET study. *Journal of Cognitive Neuroscience*, 13, 430-443.
- Sirigu, A., Duhamel, J. R., & Poncet, M. (1991). The role of sensorimotor experience in object recognition. A case of multimodal agnosia. *Brain*, 114, 2555-2573.
- Snodgrass, J. G., & Vanderwart, M. (1980). A standardized set of 260 pictures: norms for name agreement, image agreement, familiarity, and visual complexity. *J Exp Psychol Hum Learn*, 6, 174-215.
- Stephan, K. M., Fink, G. R., Passingham, R. E., Silbersweig, D., Ceballos Baumann, A. O., Frith, C. D., & Frackowiak, R. S. (1995). Functional anatomy of the mental representation of upper extremity movements in healthy subjects. *J Neurophysiol*, 73, 373-386.
- Taira, M., Kawashima, R., Inoue, K., & Fukuda, H. (1998). A PET study of axis orientation discrimination. *Neuroreport*, 9, 283-288.
- Taira, M., Mine, S., Georgopoulos, A. P., Murata, A., & Sakata, H. (1990). Parietal cortex neurons of the monkey related to the visual guidance of hand movement. *Exp Brain Res*, 83, 29-36.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. Stuttgart: Thieme.
- Warburton, E., Wise, R. J. S., Price, C. J., Weiller, C., & et al. (1996). Noun and verb retrieval by normal subjects studies with PET. *Brain*, 119, 159-179.
- Warrington, E. K., & McCarthy, R. (1983). Category specific access dysphasia. *Brain*, 106, 859-878.
- Warrington, E. K., & McCarthy, R. A. (1987). Categories of knowledge. Further fractionations and an attempted integration. *Brain*, 110, 1273-1296.
- Warrington, E. K., & Shallice, T. (1984). Category specific semantic impairments. *Brain*, 107, 829-854.
- Wise, R., Chollet, F., Hadar, U., Friston, K., Hoffner, E., & Frackowiak, R. (1991). Distribution of cortical neural networks involved in word comprehension and word retrieval. *Brain*, 114, 1803-1817.
- Wojciulik, E., & Kanwisher, N. (1999). The generality of parietal involvement in visual attention. *Neuron*, 23, 747-764.
- Worsley, K. J., Marrett, S., Neelin, P., Vandal, A. C., Friston, K. J., & Evans, A. C. (1996). A unified statistical approach for determining significant signals in images of cerebral activation. *Human Brain Mapping*, 4, 58-73.
- Yamadori, A., & Albert, M. L. (1973). Word category aphasia. *Cortex*, 9, 112-125.

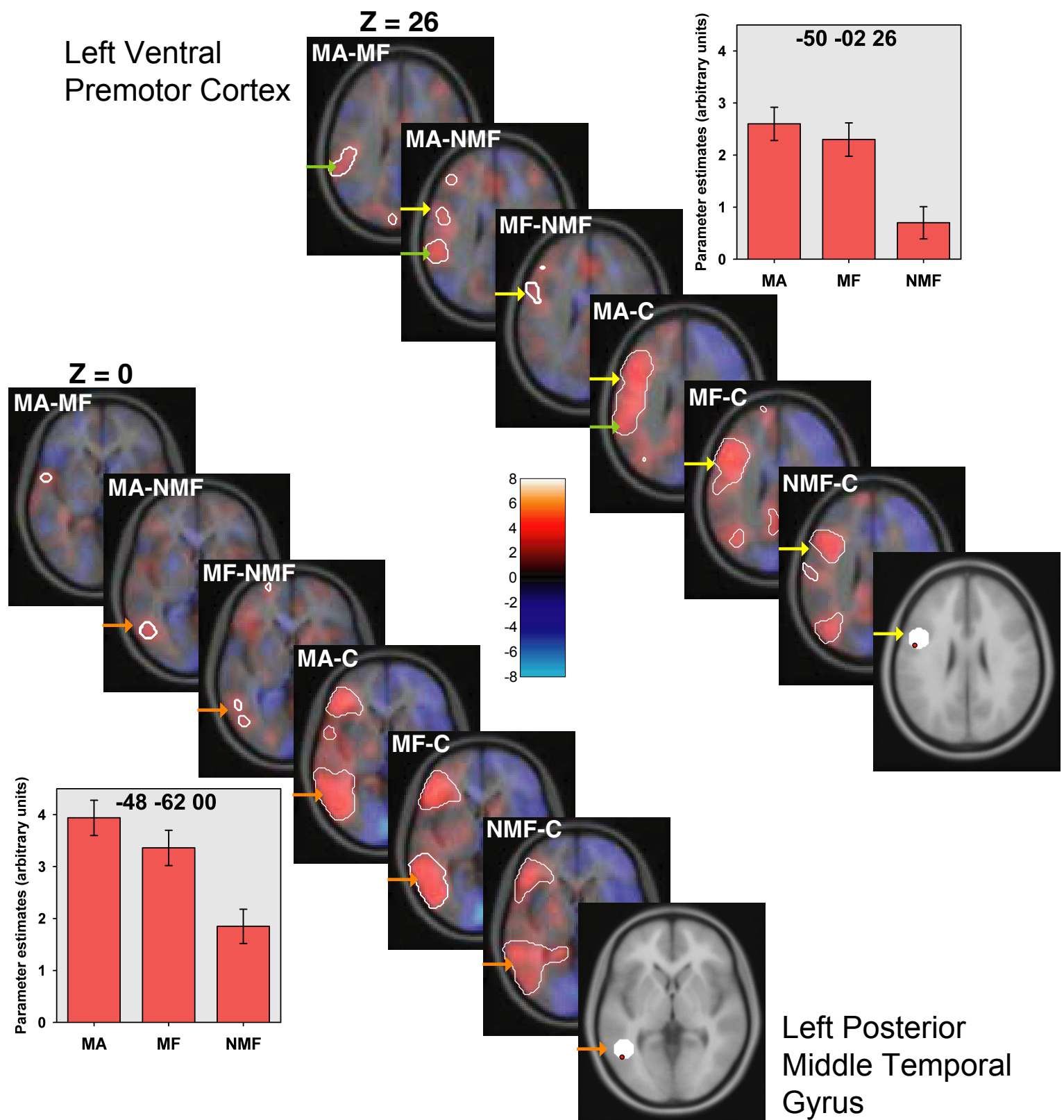


FIGURE 1

Differential activation in left ventral premotor cortex (yellow arrows) and left posterior middle temporal gyrus (orange arrows) for a range of condition contrasts. Red corresponds to higher activation for the first condition of the contrast, while blue reflects more activation for the second condition of the contrast. Colour intensity is overlaid on the MNI brain template to show activation in various key regions. The colour intensity represents the effect size at each voxel, in terms of estimated ml/min/dl blood flow change. The outlined areas show where this change is significant at the threshold determined for the 10mm radius sphere ROIs ($t = 2.94$, $p = 0.05$), and therefore where the t statistic (which is the size of effect divided by an estimate of its standard error) is above the threshold given by random field theory (Worsley et al., 1996). The green arrows indicate the ventral part of the activation observed in the inferior parietal lobule in the whole-brain analysis. The parameter estimate plots show the relative activation for each condition relative to the control condition for the left VPMCx and PMTG at the local maxima identified for the relevant ROI in the MA-NMF contrast. The level of the axial slice shown for each of the condition contrasts also corresponds to these local maxima. MA= manipulable objects, action judgement; MF= manipulable objects, function judgement; NMF= non-manipulable objects, function judgement; C = control condition. The gray-scale axial figures illustrate the position of the spherical ROIs used (white circles) and the local maximum used for both the activation figures and the parameter estimate plot (red circles).

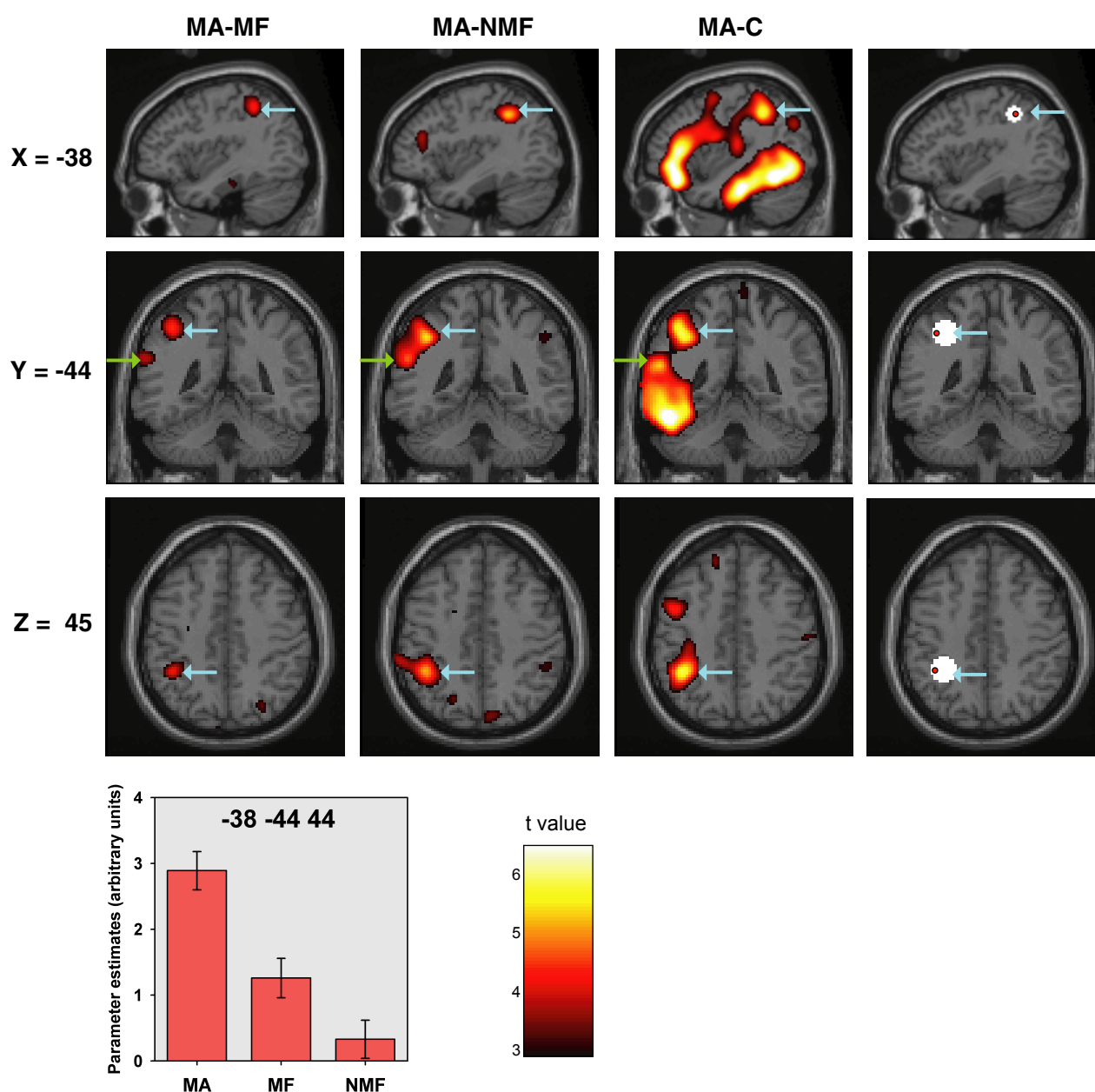


FIGURE 2

Activation in left posterior parietal cortex (intraparietal sulcus: blue pointers) associated with the action judgements to manipulable objects. The activity shown corresponds to where this condition was above the threshold determined for the 10mm radius sphere ROI ($t = 2.94$, $p = 0.05$), and therefore where the t statistic (which is the size of effect divided by an estimate of its standard error) is above the threshold given by random field theory (Worsley et al., 1996). The green pointers indicate the activation observed in the inferior parietal lobule in the whole-brain analysis. The parameter estimate plot shows the relative activation for each condition relative to the control condition at the local maximum corresponding to the indicated region in the MA-NMF comparison. MA= manipulable objects, action judgement; MF= manipulable objects, function judgement; NMF= non-manipulable objects, function judgement; C = control condition. The right-hand column of figures illustrates the position of the spherical ROI used for the intraparietal sulcus (white circles) and the local maximum used for both the activation figures and the parameter estimate plot (red circles).