

The Role of the Inferior Parietal Cortex in Linking the Tactile Perception and Manual Construction of Object Shapes

L. Jäncke^{1,3}, A. Kleinschmidt², S. Mirzazade³, N.J. Shah³ and H.J. Freund²

¹Institute of General Psychology, Otto-von-Guericke University Magdeburg, Magdeburg, ²Department of Neurology, Heinrich-Heine University Düsseldorf, Düsseldorf and ³Institute of Medicine, Research Centre Jülich, Jülich, Germany

We employed functional magnetic resonance imaging (fMRI) in 12 healthy subjects to measure cerebral activation related to a set of higher order manual sensorimotor tasks performed in the absence of visual guidance. Purposeless manipulation of meaningless plasticine lumps served as a reference against which we contrasted two tasks where manual manipulation served a meaningful purpose, either the perception and recognition of three-dimensional shapes or the construction of such shapes out of an amorphous plasticine lump. These tasks were compared with the corresponding mental imagery of the modelling process which evokes the constructive concept but lacks concomitant sensorimotor input and output. Neural overlap was found in a bilateral activity increase in the posterior and anterior intraparietal sulcus area (IPS and AIP). Differential activation was seen in the supplementary and cingulate motor areas, the left M1 and the superior parietal lobe for modelling and in the left angular and ventral premotor cortex for imagery. Our data thus point to a congruent neural substrate for both perceptive and constructive object-oriented sensorimotor cognition in the AIP and posterior IPS. The leftward asymmetry of the inferior parietal activations, including the angular gyrus, during imagery of modelling along with the ventral premotor activations emphasize the close vicinity of the circuitry for cognitive manipulative motor behaviour and language.

Introduction

Of all species, human beings are most proficient in shaping and constructing objects with their hands. This extraordinary ability is documented by a wealth of fine arts and crafts created during human history. To be successful in manual modelling several functions must be orchestrated. They comprise the ongoing mental representation of the object to be modelled, the transformation of this mental representation into appropriate motor trajectories, and the fine tuned bimanual interaction and sensorimotor dexterity to create a particular 'Gestalt'. Little is known about the underlying neural substrates controlling this ability of mankind. For instance, it is unknown whether the objects to be modelled are mentally represented in the visual and/or tactile modality or even in a supramodal way. Lesion and functional imaging studies in humans indicate that such mental representations are processed within the posterior parietal cortex, especially in the inferior parietal lobule (IPL). Lesions of the superior parietal lobe (SPL) have been reported to result in impairment of sensorimotor functions, including tactile exploration (Pause *et al.*, 1989), reaching for and grasping (Kalaska *et al.*, 1997), whereas IPL damage disturbs the correct motor response to objects reflected in mirrors (Ramachandran *et al.*, 1997; Binkofski *et al.*, 1999a). Functional imaging studies in human subjects showed involvement of the IPL cortex in location matching and in the mental rotation of two- (Alivisatos and Petrides, 1997) and three-dimensional objects (Cohen *et al.*, 1996) as well as of the body (Bonda *et al.*, 1996). Furthermore, it was shown that object-oriented action and object recognition activates the IPL, suggesting that some form of within-object

spatial analysis has to be processed by this area (Faille *et al.*, 1997a).

A further line of evidence demonstrated that the SPL and IPL are involved in the visuo-motor imagery of simple and complex finger movements, suggesting an important function of the IPL in planning of motor acts (Seitz *et al.*, 1997). Such a role has already been implicated by lesion studies showing that IPL damage of the left hemisphere is often characterized by apraxia (Kleist, 1934). This emphasizes that IPL functions may be lateralized, so that the left hemisphere is not only dominant for language but also for praxis. In contrast to this action-related IPL function, infero-temporal cortex is preferentially involved in cognitive aspects of shape and object discrimination (Gross *et al.*, 1972). Neuronal populations in these areas respond more to complex visual features than to more elementary attributes of these stimuli, like spatial position, size, luminance, colour or spatial frequency (Perrett *et al.*, 1985). Accordingly, infero-temporal areas are functionally involved in processing invariant aspects of visual stimuli, thus representing a final stage of an object identification mechanism.

In contrast to the visual modality where recognition involves the ventral stream, action-related and cognitive processed aspects of somato-sensation are housed within the parietal lobe. This is best illustrated by the dual nature of tactile object identification and manipulation in active touch. Whereas this facet of an action-recognition interdependence has been shown by lesion (Pause *et al.*, 1989) and activation (Binkofski *et al.*, 1999a) studies, the formative dimension of the control of manual three-dimensional modelling has not been studied so far. This functional magnetic resonance imaging (fMRI) study was designed to identify the neural structures subserving this ability. In particular, we were interested whether manual modelling in the absence of vision shares a common neural substrate with tactile perception and whether mental imagery is sufficient to evoke such a representation of manual creative processes independent of concomitant sensory input or execution.

We hypothesize that manual modelling comprises at least four steps of cognitive processing: memory retrieval of the tactually perceived three-dimensional object, representation of this object in working memory, conception of the motor act. Exploration involves tactile sensation, object perception, working memory and memory encoding processes.

Materials and Methods

Subjects

Twelve healthy, right-handed volunteers (two female and 10 male, mean age 36 years) took part in the study. All were consistent right-handers as measured by standard handedness questionnaires (Peters, 1998). Subjects were paid and gave written informed consent according to institutional guidelines (Ethics Committee of the University of Düsseldorf). All subjects were also tested for their proficiency with respect to imagination

and rotation of three-dimensional objects [paper-and-pencil version of the mental rotation test (Peters *et al.*, 1995)] and for the vividness of their visual imagery (Marks, 1973). These tests showed that all subjects were able to deal with three-dimensional information, as indicated by at least average proficiency in the mental rotation task for nine subjects and average performance in three subjects. None of the subjects showed any obvious deficiency with respect to his/her vividness of visual imagery.

Magnetic Resonance Imaging

fMRI was performed on a 1.5 T MRI system (Siemens Magnetom Vision; Erlangen, Germany), equipped with echo planar imaging (EPI) capabilities using the standard head coil for radio frequency (RF) transmission and signal reception. Sequences with the following parameters were employed: gradient echo EPI, repetition time $T_R = 3$ s, echo time $T_E = 66$ ms, field of view = 200×200 mm², $\theta = 90^\circ$, matrix size = 64×64 , voxel size = $3.125 \times 3.125 \times 6.5$ mm³. Using a mid-sagittal scout image, 16 axial slice positions (0.3 mm interslice gap) were oriented parallel to the bi-commissural plane with the uppermost slice aligned 2 mm below the vertex, thus covering the whole brain excluding deep brain stem nuclei and the posterior lobe of the cerebellum. In addition, three-dimensional anatomical images of the entire brain were obtained using a strongly T_1 -weighted gradient echo pulse sequence (MP-RAGE, magnetization-prepared, rapid acquisition gradient echo) with the following parameters: $T_R = 11.4$ ms, $T_E = 4.4$ ms, 15° flip angle, FOV = 256×256 mm², matrix size = 200×256 , 128 sagittal slices of 1.33 mm thickness.

Experimental protocol

For each subject series of fMRI images were acquired. Each image series (95 volumes) consisted of multiple periods of 'baseline' (OFF) alternating with periods of 'activation' (ON), during which the subjects successively performed one of the four tasks: (1) repeatedly manipulating plasticine (motor control condition, squeezing); (2) manually exploring a three-dimensional plasticine object so as to infer its shape (sensory perceptive condition, exploring); (3) imagining constructing the previously palpated three-dimensional object (imagery condition, imagining); (4) constructing the previously palpated three-dimensional object from an amorphous lump of plasticine (active constructive condition, modelling). During scanning the room lights were dimmed and the subjects' eyes were open. Subjects were not able to see the objects or plasticine lumps. For condition 1, subjects were handed ball-like lumps of plasticine with a diameter of 8 cm to both hands and they squeezed them repetitively at an individually pre-learned rate. Thus, the subjects applied slightly different movements rates (ranging from 0.8 to 1 Hz), but these movements were generated by an internalized pattern and resembled those used for modelling and exploring. During each exploring condition subjects were handed one of five objects formed of plasticine (see below). They were required to hold the object with the left hand and to explore it with the right hand in concordance with typical exploratory movement patterns Klatzky and co-workers (Lederman and Klatzky, 1987) and movement rates (Kunesch *et al.*, 1989). The objects were modelled beforehand by the experimenter (L.J.) and represented everyday objects thought to be easily recognizable in a size-invariant way (hammer, bag, cup, umbrella, car). Onset and end of condition 3 (imagery) were signalled by lightly and briefly touching the subject's left foot. During this condition, subjects were instructed to maintain both hands positioned on the right and left upper thigh without motion and to imagine manual shaping of the previously explored object. The experimenter verified whether the subjects moved their hands or not. Since all subjects completed these conditions without overt hand movements, no repetitions were necessary. During the modelling condition (condition 4) subjects were handed an amorphous lump of plasticine and modelled the previously palpated object with both hands. All subjects held the bulk with the left (sub-dominant) hand and modelled with the right (dominant) hand. Afterwards the experimenter judged the degree of success on a 3 point scale (successful, moderately successful or unsuccessful). Each series thus covered comprised four 'OFF-ON' cycles of 10/10 image volumes embedded in an initial and final 'OFF' period of 10 and 5 image volumes, respectively (total duration 285 s, duration of each condition 30s). Each session was repeated four times. Eight subjects performed squeezing as the first 'ON' condition and four as the last, but all subjects performed

Table 1

Brain areas and their stereotaxic coordinates in which significantly activated voxels were detected for the comparison performed for motor control condition (squeezing) versus rest

Anatomical region	x	y	z	Z score
l M1	-44	-24	44	7.5
l S1	-40	-36	52	7.1
l SII	-60	-24	20	5.2
l SMA	-4	-4	48	7.4
l CMA	-4	-4	40	8.4
l pre-SMA	-4	4	52	7.2
l dPMC	-40	-12	48	6.6
r M1	40	-24	44	7.1
r S1	44	-32	56	6.9
r SII	52	-20	16	5.5
r dPMC	40	-12	48	5.2

Abbreviations for this and the following tables: l, left; r, right; m, mesial; M1/S1, primary sensorimotor area; vPMC, ventral premotor area; dPMC, dorsal premotor area; SII, secondary somatosensory area; SMA, supplementary motor area; CMA, cingulate motor area; pre-SMA: rostral supplementary area; AIP, anterior intraparietal area; IPS, intraparietal sulcus; Ga, angular gyrus; SPL, superior parietal lobe; GC, cingulate gyrus; PCu, precuneus; Spo, parieto-occipital gyrus. x, y, z are stereotaxic coordinates (mm); Z scores are peak activations within the significant cluster of activated voxels; Z scores >3.09 , >4.2 and >4.6 correspond to $P < 0.001$ (uncorrected for multiple comparison), $P < 0.05$ and $P < 0.01$, respectively (corrected for multiple comparisons); peaks of activity are localized according to their position on an averaged MNI brain. The coordinates do not correspond to the Talairach and Tournoux atlas.

conditions 2-4 in that order. This systematic ordering was necessary given the specific interest of our study: in order to introduce the objects to be modelled, tactile exploration of the particular object for a given session had to precede its manual reshaping. Additionally, behavioural piloting showed that subjects had greater difficulties with pure imagery (without overt movements) once they had performed the actual shaping task. This prompted us to apply the described order of exploring, imagining and modelling across all subjects.

Image analysis

Image analysis was performed on an Ultra 4 work station (Sun Microsystems) using MATLAB (Mathworks, Natick, MA) and SPM99 software (<http://fil.ion.ucl.ac.uk/spm>). For analysis, all images were realigned to the first volume, corrected for motion artefacts, co-registered with the subject's corresponding anatomical (T_1 -weighted) images, normalized (4 mm³) to standard stereotaxic space (template provided by the Montreal Neurological Institute) and smoothed using an 8 mm full-width-at-half-maximum Gaussian kernel. Applying a box-car model, adjusted mean images (convolved with the modelled haemodynamic response and eliminating low frequency noise) were computed for each condition and each subject in the context of SPM97 ('random effects procedure'). These images were used to generate group statistical parametric maps. Activated pixels were identified by the 'General Linear Model' approach (Friston *et al.*, 1995). To test the hypotheses about region-specific condition effects, linear contrasts were employed. The resulting SPM{Z} for these effects were thresholded at a Z value of 3.09 ($P = 0.001$, uncorrected for multiple comparisons) and a spatial extent criterion of $P = 0.05$ (corrected for multiple comparisons). Activation areas were given anatomical labels only when the borders of the area followed borders of a gyral or sulcal structure in the Talairach and Tournoux atlas and the label was supported by three-dimensional inspection of the averaged anatomical data.

Results

All subjects easily identified the objects palpated and modelled them reasonably successfully (10 successfully and two moderately, as indicated by the averaged judgements across all five modelling sessions). As demonstrated in Table 1, motor control condition compared with the rest revealed activation in the left and right sensorimotor cortex (MI and SI), the medial motor wall areas, predominantly on the left side [CMA, SMA proper and pre-SMA, according to Roland and Zilles (Roland and Zilles, 1996)], and SII. Table 2 and Figures 1 and 2 summarize the

Table 2

Brain areas and their stereotaxic coordinates in which significantly activated voxels were detected for the comparison performed for exploring (E), imagining (I) and modelling (M) versus squeezing (S)

Anatomical region	E > S				I > S				M > S			
	x	y	z	Z score	x	y	z	Z score	x	y	z	Z score
l SPL									-32	-52	52	4.1
l Ga/IPSpost.	-28	-68	36	4.4	-32	-64	36	5.0	-28	-68	36	5.3
l Ga					-52	-52	28	4.5				
l IPSpost.	-28	-60	52	4.2					-28	-60	52	4.1
l AIP	-44	-40	40	4.1					-40	-44	40	4.6
r IPSpost.	32	-56	48	4.2					32	-52	52	4.3
r Ga/IPSpost.	24	-68	44	3.7					28	-64	44	3.7
r AIP	36	-44	44	3.5					32	-40	40	4.2
l vPMC					-40	0	28	4.8				
l vPMC					-40	12	32	4.0				

Abbreviations as for Table 1.

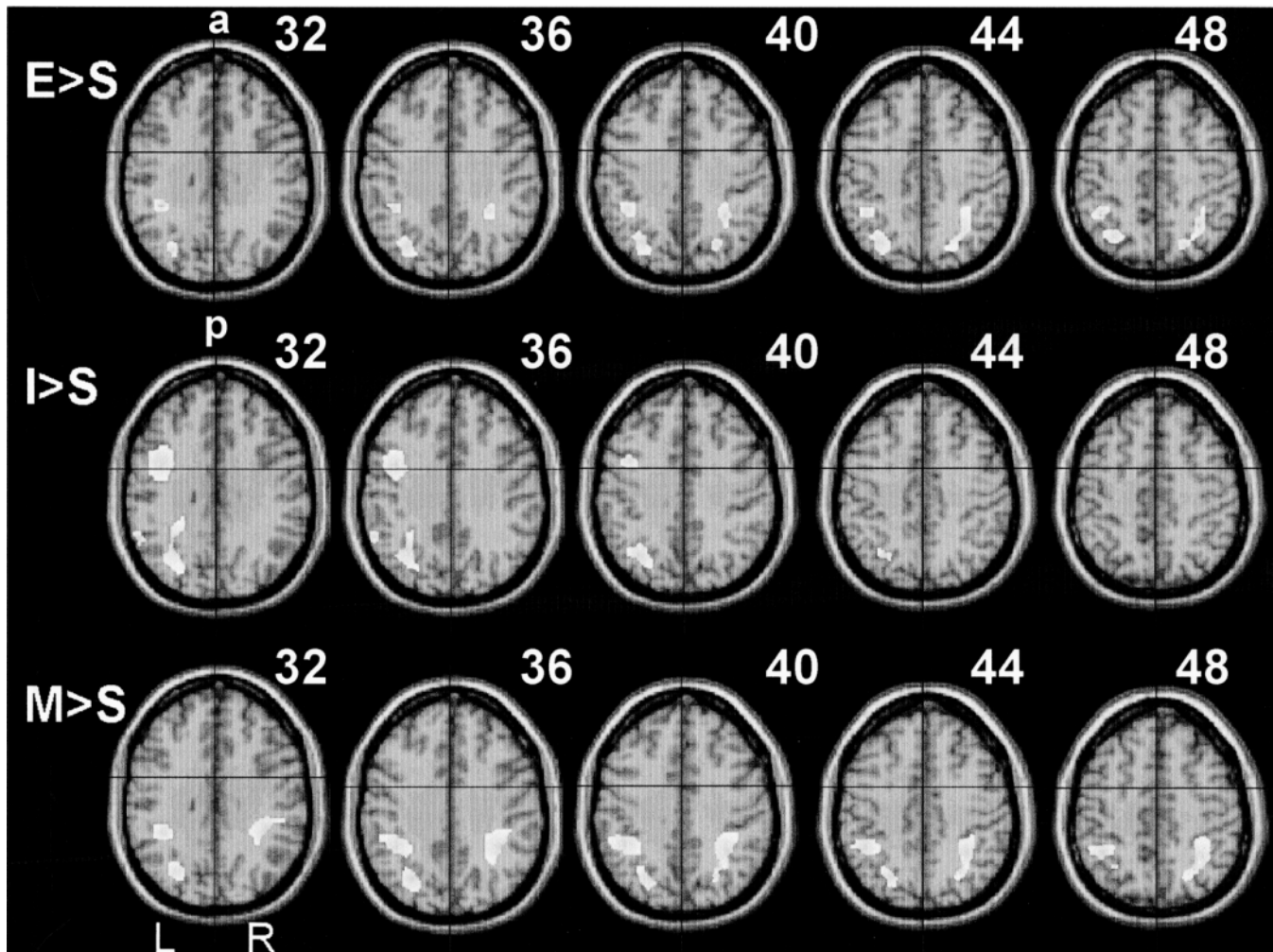


Figure 1. Areas of significant activation for the exploring (E), imagining (I) and modelling (M) conditions compared with the motor control task (squeezing, S) overlaid on transverse slices of a MNI T_1 -weighted standard brain. E > S, exploring > squeezing; I > S, imagining > squeezing; M > S, modelling > squeezing. Numbers refer to millimetres relative to the intercommisural line. Bilateral activations in the AIP and the posterior IPS for the E > S and M > S contrasts (slices 36–48) are displayed. The I > S comparison revealed activation in the left hemisphere within the posterior IPS (slices 32–44), the angular gyrus (slices 32–36) and the vPMC (slices 32–36). L, left; R, right; a, anterior; p, posterior.

significantly activated brain areas for the contrasts comparing exploring, imagining and modelling under the motor control condition.

The most prominent finding is that the exploring and

modelling conditions evoke activations in similar brain areas comprising, bilaterally, the IPS and the AIP, extending slightly into the dorsal parts of the angular gyrus. Interestingly, there were two different foci in the vicinity of the posterior IPS for the

Table 3

Brain areas and their stereotaxic coordinates in which significantly activated voxels were detected for the comparison performed for modelling (M) and imagining (I) versus exploring (E)

Anatomical region	M > E				I > E				I > M			
	x	y	z	Z score	x	y	z	Z score	x	y	z	Z score
I MI	-24	-28	56									
I SMA/CMA	-4	4	52	4.5								
I SPL	-20	-40	64	3.8								
I SPL	-32	-44	60	3.6								
I Ga					-52	-52	28	4.8	-52	-56	24	5.6
I GC/Spoa					-20	-64	20	4.7				
m PCua					4	-64	40	4.7	4	-60	36	4.9
I GCa					-16	-40	20	4.7				
I SII					-44	-12	28	4.0				
I vPMC					-44	0	40	3.9	-44	12	36	5.8
I vPMC					-40	16	32	3.4	-32	24	12	4.1

Abbreviations as for Table 1.

Significantly activated anatomical regions for the comparison imaging versus modelling (M) are also presented. Note that there was no difference for the E > M comparison.

^aThese differences are due to strong deactivations during the exploring and modelling conditions. There are no activations in these areas (relative to the motor control condition and relative to rest) during the imagining condition.

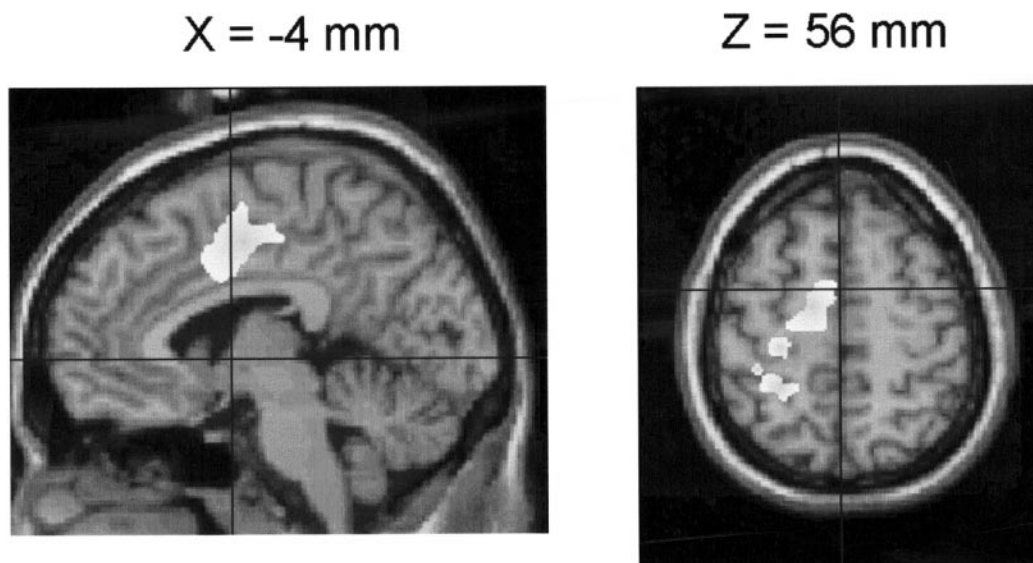


Figure 2. Areas of different activations found for the comparison of modelling with exploration (M > E) displayed on a left-sided sagittal view ($x = -4$) and on a transverse slice 56 mm above the intercommisural line. There are activations within the mesial motor wall area located in pre-SMA, SMA and CMA (sagittal view). The transverse slice shows three significant foci of activation for this contrast located in the mesial motor wall area, the mesial part of the left M1 and the left SPL.

exploring and modelling conditions, one located near the mesial parts (possibly the fundus) of the angular gyrus (-28, -68, 36) while the other focus was located more superiorly bordering the superior parietal lobe (-28, -60, 52). There were also two different foci in the right hemisphere in the vicinity of the IPS, one located more inferiorly and posteriorly (E > S, 24, -68, 44; M > S, 28, -64, 44), the other located more anteriorly and superiorly (E > S, 32, -56, 48; M > S, 32, -52, 52). As can be seen in Figure 1, these peaks are part of a cluster lining the posterior IPS. The inferior voxels border the fundus of the angular gyrus. The different locations with respect to the superior-inferior axis might reflect the between-hemisphere difference in the angulation of the Sylvian fissure. Comparing these peak activations in terms of right-left differences revealed no significant left-right difference [$Z_{\text{Left}} - Z_{\text{Right}}/\sqrt{2}$ according to Rosenthal (Rosenthal, 1991)]. Besides these activations within the posterior IPS we also found consistent bilateral activations in the AIP (left hemisphere,

E > S, -44, -40, 40; M > S, -40, -44, 40; right hemisphere, E > S, 36, -44, 44; M > S, -32, -40, 40). The coordinates of these activations are similar to those found in previous studies by our group (Binkofski *et al.*, 1998). For the modelling condition the activated cluster also extended into the superior parietal lobe (SPL, -20, -40, -64).

As one can see from Table 2, the imagining condition revealed only two activation peaks within the inferior parietal lobe, one of which was close to the posterior IPS peaks found for the aforementioned contrasts (-32, -64, 36) and the other was located exactly within the convexity of the angular gyrus (-52, -52, 28). For this contrast we also found activations in the left inferior frontal gyrus (ventral premotor cortex, vPMC). Comparison of the coordinates of the activated foci located in the vPMC (-40, 0, 28 and -40, 12, 32) with the coordinates of the probability maps of Broca's area (Amunts *et al.*, 1999) demonstrated that these activation foci are at the outer edges

Table 4

Brain areas and their stereotaxic coordinates in which significantly activated voxels were detected for the comparison performed for exploring (E) and modelling (M) versus imagining (I)

Anatomical region	E > I				M > I			
	x	y	z	Z score	x	y	z	Z score
r M1/SI	40	-28	40	6.0	40	-28	40	7.0
r IPS	32	-48	56	4.9				
r SII	52	-20	16	4.3	56	-24	28	6.6
r Pulvinar	8	-24	4	5.8	8	-24	4	6.3
r AIP	40	-32	40	5.9	40	-40	40	4.2
l IPS	-40	-40	52	5.9	-32	-48	60	6.3
l AIP	-44	-32	40	5.9	-48	-32	40	6.7
l M1	-44	-24	44	5.7	-32	-16	56	6.1
l SII	-60	-24	20	3.8	-64	-24	20	6.3
l dPMC	-	-	-	-	-36	-8	52	4.1
r dPMC	-	-	-	-	40	-8	52	3.3
l SMA/CMA	-4	-4	48	5.4	-4	-4	48	7.3

(but within the variability zone) of Broca's area, extending into the vPMC.

A comparison between the modelling and the exploring conditions (Table 3) revealed an extended cluster comprising the left mesial motor wall areas (CMAr, CMAc, SMA proper and pre-SMA) and a mesial part of M1 (-24, -28, 56), as well as mesial parts of the SPL (the same location as for the modelling > squeezing contrast; see Table 2 and Figure 2). There was no significant difference for the contrast seeking for stronger activations during the exploring compared with the modelling condition. Comparing the imagining condition with the exploring and modelling conditions revealed roughly similar results to the imagining versus squeezing contrast, with activation foci in the left angular gyrus and the left vPMC. These contrasts uncovered two additional foci in the vicinity of the parieto-occipital sulcus and the precuneus area (Table 3). Because these activation differences were due to strong deactivations during the exploring and modelling conditions relative to baseline and deactivations are known to be unreliable in cognitive studies (Sadato *et al.*, 1998), we refrained from drawing too strong conclusions from these findings. For the squeezing > exploring comparison there was no significant difference.

As a cross-validation we also compared exploring and modelling with imagining (Table 4). These comparisons revealed similar bilateral activations within the M1/S1 area, in SII, the AIP, the posterior IPS, the left dorsal premotor cortex (dPMC), the mesial motor wall and the left pulvinar. Thus, these contrasts uncovered all anatomical regions responsible for basic motor control as well as those regions responsible for modelling and exploring. Significant activation in the pulvinar was due to a profound deactivation in this area during the imagining condition. As expected, the regions predominantly involved during the imagining process (i.e. left angular gyrus and left vPMC) were not activated.

Discussion

The purpose of the present study was to evaluate the neural control of manual modelling of three-dimensional objects in the absence of vision and to compare this with an imagery task of the constructive process to dissociate the conceptual component of object construction and perception from the concomitant low level sensorimotor processing involved in both construction and exploration. Comparing the haemodynamic responses obtained during the modelling, exploring and imagining conditions with

those of the motor control condition revealed the following main findings: (i) both modelling and exploring bilaterally activated posterior and anterior parts of the IPS (posterior IPS and AIP), slightly extending into dorsal parts of the angular gyrus; (ii) imagining evoked a left-sided network including the left posterior IPS, similar to the modelling and exploring conditions, the angular gyrus and the vPMC slightly above, but nevertheless within, the variability zone of Broca's area; (iii) manual modelling as compared with tactile exploration revealed additional activation within the mesial motor wall areas (SMA proper and CMA) and also within the superior parietal lobe. In the following we will first discuss the motor paradigm before we discuss the neurophysiological findings and how they relate to published findings in the neurophysiological and psychological literature.

The Motor Paradigm

The basic manipulative pattern was similar in all conditions where explicit motor behaviour was required. At present there is no technique available to measure these fine tuned finger movements in relation to an object within the MRI scanner. One can therefore only assume a basic pattern of similarity, both in terms of spatial trajectories and for the temporal profile of the manipulation paths. Kunesch *et al.* have measured eight manipulative serial hand/finger movements with respect to their temporal characteristics (Kunesch *et al.*, 1989). They found a clear grouping into two distinct temporal profiles: when the hand was used as a sense organ during active touch, finger movements across objects were restricted to a slow performance range scattering closely around 1 Hz. Recordings from single mechano-receptive afferents from the finger tips and calculations of the receptor densities indicated that these movements have to match the temporal requirement of the sequential sampling process from the mechano-receptor population of the finger tips. In contrast, manual skills for extrinsic hand movements employing the hand as a whole (typing, writing and hammering) had distinctly faster frequencies, between 4 and 7 Hz. Since intersubject variability was fairly low for the slow explorative movements we assume that the different manipulative tasks did not imply major differences in sensorimotor performance. If differences occurred they may be largely reflected in different activations of the primary sensory motor cortex rather than in distinct patterns of posterior parietal cortex activations.

The only major difference for the manipulative performance in the three different tasks employing explicit manipulation was for exploration, where the left hand served to hold the object while the right hand was used for exploration. For the simple manipulation task and modelling, both hands were equally active. Again, this difference should be mainly reflected in right/left asymmetries of primary sensorimotor cortex and possibly in a different activation of the medial wall motor areas known to be involved in bi-manual interactions (Stephan *et al.*, 1999). However, contrasting the exploring with the motor control condition did not disclose significant differences with respect to activations in primary cortical somatosensory areas. This may depend on the fact that fMRI block design experiments as used here are not sensitive enough to uncover subtle differences in somatosensory cortical activations.

Similar Intraparietal Sulcus Activations for Modelling and Exploring

The present study has demonstrated for the first time in humans that the left and right AIP is active during both explicit creative manual modelling and tactile exploration of three-dimensional

objects. The AIP was found to be active in previously published studies of one of the authors (Binkofski *et al.*, 1998) in which lesion and fMRI studies revealed that the AIP is involved in the control of hand movements during grasping, manipulation and exploration of three-dimensional objects. It was concluded that this region represents the likely human homologue of the AIP as defined in the monkey (Gallese *et al.*, 1994). The latter studies demonstrated specific hand manipulation neurons in the macaque AIP area, whereas a subset of neurons responded to specific visual three-dimensional stimuli. A third category fired both during active finger/hand movements and in response to three-dimensional stimuli congruent in size and shape with the encoded grasping movement. Unfortunately, the spatial resolution of current fMRI methods is too crude to delineate these different neuronal networks within the AIP. However, the AIP and adjacent areas seem to be involved in explicit, complex hand manipulation operations both during manual modelling and exploration, but not during the imagining of complex hand movements.

The modelling and exploring conditions also evoked bilateral activations within posterior parts of the IPS. Since the posterior IPS is involved in a variety of mental operations, this area does not represent a dedicated modelling or exploration module in the brain. Participation of this region has been shown when the subjects were required to perform mental rotation of two- (Alivisatos *et al.*, 1997) or three-dimensional figures (Cohen *et al.*, 1996), to imagine motor acts (Deiber *et al.*, 1998), to learn trajectorial movements (Seitz *et al.*, 1997), to control self-determined finger movements (Schubert *et al.*, 1998), to generate internal body representations (Bonda *et al.*, 1995), to recognize objects in relation to actions (Faillenot *et al.*, 1997b), to perform cross-modal matching tasks (Banati *et al.*, 2000) and during spatial attention, as well as spatial working memory, processes (Coull and Frith, 1998; Mattingley *et al.*, 1998).

Single cell recording in monkeys revealed that a posterior part of monkey IPS (c-IPS) is a higher centre of stereopsis, integrating various binocular disparity signals received from V1, V2 and V3, possibly representing the neural codes of three-dimensional features of objects to be sent to area AIP for visual guidance of hand movements. Most interestingly, they identified two classes of neurons within the c-IPS of monkeys: axis orientation-selective (AOS) neurons and surface orientation-selective (SOS) neurons (Sakata *et al.*, 1999). The common denominator of the tasks used in these studies to evoke posterior IPS or c-IPS activation may be that they require the generation of a mental representation of a three-dimensional object which should either be grasped, explored or manipulated (explicitly or implicitly). It may be possible that this mental object representation is established in the posterior IPS region in both humans and monkeys. It is interesting to note that there was no explicit visual input in our study which might have caused the posterior IPS activation. Thus, this area serves as a supra-modal integration centre, especially for three-dimensional information relevant to motor control. This action-oriented object representation is clearly different from the object recognition processes linked with the ventral stream (Goodale and Milner, 1992). In the case of manual modelling this supra-modal mental representation must first be recalled, kept in mind and then transformed into appropriate motor commands. For tactile exploration similar processes, although in different causal order, are necessary. Somewhat simplistically one might say that in exploration motor function serves a somatosensory modality and vice versa in construction.

Differences Between Modelling and Exploring

Although manual modelling and exploration of three-dimensional objects shared neural substrates within the intraparietal areas, there are nevertheless striking differences between the two conditions in terms of medial motor wall and SPL activations during manual modelling. The medial wall motor area, including the cingulate motor areas (CMA), pre-SMA and SMA proper, are known to be involved in various motor tasks, among them motor imagery (imagining-doing or imagining-seeing-doing) (Stephan *et al.*, 1995), movement preparation, movement planning (internal rehearsal or simulation) (Stephan *et al.*, 1995), control of complex versus simple sequences of movements (Shibasaki *et al.*, 1993), control of faster finger movements (Leonardo *et al.*, 1995) and control of self-generated movements compared with externally cued movements (Stephan *et al.*, 1999). Modelling requires movements guided by internal models, while exploration is guided by the shape of the palpated object. Thus, modelling basically requires self-generated movements while exploration is guided externally. In addition, during modelling subjects have to rehearse the movement they are going to execute and they are also continuously involved in planning and preparing the next movement. Lastly, all subjects were explicitly required to perform the exploration movements with the left hand holding the object while the right hand performed the palpation. This stereotypical movement pattern is less complex than the modelling movement, which requires constantly changing bi-manual interactions. Bi-manual activity is known to be associated with strong activation of the medial wall motor area (Stephan *et al.*, 1999). A second major difference between the modelling and exploration conditions was increased activation within the SPL. Recent brain imaging studies showed that complex hand movements compared with less complex movements are associated with increased SPL activation (Dassonville *et al.*, 1998). On the other hand, it was also shown that increased motor skill proficiency is associated with less activation in this area (Jäncke *et al.*, 2000). Thus we conclude that the SPL activation found during the manual modelling condition is due to increased computational demands placed on the modelling process.

Left Fronto-parietal Network During Imagining

The imagining condition turned out to evoke activation in a left-sided fronto-parietal network including the angular gyrus, the posterior IPS and the left vPMC. It is interesting to note that there was little overlap in activation between the exploration, modelling and imagining conditions within a small region in the left posterior IPS. This might indicate two aspects, one which is similar across all conditions and one which emphasizes the different psychological functions operative during imagining as compared with modelling and exploring. This left-sided activation in the posterior IPS is present without any visual input, leaving mental imagery or somatosensory input as other candidates. In addition, there are remarkable differences between imagining and the other conditions, emphasizing that imagining modelling previously perceived objects predominantly requires different psychological functions as compared with the actual modelling and exploration conditions.

The angular gyrus has been shown to be involved in short term memory and priming processes (Markowitsch *et al.*, 1999). The strong participation of this area during imagining might indicate that the subjects in our study were relying on intensive memory processes to retrieve the objects for imagining. A further plausible suggestion for angular gyrus activation would

be that this area is involved in the ideation or formation of actions, as suggested by human lesion data (Goldenberg and Hagmann, 1997) or recent brain imaging studies (de Jong *et al.*, 1999). Additionally, one may suggest that the subjects are generating a vivid and, compared with the other conditions, longer lasting mental representation of the previously tactually perceived object. This interpretation fits with lesion and imaging data and indicates participation of the angular gyrus during tactile perception (Endo *et al.*, 1992). Finally, it might also be that mental simulation of the up-coming movements necessary to model the object requires the angular gyrus, an interpretation which is supported by data demonstrating angular gyrus activation during mental imaging of events and complex actions (Crozier *et al.*, 1999). Which of these suggestions is most suitable to explain the angular gyrus activation found during the imagining condition has to be elucidated in future experiments.

A further interesting finding of our study is the left-sided activation in the vPMC in the vicinity of Broca's area during imagining. The activation focus is slightly higher but nevertheless within the variability range of Broca's area, as indicated by a probability map of Broca's area (Amunts *et al.*, 1999). Whether this activation is due to language or more specific dominant hand movement processes is not discernible from the present data. Recently, evidence has been provided that a fronto-parietal circuit for hand-object interaction also exists in the human (Binkofski *et al.*, 1999b) and represents the likely homologue of such a circuitry previously described in the monkey (Gallese *et al.*, 1994). In the ventral premotor cortex (area F5) a subset of neurons was designated as 'mirror neurons' (Rizzolatti *et al.*, 1996), because they discharged both when the monkey performed an action and also when it observed another monkey or the experimenter doing so. This property was regarded as the basis for the understanding of motor behaviour in an ancient communication system for the recognition and production of hand and face gestures that provided the grounding for the later development of a verbal communication system.

Notes

This study was financed by the Deutsche Forschungs- gemeinschaft (DFG JA 737/7-1 and JA 737/7-2).

Address correspondence to Lutz Jäncke, Institute of General Psychology, Otto-von-Guericke University Magdeburg, Universitätsplatz 2, D-39106 Magdeburg, Germany. Email: lutz.jaencke@nat.uni-magdeburg.de.

References

- Alivisatos B, Petrides M (1997) Functional activation of the human brain during mental rotation. *Neuropsychologia* 35:111-118.
- Amunts K, Schleicher A, Burgel U, Mohlberg H, Uylings HB, Zilles K (1999) Broca's region revisited: cytoarchitecture and intersubject variability. *J Comp Neurol* 412:319-341.
- Banati RB, Goerres GW, Tjoa C, Aggleton JP, Grasby P (2000) The functional anatomy of visual-tactile integration in man: a study using positron emission tomography [In Process Citation]. *Neuropsychologia* 38:115-124.
- Binkofski F, Dohle C, Posse S, Stephan KM, Heftner H, Seitz RJ, Freund HJ (1998) Human anterior intraparietal area subserves prehension: a combined lesion and functional MRI activation study. *Neurology* 50:1253-1259.
- Binkofski F, Buccino G, Dohle C, Seitz RJ, Freund HJ (1999a) Mirror agnosia and mirror ataxia constitute different parietal lobe disorders. *Ann Neurol* 46:51-61.
- Binkofski F, Buccino G, Posse S, Seitz RJ, Rizzolatti G, Freund HJ (1999b) A fronto-parietal circuit for object manipulation in man: evidence from an fMRI-study. *Eur J Neurosci* 11:1-11.
- Bonda E, Petrides M, Frey S, Evans A (1995) Neural correlates of mental transformations of the body-in-space. *Proc Natl Acad Sci USA* 92:11180-11184.
- Bonda E, Frey S, Petrides M (1996) Evidence for a dorso-medial parietal system involved in mental transformations of the body. *J Neurophysiol* 76:2042-2048.
- Cohen MS, Kosslyn SM, Breiter HC, DiGirolamo GJ, Thompson WL, Anderson AK, Brookheimer SY, Rosen BR, Belliveau JW (1996) Changes in cortical activity during mental rotation. A mapping study using functional MRI. *Brain* 119:89-100.
- Coull JT, Frith CD (1998) Differential activation of right superior parietal cortex and intraparietal sulcus by spatial and nonspatial attention. *Neuroimage* 8:176-187.
- Crozier S, Sirigu A, Lehericy S, van de Moortele PF, Pillon B, Grafman J, Agid Y, Dubois B, LeBihan D (1999) Distinct prefrontal activations in processing sequence at the sentence and script level: an fMRI study [In Process Citation]. *Neuropsychologia* 37:1469-1476.
- Dassonville P, Lewis SM, Zhu XH, Ugurbil K, Kim SG, Ashe J (1998) Effects of movement predictability on cortical motor activation. *Neurosci Res* 32:65-74.
- de Jong BM, Willemsen AT, Paans AM (1999) Brain activation related to the change between bimanual motor programs. *Neuroimage* 9:290-297.
- Deiber MP, 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.
- Endo K, Miyasaka M, Makishita H, Yanagisawa N, Sugishita M (1992) Tactile agnosia and tactile aphasia: symptomatological and anatomical differences. *Cortex* 28:445-469.
- Faillenot I, Toni I, Decety J, Gregoire MC, Jeannerod M (1997a) Visual pathways for object-oriented action and object recognition: functional anatomy with PET. *Cereb Cortex* 7:77-85.
- Faillenot I, Sakata H, Costes N, Decety J, Jeannerod M (1997b) Visual working memory for shape and 3D-orientation: a PET study. *NeuroReport* 8:859-862.
- Friston KJ, Holmes AP, Poline JB, Grasby PJ, Willman SCR, Frackowiak RSJ, Turner R (1995) Analysis of fMRI time-series revisited. *Neuroimage* 2:45-53.
- Gallese V, Murata A, Kaseda M, Niki N, Sakata H (1994) Deficit of hand reshaping after muscimol injection in monkey parietal cortex [see comments]. *NeuroReport* 5:1525-1529.
- Goldenberg G, Hagmann S (1997) The meaning of meaningless gestures: a study of visuo-imitative apraxia. *Neuropsychologia* 35:333-341.
- Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. *Trends Neurosci* 15:20-25.
- Gross CG, Rocha-Miranda CE, Bender DB (1972) Visual properties of neurons in inferotemporal cortex of the Macaque. *J Neurophysiol* 35:96-111.
- Jäncke L, Shah NJ, Peters M. (2000) Cortical activations in primary and secondary motor areas for complex bimanual movements in professional piano players. *Brain Res Cogn Brain Res* 10:177-183.
- Kalaska JF, Scott SH, Cisek P, Sergio LE (1997) Cortical control of reaching movements [In Process Citation]. *Curr Opin Neurobiol* 7:849-859.
- Kleist K (1934) *Gehirnpathologie. Vornehmlich auf Grund der Kriegserfahrungen.* Leipzig: Verlag von Johann Ambrosius Barth.
- Kunesch E, Binkofski F, Freund HJ (1989) Invariant temporal characteristics of manipulative hand movements. *Exp Brain Res* 78:539-546.
- Lederman SJ, Klatzky RL (1987) Hand movements: a window into haptic object recognition. *Cognit Psychol* 19:342-368.
- Leonardo M, Fieldman J, Sadato N, Campbell G, Ibanez V, Cohen L, Deiber MP, Jezzard P, Pons T, Turner R, Le Bihan D, Hallett M (1995) A magnetic resonance functional neuroimaging study of cortical regions associated with motor task execution and motor ideation in humans. *Hum Brain Map* 3:83-92.
- Markowitsch HJ, Kalbe E, Kessler J, Stockhausen vH, Ghaemi M, Heiss WD (1999) Short-term memory deficit after focal parietal damage. *J Clin Exp Neuropsychol* 21:784-797.
- Marks DF (1973) Visual imagery differences in the recall of pictures. *Br J Psychol* 64:17-24.
- Mattingley JB, Husain M, Rorden C, Kennard C, Driver J (1998) Motor role of human inferior parietal lobe revealed in unilateral neglect patients. *Nature* 392:179-182.
- Pause M, Kunesch E, Binkofski F, Freund HJ (1989) Sensorimotor disturbances in patients with lesions of the parietal cortex. *Brain* 112:1599-1625.

- Perrett DI, Smith PA, Potter DD, Mistlin AJ, Head AS, Milner AD, Jeeves MA (1985) Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proc R Soc Lond B Biol Sci* 223:293-317.
- Peters M (1998) Description and validation of a flexible and broadly usable hand preference questionnaire. *Laterality* 3:77-96.
- Peters M, Laeng B, Latham K, Jackson M, Zaiyouna R, Richardson C (1995) A redrawn Vandenberg and Kuse mental rotations test: different versions and factors that affect performance. *Brain Cognit* 28:39-58.
- Ramachandran VS, Altschuler EL, Hillyer S (1997) Mirror agnosia. *Proc R Soc Lond B Biol Sci* 264:645-647.
- Rizzolatti G, Fadiga L, Gallese V, Fogassi L (1996) Premotor cortex and the recognition of motor actions. *Brain Res Cognit Brain Res* 3:131-141.
- Roland PE, Zilles K (1996) Functions and structures of the motor cortices in humans. *Curr Opin Neurobiol* 6:773-781.
- Rosenthal R (1991) *Meta-analytical procedures for social research*. Newbury Park: Sage Publications.
- Sadato N, Yonekura Y, Yamada H, Nakamura S., Waki A, Ishii Y (1998) Activation patterns of covert word generation detected by fMRI: comparison with 3D PET. *J Comput Assist Tomogr* 22:945-952.
- Sakata H, Taira M, Kusunoki M, Murata A, Tsutsui K, Tanaka Y, Shein WN, Miyashita Y (1999) Neural representation of three-dimensional features of manipulation objects with stereopsis. *Exp Brain Res* 128:160-169.
- Schubert T, Von Cramon DY, Niendorf T, Pollmann S, Bublak P (1998) Cortical areas and the control of self-determined finger movements: an fMRI study. *NeuroReport* 9:3171-3176.
- Seitz RJ, Canavan AG, Yaguez L, Herzog H, Tellmann L, Knorr U, Huang Y, Homberg V (1997) Representations of graphomotor trajectories in the human parietal cortex: evidence for controlled processing and automatic performance. *Eur J Neurosci* 9:378-389.
- Shibasaki H, Sadato N, Lyshkow H, Yonekura Y, Honda M, Nagamine T, Suwazono S, Magata Y, Ikeda A, Miyazaki M (1993) Both primary motor cortex and supplementary motor area play an important role in complex finger movement. *Brain* 116:1387-1398.
- Stephan KM, Fink GR, Passingham RE, Silbersweig D, Ceballos-Baumann AO, Frith CD, Frackowiak RS (1995) Functional anatomy of the mental representation of upper extremity movements in healthy subjects. *J Neurophysiol* 73:373-386.
- Stephan KM, Binkofski F, Halsband U, Dohle C, Wunderlich G, Schnitzler A, Tass P, Posse S, Herzog H, Sturm V, Zilles K, Seitz RJ, Freund HJ (1999) The role of ventral medial wall motor areas in bimanual co-ordination. A combined lesion and activation study. *Brain* 122:351-368.