

Motor Affordance and its Role for Visual Working Memory:

Evidence from fMRI studies

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Abstract. We examined the role of motor affordances of objects for working memory retention processes. Three experiments are reported in which participants passively viewed pictures of real world objects or had to retain the objects in working memory for a comparison with an S2 stimulus. Brain activation was recorded by means of functional magnetic resonance imaging (fMRI). Retaining information about objects for which hand actions could easily be retrieved (manipulable objects) in working memory activated the hand region of the ventral premotor cortex (PMC) contralateral to the dominant hand. Conversely, nonmanipulable objects activated the left inferior frontal gyrus. This suggests that working memory for objects with motor affordance is based on motor programs associated with their use. An additional study revealed that motor program activation can be modulated by task demands: Holding manipulable objects in working memory for an upcoming motor comparison task was associated with left ventral PMC activation. However, retaining the same objects for a subsequent size comparison task led to activation in posterior brain regions. This suggests that the activation hand motor programs under top down control. By this they can flexibly be adapted to various task demands. It is argued that hand motor programs may serve a similar working memory function as speech motor programs for verbalizable working memory contents, and that the premotor system mediates the temporal integration of motor representations with other task-relevant representations in support of goal oriented behavior.

Key words: , , , ,

Everyday situations require doing several things in parallel. For example, listening to a person, maintaining a memory of what he/she said, accessing information in long-term-memory, and initiating new task-appropriate behavior whenever something new is happening. The system that allows us to coordinate various activities, to keep information in mind, and to initiate goal-oriented behavior is called working memory. It is an extremely flexible system, adaptable to a large variety of tasks and situations.

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On a functional level, working memory can be decomposed into *storage* and *manipulation* processes. Manipulation processes, on a very broad level, can be defined as processes that act on the contents of storage, like updating and rechecking of working memory contents, focusing attention on relevant events and inhibiting irrelevant ones, or the planning of sequences of subtasks to accomplish goals. These manipulation processes – also referred to as executive control (Baddeley; 2000) or executive memory (Fuster, 2002) – are ascribed to different and hierarchical levels of the frontal (e.g., Smith & Jonides, 1999).

Storage processes in human working memory, on the other hand, have been extensively studied with verbal materials that can be encoded phonologically. Due to the direct mapping between hearing and articulation (inherent to phonemes) phonological codes can be accessed and repeatedly refreshed by an articulatory rehearsal mechanism. This enables the main-

tenance of verbal information in working memory. Conversely, not much is known in which format visual memoranda, for which no phonological codes are accessible, are maintained in working memory. To overcome this apparent discrepancy between storage of verbalisable and nonverbalisable contents, the concept of motor rehearsal was introduced: This concept suggests that visual-spatial working memory contents can be maintained by activating spatially selective eye movements towards memorized locations.

The empirical evidence for a motor-rehearsal account, however, is mixed: Studies in humans have shown stronger interference of a sensorimotor tracking task (Quin, 1994) and of concurrent eye movements (Lawrence, Myerson, Oonk, & Abrams, 2001) for spatial than for verbal working memory contents. Neurophysiological studies with animals, in contrast, have revealed no correlation between single cell activity in the prefrontal cortex (PFC) during spatial rehearsal periods and during movement periods (Carlson, Rämä, Tanica, Linnankoski, & Mansikka, 1997). While these data suggest that spatial working memory representations are to some extent independent from motor-based processes, they do not rule out the possibility that motor-based processes are important for the rehearsal of visual materials.

A different view on working memory retention processes and the role of motor processes can be derived by considering working memory in its relation to other memory systems. Fuster (1997) proposed considering working memory as part of a perception-action cycle. According to this view, the main purpose of working memory is to bridge a period between the encoding of information and the time when such information has to be acted upon. In other words, maintaining a stimulus in working memory activates a network of hierarchical perceptual and motor memories associated with that stimulus, which are housed by posterior and frontal brain regions, respectively.

This model not only emphasizes the temporal integration function of the PFC, that is, the integration of perceptual, motor, or cognitive units into a sequence towards a goal (Fuster, 2002). It also has clear implications for the role of motor memories for working memory retention: Maintaining a stimulus in working memory should activate ensembles of perceptual and motor representations associated with that stimulus, with the hierarchical level and the extensiveness of these representations being dependent on the stimulus characteristics and the motor acts to be performed.

The present report aims at specifying the role of motor memories for the maintenance of information about every day objects in working memory. The question arises what the nature of motor memories for every day objects might be and at what level of

the motor hierarchy these motor memories are located. Are motor programs for object use, that is, information on the trajectories of movements to be performed with an object represented in the human brain? If so, are these motor affordances of objects automatically recognized by perceiving action-relevant object features? Are representations of motor acts of relevance for maintaining information about object identity in working memory?

These issues were addressed in a series of fMRI studies in which either photographs or line drawings denoting real world objects were presented and task demands were systematically varied across experiments. All stimuli were carefully selected by means of preexperimental rating studies in which participants indicated whether or not they can pantomime the action associated with the object. Based on the outcome of these ratings, objects were assigned to groups of manipulable and nonmanipulable objects. The participants in the fMRI studies were not informed about this aspect of the stimulus material. Experiment 1 examined visual discrimination of manipulable and nonmanipulable objects using photographs as stimulus materials. In Experiment 2, we examined working memory retention for both types of objects. Using photographs of manipulable objects; Experiment 3 examined whether motor programs for object use can be flexibly adapted to changing task demands.

Experiment 1

In Experiment 1 we examined brain activation evoked by passively viewing tool-like manipulable objects and nonmanipulable objects. Imaging studies in humans revealed enhanced activation in the hand area of the ventral premotor cortex (PMC) during the observation of tools and when an action is performed with a tool (Grafton, Arbib, Fadiga, & Rizzolatti, 1996). Given this, we predicted higher activation in the hand area of the ventral PMC for viewing manipulable than nonmanipulable objects.

Methods

Subjects

Twelve right-handed subjects (7 male, mean age: 25 years) participated in Experiment 1. They were paid 15 DM/h.

Stimulus Materials

Two hundred and twenty color photographs of real world objects were used as stimulus materials. There

were two sets of 60 photographs with manipulable (e.g., *hammer*; *hair dryer*; *comb*) and nonmanipulable objects (e.g., *ice bear*; *house*). A third group of 80 objects was comprised of neutral objects, i.e., objects that had a mean manipulability score in the preexperimental rating. (e.g., *shuttlecock*, *mussel*). The remaining 20 stimuli were photographs of male (10) and female faces. All photographs were 94 mm in height and width.

Procedure

All objects were presented for 400 ms in a quasi-randomized order. The subjects task was to watch the train of stimuli and to press a button whenever a face is presented (go/nogo task). As the main interest in the present study was in PMC activation contralateral to the dominant (right) hand, the index finger of the left hand was used for responding. The ISI was variable and ranged from 2.5 s to 5 s (steps of 500 ms). By this, the mean trial duration was 4 s. To get a better estimate of the hemodynamic response evoked by the object, 40 null events without stimulus presentation were randomly inserted in the stimulus train. These null events served as a control condition for statistical analyses. At least three target objects and neutral objects were interposed between two manipulable or two nonmanipulable objects. The experiment had a duration of 17 minutes.

fMRI Procedure and Statistical Analyses

Imaging was performed with a 3T MR scanner (Brocker) and a T2* sensitive echo planar sequence was used for functional imaging (TR: 1000 ms; TE: 30 ms). Structural whole brain images were acquired using a T1-weighted three-dimensional segmented MDEFT in a separate session. A standard birdcage head coil was used and the participants were supine on the scanner bed, with a stereotactic fixation system used to reduce head motion. An acquisition volume consisted of 16 axial slices (parallel to the AC-PC line), with 5mm thickness and 1 mm interslice distance. Seven slices were positioned above the AC-PC line, resulting in a voxel size of $3 \times 3 \times 5$ mm. The variable ISI allowed oversampling and increased the temporal resolution. Throughout the experiment, 530 acquisition volumes could be taken.

The fMRI data were processed using the software package LIPSIA (Lohmann et al. 1999). During preprocessing low-frequency artifacts were removed by applying a 1/55 s high pass filter. For spatial smoothing, a Gaussian filter was applied (FWHM: 5.28 mm). For each subject, the fMRI signals evoked by the objects were correlated with a Gaussian reference

function. The reference function resembled the time course of the hemodynamic response evoked by the objects. To account for the physiological delay of the hemodynamic response, the reference function was shifted by 6 s. Using this reference function orthogonal contrasts were calculated between both object types and null events and between manipulable and nonmanipulable objects. Group analyses were performed with a random effect model one-sample *t* test across individual *z* scores (Bosch, 2000). The resulting *t* statistics were normalized to *z* scores and for each participant the *z* maps were coregistered with the individual anatomical data sets and transformed into stereotactic Talairach space. For the statistical analyses of the contrasts between both object types and the null events a height threshold of $p < .005$ ($z = 2.6$) (uncorrected) and a spatial extend threshold of 5 voxels (corresponding to an activated volume of 225 mm³) was defined. In order to test the hypothesis that viewing manipulable objects activates the hand area of the premotor cortex, a region of interest (ROI) for this area was defined a priori. On the basis of recent studies (Rizzolatti, Fogassi, & Gallese, 2002; Schubotz & von Cramon, 2003), activation was considered to be in the left PMC hand area when it was smaller than $z = 50$ mm, between -2 mm and 10 mm in the sagittal (*y* axes) plane and smaller than $x = -20$ mm in Talairach space. The conventional $p < .05$ level was used to test the hypotheses.

Results

All participants performed with high accuracy. The hit rate was 100% and mean reaction times were 591 ms. The contrast between manipulable objects and null events and between nonmanipulable objects and null events revealed enhanced activation in a large and overlapping bilateral network of brain regions. The anterior parts included the left inferior frontal sulcus (BA 6/9/46), the inferior frontal gyrus (BA 45), and the frontopolar PFC (BA 47). In the posterior cortex, there was activation in the precuneus (BA 7), and in the superior parietal lobe (BA 7). In addition, both classes of objects relative to null events also activated the posterior parts of the occipital gyri, the lingual gyrus, and the fusiform gyrus (BA 17, 18, 19). For nonmanipulable objects, there was activation in the medial frontal gyrus (BA 6). Interestingly, activation in the left ventral PMC (BA 6, Talairach coordinates: -38 mm, -1 mm, 32 mm; z max: 4.2) was found for manipulable objects only. This latter activation was in the posterior wall of the precentral gyrus and by this about 1 cm more posterior and about 1.5 cm more superior than the adjacent left inferior frontal gyrus (BA 44).

As illustrated in Figure 1, the direct contrast of both classes of objects revealed enhanced activation for manipulable objects in the left ventral PMC (BA 6) and in the temporo-occipital junction (BA 18 & 37; z max: 3.24 and 3.27). Confirming our hypothesis, the ventral PMC activation (Talairach coordinates: -52 mm, -1 mm, 38 mm; z max: 3.24, $p < .005$) was within the a priori defined ROI.

Discussion

Consistent with our hypothesis, passive viewing of manipulable objects activates the hand region of the PMC contralateral to the dominant hand. As the objects in this experiment did not require an overt response and the target response had to be given with the left hand, any contribution of task-initiated motor processes to the present PMC activation can be ruled out. This result supports the view that motor programs for object use are a constituent component of object representations in the human brain. Consistent with the present findings, the ventral PMC contralateral to the dominant hand was also activated in various perceptual tasks, like viewing tool-like objects (Chao & Martin, 2000), naming tools (Grafton et al., 1996; Martin, Wiggs, Unterleider, & Haxby, 1996), or semantic classifications of tools (Gerlach, Law, Gade, & Paulson, 2000). An important next issue to be addressed is whether PMC activation of a similar kind is also obtained without sensory input, when information about objects is maintained in working memory.

Experiment 2

In Experiment 2, participants were required to maintain the objects in working memory for several seconds and, upon presentation of a test stimulus, retrieve this information from working memory. We used line drawings of familiar objects that were matched for name agreement, familiarity, and complexity (Snodgrass & Vanderwart, 1980). To reduce the likelihood of verbal recoding and rehearsal of the object name, a task was designed in which the object was held constant within each trial, and its physical appearance was varied between S1 and S2. In this task, a brief verbal cue is presented visually within the retention interval that indicates the type of task to be performed. Time locking the analysis of the hemodynamic response to that cue should enable retention-related activation to be examined without contaminations from perceptual encoding processes.

Methods

Stimulus Materials

Ninety six line drawings of every day objects were selected from a total of 240 objects, which were tested for manipulability in a pilot study (see Magnié, Besson, Poncet, & Dolisi, 2002, for details). The stimuli were assigned to two groups of 48 manipulable and 48 nonmanipulable objects.

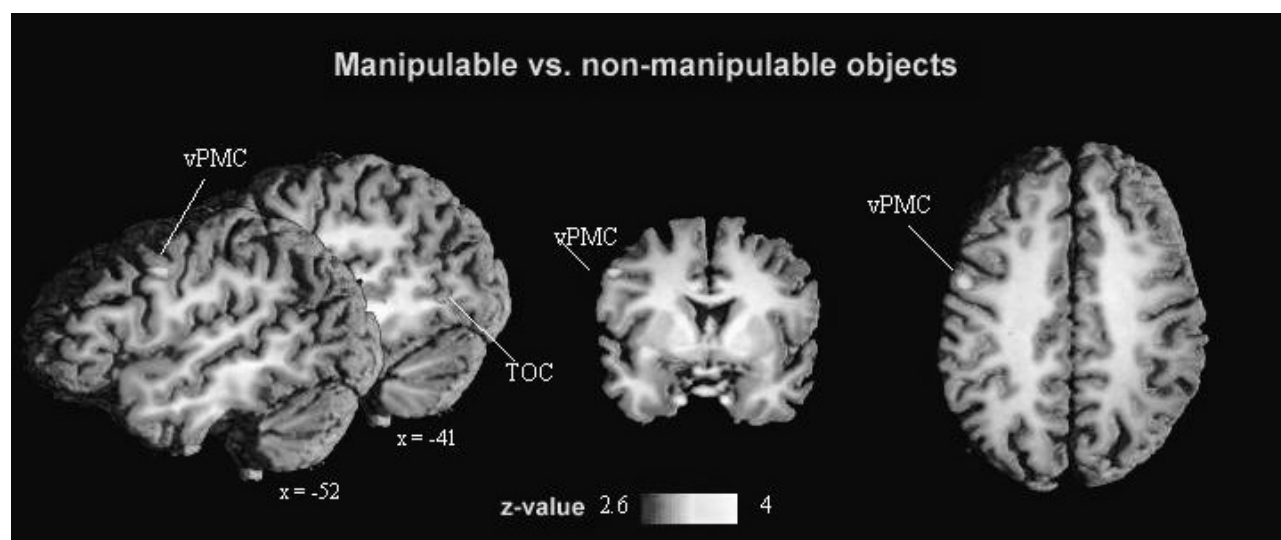


Figure 1. Mean activation for manipulable vs. nonmanipulable objects in Experiment 1 (passive viewing). Manipulable objects activate the left ventral PMC (vPMC) and the junction between the temporal and occipital cortices (TOC).

Procedure

Each trial started with an object presented for 100 ms. Four seconds thereafter, a task cue was shown that indicated the type of task to be performed upon presentation of S2 (6 s after the task cue). In the memory task, the cue (MEM) indicated that subjects had to judge whether the object presented at S2 is identical to the one maintained in working memory or its mirror version. In the control task (ZIF), subjects had to indicate whether two digits presented to the left and right of the object at S2 are identical or not. In both tasks, subjects responded with the index and middle finger of their right hand. Subjects performed a total of 192 trials. Half of them were memory trials, the other half control trials. In both types of trials, half of the objects were manipulable and the other half nonmanipulable. The order of memory and control trials was randomized.

fMRI Procedure and Statistical Analyses

The fMRI procedure was the same as in Experiment 1, with the following exceptions. A voxel size of $3 \times 3 \times 5$ mm was used and the lower edge of the most inferior slice was identical with the AC-PC line. The fMRI analyses focused on the hemodynamic response evoked by the task cues. The fMRI signals evoked by the task cues for each subject were correlated with a reference function, i.e., a rectangular (boxcar) function convolved with a Gaussian kernel that followed the time course of the cue-S2 interval of 6 s. The reference function was shifted by 4 s in order to account for the delay in the hemodynamic response. Orthogonal contrasts between memory trials and control trials and between memory trials with manipulable and nonmanipulable objects were calculated. Only trials with correct performance entered this analysis.

A two-step procedure was applied for all statistical analyses: First the main effects of memory task vs control task (collapsed across both classes of objects) were conducted at a threshold of $p < .001$ (uncorrected). Only voxels that showed this overall effect of memory vs control task were selected for further analyses. Specific contrasts were then calculated with a threshold of $p < .01$ and a spatial extent threshold of 5 voxels corresponding to an activated volume of 225 mm^3 .

Results and Discussion

The mean response times were 913 ms (manipulable objects) and 924 ms (nonmanipulable objects). The

corresponding error rates were 9.4% (manipulable) and 12.3% (nonmanipulable). As expected, response times were lower in the control trials (878 ms and 882 ms for manipulable and nonmanipulable objects, respectively). As the present task required the subjects to judge whether or not the object presented at S2 is identical or a mirror image of the object presented at S1, we assumed that task demands may differ for objects with high and low symmetry along their vertical axis.

To test this possibility, we performed a median split of the stimulus materials and contrasted performance measures for objects with low and high symmetry. Confirming our prediction, subjects performed faster (884 ms) and committed less errors (6.4%) for low than for high symmetry objects (958 ms/15.2%). In the following, we will present the fMRI data for objects with high only symmetry. (For a full report of the experimental results, see Mecklinger et al., 2002.)

Figure 2 shows the mean activation patterns for memory relative to control trials for manipulable and nonmanipulable objects with high symmetry. There was pronounced activation in the left ventral PMC (BA 6, -44 mm, 3 mm, 31 mm; z max: 3.13) for manipulable objects. In contrast, nonmanipulable objects were associated with enhanced activation in the adjacent left inferior frontal gyrus (Broca's area BA 44, -45 mm, 12 mm, 9 mm; z max: 3.75).

Taken together, the present results show that activation in the ventral PMC is modulated by an object's manipulability. Even more important, ventral PMC activity is also revealed when encoding processes are controlled for. By this, the present results extend those of Experiment 1 and show that, in a classical case for visual working memory, in which object information has to be retained for an prospective action and sustained activity is not contaminated by encoding processes, higher order motor memories are a constituent part of the working memory network. Conversely, premotor cortex activation is absent for nonmanipulable objects, for which motor schemata are not part of the object representation. These objects are associated with enhanced activation in Broca's area, suggesting that speech motor programs may have played a role for the maintenance of nonmanipulable objects.

A common feature of the two experiments presented so far, was that qualitatively different objects were used to probe the relevance of motor memories for object representation in the human brain. In both studies ventral PMC activation was obtained by contrasting manipulable and nonmanipulable objects under different task demands. An important issue, however, is whether motor memories can also be activated intentionally to support goal-oriented actions. We addressed these issue, by examining hemody-

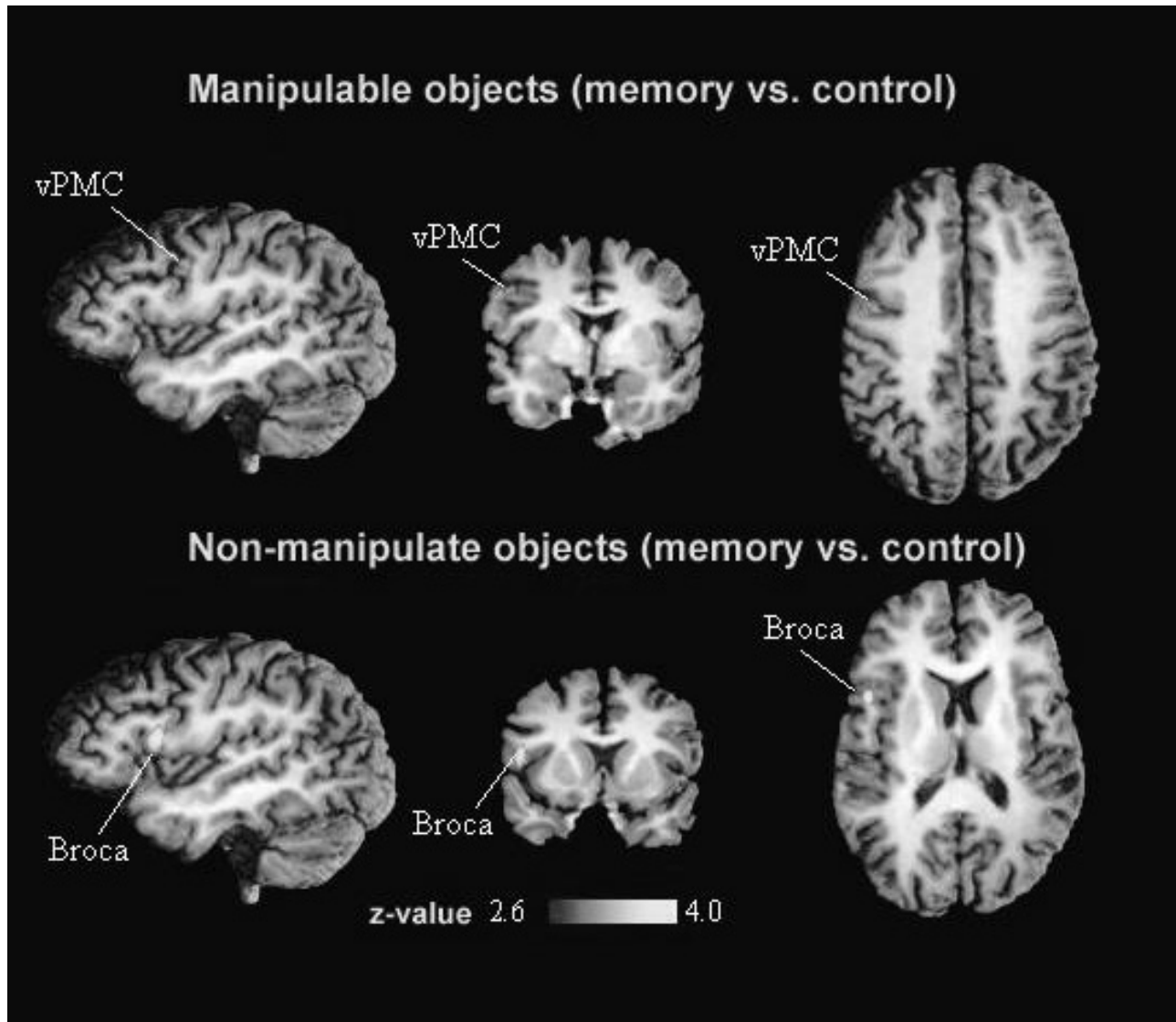


Figure 2. Mean activation for manipulable and nonmanipulable objects with high symmetry in the retention interval of Experiment 2. Contrasts between working memory and control trials are shown for both object types.

dynamic activation evoked by the same (manipulable) objects under two different working memory conditions, that either required the maintenance of action features or sensory features of an object.

Experiment 3

Methods

Subjects

Eleven subjects (mean age: 30 years; range: 26–36 years, 4 male) participated in the study. All subjects were right handed and gave informed consent prior to participation.

Stimuli

The stimuli were 240 photographs denoting real world objects. They included the 60 manipulable objects also used in Experiment 1 plus 180 new manipulable objects that were selected from a larger set of photographs based on a pilot rating study that was identical with respect to the manipulability criteria in the pilot study used to select the stimulus materials of Experiment 1. In addition, name agreement was assessed. The photographs were divided in two sets of 120 stimuli. For both sets, 20 pairs of objects were created with which similar hand movements can be performed (e.g., *fork & spoon/can & drinking glass*). Another 20 pairs of objects were created, which were about equal in size in their real world

appearance (e.g., *lipstick & whistle/passport & cigarette box*). Special care was taken to instruct the subjects to judge similarities of movements rather than actions.

Procedure

Each trial started with the presentation of an object (2 s), 500 ms after its offset a task cue was shown that indicated that upon presentation of S2 (5.8 s after the task cue onset) either of two memory tasks (HAN/GRÖ) or the control task (ZIF) had to be performed. At S2 only object names were presented. In one memory task (HAN), participants indicated whether or not the same hand movement can be performed with the objects represented at S1 and S2. In the other memory task (GRÖ), they indicated whether or not the two objects presented at S1 and S2 are equal in size. In the control task, participants indicated whether the two digits presented to the left and right of the object were identical or not. In all three tasks, the subjects responded by pressing one of two response buttons with the index and middle finger of their right hand. The next trial started 6 s after S2 onset. Subjects performed 40 trials in each of the three tasks. Task order was randomized and within each task there was an equal amount of “identical” and “nonidentical” responses. Words for which nonidentical responses had to be given were randomly drawn from the other object group (size words from the group of movement words and vice versa) and the two stimulus sets were counterbalanced across subjects.

FMRI Procedures

Imaging was performed with a Siemens Trio 3T MR scanner at the Medical School at Tübingen University. A T2* sensitive echo planar sequence was used for functional imaging (TR: 1000 ms; TE: 30 ms; flip angle: 70°; 4 runs). A total of 1724 volumes, subdivided in four runs, were recorded. High-resolution structural images were acquired using a MP-RAGE 3-D sequence. A standard birdcage head coil was used and the participants were supine on the scanner bed, with a stereotactic fixation system used to reduce head motion. An acquisition volume consisted of 16 axial slices (parallel to the AC-PC line) with 4 mm slice thickness, 1 mm interslice distance, and an in-plane resolution of 3 × 3 mm, resulting in a voxel size of 3 × 3 × 4 mm.

FMRI time-series analysis was performed with Statistical Parametric Mapping (SPM2; Friston, Penny, Kiebel, Hinton, & Ashburner, 2002). First, time series were corrected to account for the different

sampling time of the slices and realigned to minimize movement-related artifacts. After coregistering anatomical images to the mean functional image, resulting images were normalized to the standard MNI-T1 template (Cocosco, Kollokian, Kwan, & Evans, 1997). Based on the determined parameters, the normalization algorithm was then applied to the functional volumes. Finally, the normalized images were resampled into 2 mm isotropic voxels and spatially smoothed with an isotropic 8-mm FWHM Gaussian kernel. Due to technical artifacts, one subject had to be excluded from statistical analyses.

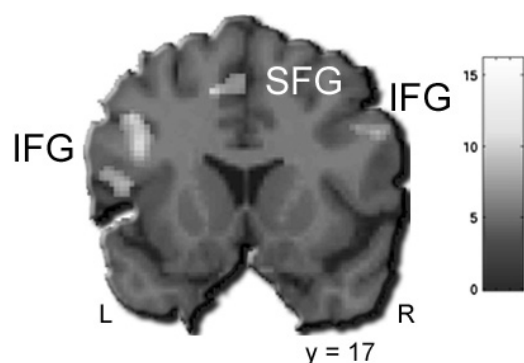
Statistical analysis was performed in two steps in a mixed-effects model. Hemodynamic activation was modeled as an epoch time-locked to the on- and offset of the cue interval, separately for both memory conditions and the control condition. Time series were high-pass filtered to 1/128 Hz and proportionally scaled to a grand mean of 100 (across all measured volumes). After estimating parameters for each covariate using a subject-specific fixed-effects model, linear contrast of the parameter estimates entered into a second-level random-effect analysis. One-sample *t* tests on contrast images were performed for all comparisons. *t* tests on contrast images are considered to be less powerful than *t* tests on individual *z* scores (Bosch, 2000), employed in the data analyses of Experiment 1 and 2. For that reason the height thresholds for the overall comparison of memory tasks and control task, statistical parametric maps (SPMs) were set to a higher threshold of $p < .0001$, as compared to the corresponding value in Experiment 2. ($p < .001$). In an analogous way, the height value for the direct contrasts of the two memory tasks was increased to $p < .001$ (all *p* values uncorrected). An extend threshold of 30 voxels (corresponding to an activation volume of 240 mm³, that was similar in its spatial extent to the corresponding threshold in Experiments 1 and 2, was used for all comparisons.

Results and Discussion

Mean RTs were 1368 ms (movement task) and 1476 ms (size task) and significantly longer in the size task ($p < .004$). Similarly, error rates were higher in the size task (28%) than in the movement task (19%; $p < .01$). As expected, mean reaction times were fastest (930 ms) and error rates lowest (5%) in the control task.

Figure 3 and Table 1 show the across-subject activation patterns for both memory tasks relative to the control task. For the movement task there was an activation in the lower limb of the left superior frontal gyrus (BA 8) and along the left and right inferior

(a) Movement > Control



(b) Size > Control

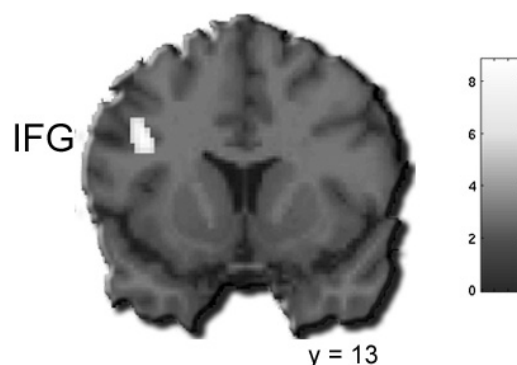


Figure 3. Contrasts between both memory tasks (movement and size) and the control task in Experiment 3. The Talairach y coordinate value is given below the slices. In the movement task the left *and* right inferior frontal gyri (IFG) and the left superior frontal gyrus (SFG) are activated. In the size task (Fig 4b) the left inferior frontal gyrus was activated.

frontal gyri (BA 44/45). Conversely, the size task activated the left inferior frontal gyrus (BA 45/44/9). In a following step, we directly contrasted the activation patterns in both memory tasks. The movement task relative to the size task activated the ventral PMC (BA 6), the left superior frontal gyrus (BA 8), the left and right inferior frontal gyri (BA 45), the anterior (ascending) and posterior branches of the left intra-parietal sulcus (BA 40), and the left middle temporal gyrus (BA 37). The reversed contrast (size task vs movement task) revealed enhanced activation in the right inferior precuneus (BA 31), the right lingual gyrus (BA 18), the left posterior cingulate gyrus (BA 23/31), the right superior parietal lobule (BA 7) and the left middle occipital gyrus (BA 19). Notably, no activation in left prefrontal and premotor regions was obtained for this contrast, even with lowered statistical thresholds. However, the size vs movement contrast revealed pronounced activation in the medial

frontal gyrus, close to the frontal pole. Given the close proximity of this region to the orbital cavity, we are inclined to consider this latter activation to be resulting from regionally heterogeneous $T2^*$ sensitivity, i.e., susceptibility artifacts (Mandeville & Rosen, 2002).

To further illustrate the differential hemodynamic activation in the movement and size tasks, we plotted the activation time course (% signal change) for two brain regions, significantly activated in the direct comparisons, i.e., the left ventral PMC (movement task) and the lingual gyrus (size task). The time course of the hemodynamic response elicited by the task cues in the ventral PMC and in the lingual gyrus is shown in Figure 4c. The BOLD response in the ventral PMC showed two pronounced peaks at around 3 s after task cue onset and 10 s after task cue onset, at the time the subjects responded. Notably, the activation patterns of both tasks start to differ

Table 1. Anatomical Location (in Talairach Coordinates) of the Regions Activated by the Contrast ($p < .0001$) and Contrasts (3) & (4) ($p < .001$)

Cortical region	Brodmann Area	Talairach coordinate			Z score
		x	y	z	
(1) Movement > Control					
Superior frontal gyrus	8	-12	20	41	4.78
Inferior frontal gyrus	45	-42	20	22	5.42
	44	48	15	29	4.37
(2) Size > Control					
Inferior frontal gyrus	45	-46	20	10	4.35
	9/44	-40	13	27	4.42
(3) Movement > Size					
Superior frontal gyrus	8	-4	29	45	4.44
Inferior frontal gyrus	45	-32	23	-3	4.70
	45	55	18	18	4.22
Ventral premotor cortex	6	-46	5	22	3.58
Anterior intraparietal sulcus	40	-46	-31	33	4.40
Posterior intraparietal sulcus	40	-40	-59	32	4.39
Middle temporal gyrus	37	-55	-62	7	3.68
(4) Size > Movement					
Posterior cingulate gyrus	23/31	-4	-49	30	3.45
Cuneus	31	8	-59	21	3.67
Lingual gyrus	18	10	-60	1	5.16
Superior parietal lobule	7	8	-73	50	3.63
Middle occipital gyrus	19	-38	-77	9	3.57

Note. Size > 30 voxels for all comparisons.

at around 3 s after cue onset and the enhanced PMC activation in the movement task was present until about 7 s after cue onset. Conversely, in the lingual gyrus, there was a peak at around 5 s after the task cue, which was larger in amplitude for the size than the movement task.

Taken together, these results argue against the view that the activation of motor programs for object use is an obligatory process evoked by action-relevant object features. No ventral PMC activation was obtained when subjects maintained features of manipulable objects in working memory for an upcoming size comparison. This suggests that motor program activation can be attenuated in favor of other task-relevant activation patterns. Conversely, pronounced ventral PMC activation was obtained when the same objects were retained in working memory for an upcoming movement comparison.

Retaining object information in working memory for a subsequent size comparison selectively activated the posterior cingulate gyrus and a number of parietal and occipital brain regions, i.e., the precuneus, the lingual gyrus, the superior parietal lobule, and the middle occipital gyrus.

The precuneus is a multimodal association area that enables the integration of current input with a

previously established situation model (see Maguire, Frith, & Morris, 1999). Precuneus activation in the present study may reflect the higher demands in visualizing object features when subjects anticipate a size comparison. The activation in the lingual gyrus and in the middle occipital gyrus, i.e., two areas of the ventral “object processing” pathway (Ungerleider & Haxby, 1994), in the size task may reflect the reactivation and selective processing of object form information, required for the upcoming size comparison.

General Discussion

The present report aims at specifying the role of motor memories for the maintenance of object information in working memory. In all three studies, objects with high motor affordance activated the hand region of the left ventral PMC, a higher order motor area that is also activated when actions with the corresponding objects have to be performed (Passingham, 1998). While the results of Experiment 1 and 2 at first glance suggest that motor memory activation is an obligatory and bottom-up driven brain response to movement relevant features of an object, Experi-

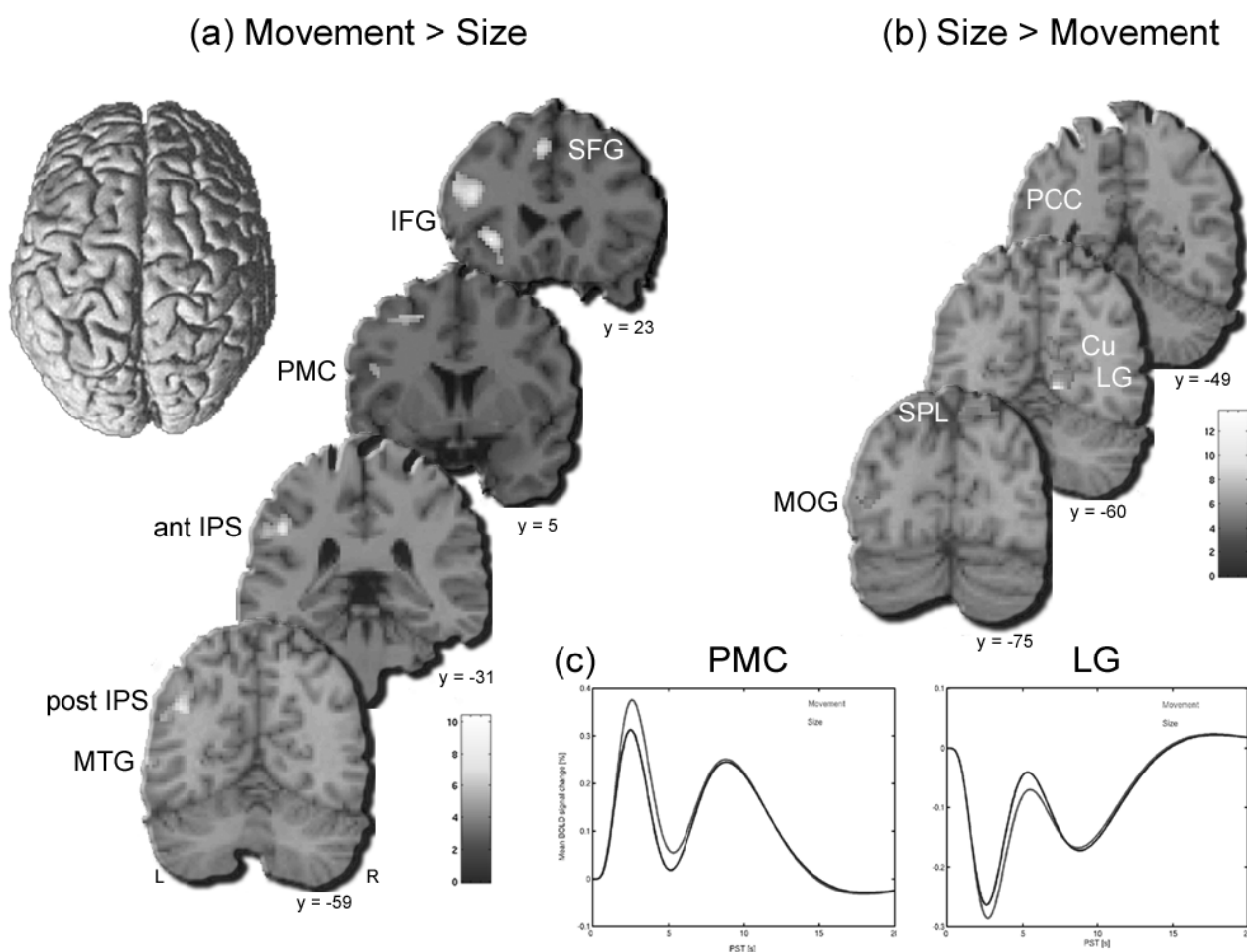


Figure 4. Direct comparisons between both memory tasks in Experiment 3. The Talairach y coordinates are indicated below each coronar section. (a) The contrast between the movement and the size condition revealed activations in the left and right inferior frontal gyri (IFG), the left superior frontal gyrus (SFG), the left ventral premotor cortex (PMC), the left anterior intraparietal sulcus (ant IPS), the left posterior intraparietal sulcus (post IPS) and the left middle temporal gyrus (MTG). (b) In the reversed comparison (size > movement) activations in the posterior cingulate gyrus (PCC), the right lingual gyrus (LG), the right precuneus (PCu), the right superior parietal lobule (SPL) and in the middle occipital gyrus (MOG) could be observed. (c) Across-subject time courses (20 s) of the fitted hemodynamic response for the left PMC and the right LG are plotted separately for the movement (red) and size (blue) condition. The vertical axis denotes the onset of the task cues.

ment 3 contradicts this view: The data show that motor memory activation can be modulated intentionally and by this flexibly adapted to changing task demands: When subjects retain information for a subsequent movement discrimination task, manipulable objects activate the ventral PMC as well as inferior frontal and posterior parietal areas. When information is retained for a size discrimination task, the same objects activate occipital and posterior parietal brain regions, presumably reflecting the selective processing of sensory object features. These results argue for a top-down attentional control on the processing of motor affordances.

Recent neurophysiological studies have shown that the ventral premotor cortex of monkeys (F5)

houses two kinds of neurons: “Canonical neurons” are active when the animal observes graspable objects and when they grasp the object. “Mirror neurons” fire when the monkey observes another individual grasping an object and when the monkey grasps the object (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Area F5 in the monkey brain receives direct input from the parietal area AIP. It has been suggested that AIP-F5 in the monkey brain constitutes a neuronal network that transforms action-relevant object properties into hand movements (Rizzolatti, Luppino, & Matelli, 1998). Even though there is some controversy on homologies between primate and human prefrontal brain regions (Amunts & Zilles, 2001; Rizzolatti et al., 1995), we take the present

results to support the view that the AIP-F5 circuitry also exists in the human brain (see Grèzes et al., 2003, for a similar view). Our ventral premotor activation may be the human homologue of the high neuronal discharge in the area F5 in the monkey brain. Similarly, the enhanced hemodynamic response in the anterior IPS (Experiment 3) may correspond to the enhanced firing rates in the monkey's area AIP (Mecklinger et al., 2002).

In extension to other studies examining the functional characteristics of the premotor systems, the present results provide evidence for the view that motor schemata for object use are a constituent component of a working memory retention network. They are part of object representations when information about manipulable object forms has to be retained in working memory. Recent models of working memory agree that the temporary maintenance of information is a joint function of the posterior and prefrontal cortex (D'Esposito & Postle, 2002; Fuster, 2002; Goldman-Rakic, 1987; Smith & Jonides, 1999), and pay little attention to lateral premotor activation. This may be a reflection of the poor spatial resolution of some imaging and analysis techniques. In fact, the anatomical segregation within left inferior frontal/premotor regions is difficult and occasional misclassifications of the ventral limb of the precentral sulcus as inferior frontal gyrus cannot be excluded. In addition, most previous studies used stimulus materials that did not contain motor associative elements.

The present results support the view that working memory emerges from a coactivation of perceptual and motor memories, which are activated to accomplish goal-oriented action (Mecklinger & Opitz, 2003). According to Fuster (2002) perceptual and motor memories are hierarchically organized and can be dynamically linked whenever stored information becomes behaviorally relevant. From the present lateral premotor cortex activation, it can be inferred that motor memories relevant for object representation do not entail movement information for specific muscle groups. Rather they are comprised of more abstract sequences of movements that are subdivided into different action domains, (i.e., speech motor programs, hand motor programs, eye movements). The activation in Broca's area obtained for nonmanipulable objects in Experiment 2 can be reconciled as the activation of speech motor programs, which presumably serve a similar working memory function than hand motor programs for manipulable objects. The main function of the premotor system is the temporal integration of motor representations with other task-relevant representational units into a sequence towards a goal (Fuster, 2002).

An open issue to be addressed is why no lateral PFC activation was obtained when manipulable ob-

jects were retained in working memory. A large number of brain imaging studies have substantiated the role of the lateral PFC for a variety of working memory processes (for overviews see: D'Esposito et al., 1998; Smith & Jonides, 1999). The absence of PFC activation may suggest that temporal integration, as required in the present delayed matching task, does not involve highest order motor memories (plans and concepts), but can be accomplished by lower level memories involving sequences and their goals. This view implies that higher order motor representations come into play with higher temporal integrations demands, like in n-back tasks that require the integration of informational units within and across trials (Petrides, 1994).

Even though the present model substantiates the role of motor memories for working memory retention processes, it is still unclear how exactly rehearsal of hand motor programs is accomplished. For phonological codes there is a direct mapping between hearing and articulation by which these speech motor programs can be directly accessed by an articulatory rehearsal mechanism. A similar role has been proposed for eye movement programs in the case of spatial rehearsal. Both mechanisms allow the repeated refreshment of verbal and spatial memory traces. Examining the mechanisms by which hand motor programs are accessed and continuously refreshed in favor of temporary storage remains an important endeavor and is of high relevance for our understanding of working memory.

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