

## FEATURE ARTICLE

# Kinesthetic Working Memory and Action Control within the Dorsal Stream

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**There is wide agreement that the “dorsal (action) stream” processes visual information for movement control. However, movements depend not only on vision but also on tactile and kinesthetic information (=haptics). Using functional magnetic resonance imaging, the present study investigates to what extent networks within the dorsal stream are also utilized for kinesthetic action control and whether they are also involved in kinesthetic working memory. Fourteen blindfolded participants performed a delayed-recognition task in which right-handed movements had to be encoded, maintained, and later recognized without any visual feedback. Encoding of hand movements activated somatosensory areas, superior parietal lobe (dorsodorsal stream), anterior intraparietal sulcus (aIPS) and adjoining areas (ventrodorsal stream), premotor cortex, and occipitotemporal cortex (ventral stream). Short-term maintenance of kinesthetic information elicited load-dependent activity in the aIPS and adjacent anterior portion of the superior parietal lobe (ventrodorsal stream) of the left hemisphere. We propose that the action representation system of the dorso-dorsal and ventrodorsal stream is utilized not only for visual but also for kinesthetic action control. Moreover, the present findings demonstrate that networks within the ventrodorsal stream, in particular the left aIPS and closely adjacent areas, are also engaged in working memory maintenance of kinesthetic information.**

**Keywords:** haptic, human fMRI, intraparietal sulcus, perception and action, primary somatosensory cortex, sensorimotor transformation

### Introduction

Visual information is processed in 2 functionally distinct streams. A ventral “perceptual” stream, which projects from early visual areas to the inferotemporal cortex and is central for object recognition, and a dorsal “action” stream, which projects from early visual areas to the posterior parietal cortex and is engaged in visually guided actions (Schneider 1969; Ungerleider and Mishkin 1982; Goodale and Milner 1992). Rizzolatti and Matelli (2003) refined this theory on the basis of electrophysiological data in monkeys and clinical data in humans. They proposed an anatomical and functional distinction of the dorsal stream in the dorsodorsal stream (d-d stream) and the ventrodorsal stream (v-d stream). The d-d stream that projects to the superior parietal lobe is supposed to be involved in fast online sensorimotor processing with little computational demand, as proposed by Goodale and Milner (1992) for the dorsal stream. In contrast, the v-d stream has its nodal points in the inferior parietal lobe including the anterior intraparietal sulcus (aIPS). Like the d-d stream, the v-d stream is responsible for action control by performing spatial computations in order to organize movements, such as object grasping and manipulation. The v-d

stream, however, has also been discussed as neural correlate of action recognition.

The majority of studies on sensorimotor processing focussed on visually guided actions. Although vision is the most dominant sensory modality, humans also rely on tactile and kinesthetic information (=, haptics; Gibson 1966) to explore object features, e.g., texture or contours, and to control motor acts. Among others, tactile and kinesthetic signals from the hand and the fingers are most critical for manual exploration (e.g., Johansson et al. 1992). Haptics and vision provide complimentary sources of information; the former refers to near peripersonal space only, whereas the latter comprises information from both proximate and distant space. Nevertheless, there is evidence that both the visual and the haptic system utilize the same processing streams subserving perception and action.

Behavioral experiments (Easton et al. 1997; Reales et al. 1999) and neuroimaging studies (Amedi et al. 2001; James et al. 2002) suggest a common neural substrate for visual and haptic object recognition in areas of the ventral stream. Accordingly, activation in the dorsal visual stream was found during exploratory hand movements performed without visual feedback (Binkofski et al. 1999; Jäncke et al. 2001; Stoekel et al. 2003). The results consistently showed activity in the superior parietal lobe, a nodal point of the d-d stream, and in the aIPS and adjacent inferior parietal lobe, areas captured by the v-d stream. Previous experiments, however, have mainly studied sensorimotor processes on the basis of tactile information. In the present study, we want to focus on the role of the dorsal stream in kinesthetic action control.

Beyond the proposed function of the dorsal stream in online action control, that is, a crude, fast, and automatic visuomotor transformation process, research in nonhuman primates suggests that posterior parietal cortex is also engaged in memory-guided actions. Neuronal activity in the anterior intraparietal (AIP) area was observed during a delayed hand manipulation task, in which monkeys were required to manipulate the remembered object in the dark relying on kinesthetic and tactile information (Murata et al. 1996). Many of the visually responsive neurons that were selective to the shape and orientation of objects were active during the delay period in the dark before object manipulation starts. A small subset of neurons showed delay period activity related to the preparation of the forthcoming hand manipulation. The majority of these neurons, however, elicited sustained activity in the dark even without the intention to remember object features. These results indicate that monkey area AIP, as part of the v-d stream, is involved in haptic working memory maintenance of spatial characteristics that guide hand actions in relation to objects. A functionally similar area has been proposed in humans as well

(human AIP; Grefkes et al. 2002). However, clinical studies have shown that a patient, DF, who has a lesion in the inferior temporal cortex, but an intact aIPS cannot recognize objects but can accurately grasp them in real time (Goodale et al. 1991; James et al. 2003). However, DF's performance deteriorates when a delay was introduced (Goodale et al. 1994), indicating that the ventral but not the dorsal stream may be engaged in the representation of delayed actions.

Functional imaging studies in humans consistently found activity in the posterior parietal cortex for both visual and tactile spatial working memory, suggesting its function in short-term maintenance of spatial information irrespective of the input modality (Macaluso et al. 2003; Ricciardi et al. 2006). Similar results have been also demonstrated for long-term memory retrieval (Stock, under review). Studies using delayed saccade tasks further indicate that visuospatial information represented in posterior parietal areas are maintained for prospective motor acts (for a review, see Curtis et al. 2006). This finding was supported by brain-imaging experiments on delayed pointing movements (Lacquaniti et al. 1997; Connolly et al. 2003). Recent studies on the tactile discrimination evidenced a decisive role of the posterior parietal cortex in working memory processes focusing on the somatosensory modality (Stoeckel et al. 2003, 2004; Kaas et al. 2006; Preuschhof et al. 2006). In the study by Stoeckel et al. (2003), participants were presented with pairs of parallelepipeds that were manually explored for subsequent object discrimination based on specific macrogeometric features. Between the presentation of the first and the second stimulus, a variable delay was introduced ranging from 12 to 17 s. Delay-related activity occurred in the left aIPS, bilateral fusiform gyrus, and left frontal regions. In a later study of the same group, short-term maintenance of tactile information activated a parietal region contiguous to the intraparietal sulcus (IPS), that is, the anterior portion of the superior parietal lobe (aSPL; Stoeckel et al. 2004).

Here, we used a delayed-recognition task in which hand movements had to be encoded, maintained, and recognized on the basis of kinesthetic information only, that is, all visual input was excluded. To uncover cortical regions related to working memory processes, we parametrically varied the memory load. We will focus on cortical activation of the dorsal stream during encoding and maintenance of the kinesthetic information. Our results suggest a functional generalization of the current theoretical framework of the dorsal stream. First, beyond its function in fast visual action control, the d-d and v-d streams seem also to be involved in kinesthetic-motor coupling in order to guide hand actions without vision. Second, areas within the v-d stream, in particular the left aIPS and closely adjacent regions, are also recruited for short-term maintenance of kinesthetic information.

## Materials and Methods

### Participants

Fourteen right-handed (Oldfield 1971), healthy young volunteers (9 males, 5 females; age range: 20–28 years, mean age: 24 years) participated in the study. They reported no history of medical, neurological, or psychiatric disorders and were free from prescription medications. Written informed consent according to the declaration of Helsinki was obtained from each volunteer before participating in the experiment. Volunteers were paid for their participation.

### Stimuli and Experimental Setup

Blindfolded participants laid supine in the scanner with their upper arm next to the body and their right forearm flexed to reach the experimental apparatus with the stylus held in the right hand (Fig. 1, left). The stimulus set comprised of 29 different line patterns that were engraved in small plastic cards (95 × 150 mm; width × height) (Fig. 1, right). There were 2 types of line patterns: 1 circular and 28 multisegment patterns. Line length was kept constant for all patterns (120 mm). To ensure comparable task complexity, each multisegment pattern was constructed with the same features: 4 segments (1 short, 2 medium, and 1 long segment of 15, 30, and 45 mm length) connected by one acute (45°), one right (90°), and one obtuse (135°) angle. To ease tracing requirements, the beginning of each line pattern was located at the left side of the card at a constant height of 75 mm and marked by a small plastic pin. Three line pattern cards were attached to a cardholder, which was uprightly fixed on a base. The base was attached comfortably to the abdomen of the participants by 2 hook-and-loop strips. The cardholder could be adjusted in 3 directions by a 120° turn on its own axis so that 3 line patterns could be successively presented per trial.

Due to the small size of the line patterns, participants mainly used finger, hand, and wrist movements only, whereas the upper arm remained motionless. In addition, head and shoulder motion was restricted by means of a Tempur foam head cushion (Tempur Deutschland GmbH, Steinhagen, Germany) and 4 arm cushions mounted to the right and left arm.

### Procedure

The time course of the delayed-recognition task is depicted in Figure 2A. Each trial started with a tone for 1000 ms, indicating the beginning of the encoding period. During this period, participants traced in succession 3 line patterns with a stylus in their right hand. After 14000 ms, a second tone of 1000 ms signaled the beginning of the delay period. Participants were instructed to maintain a vivid mental representation of the hand movements across a variable 7500–8500 ms delay period, whereas the right hand rested on their abdomen. Following the delay, a third tone of 1000 ms signaled the start of the recognition period. During recognition, participants traced one line pattern and finally pressed one of 2 buttons on a response box with their left hand to indicate whether the last line pattern matched one of the memory set items. Applying a variable inter-trial-interval of 8500–9500 ms, the total trial length was 34 000 ms. Participants held the stylus in their right hand during the entire experiment.

The memory sets always consisted of 3 stimuli, with 1 (Set 1), 2 (Set 2), or 3 (Set 3) multisegment patterns and 2, 1, or 0 circles, respectively (Fig. 1, right). None of the multisegment patterns was repeated within the same trial. As baseline condition 3 circular patterns were presented. The order of the different stimulus sets was randomized so that the participants did not know how many complex line patterns were presented during the encoding period. During the recognition period, a probe stimulus was presented which was a multisegment pattern in the Set 1, Set 2, and Set 3 condition and either a multisegment or a circular pattern in the baseline condition. There were 12 trials per condition and run, and 2 runs per participant, resulting in 96 trials per participant. To guarantee comparable task requirements, 2 filler trials per Set 1, Set 2, and Set 3 conditions and runs were inserted with a circle presented as probe stimulus. Thus, there were a total of 102 trials per participant. Trials were balanced for the number and position of complex line patterns and the position of the match stimulus within the encoding stimulus set. Furthermore, the number of match/non-match motor responses and the direction of the match/nonmatch response buttons were counterbalanced across the experiment.

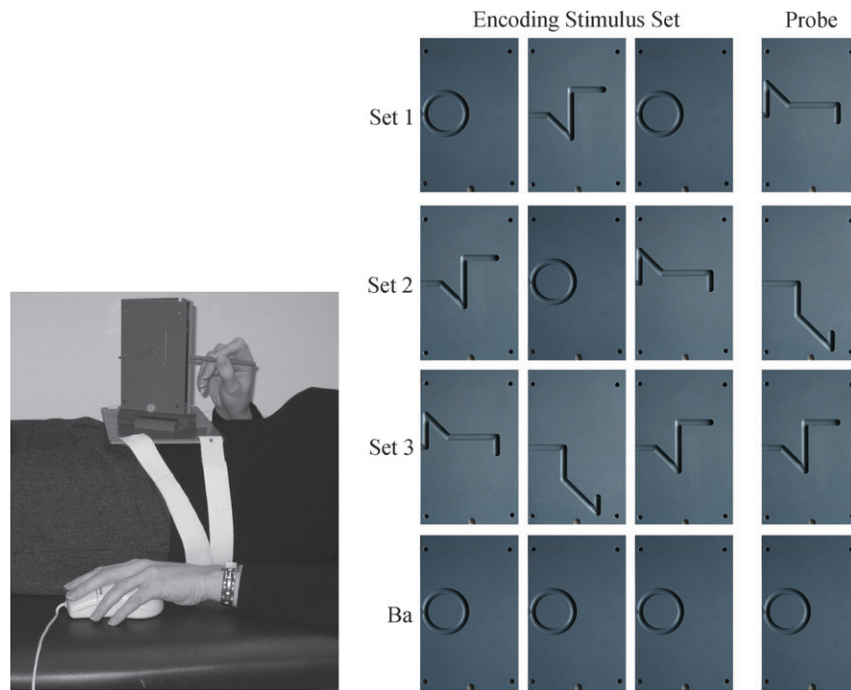
Prior to functional magnetic resonance imaging (fMRI) scanning, participants were trained in the experimental procedure outside the scanner while lying in a supine position. The practice session lasted 30–60 min depending on the participants' performance. Performance criteria were a percent correct rate more than 90% for the baseline and more than 60% for the Set 3 condition. Stimuli presented during the practice session were not used during the scanning session.

### Imaging

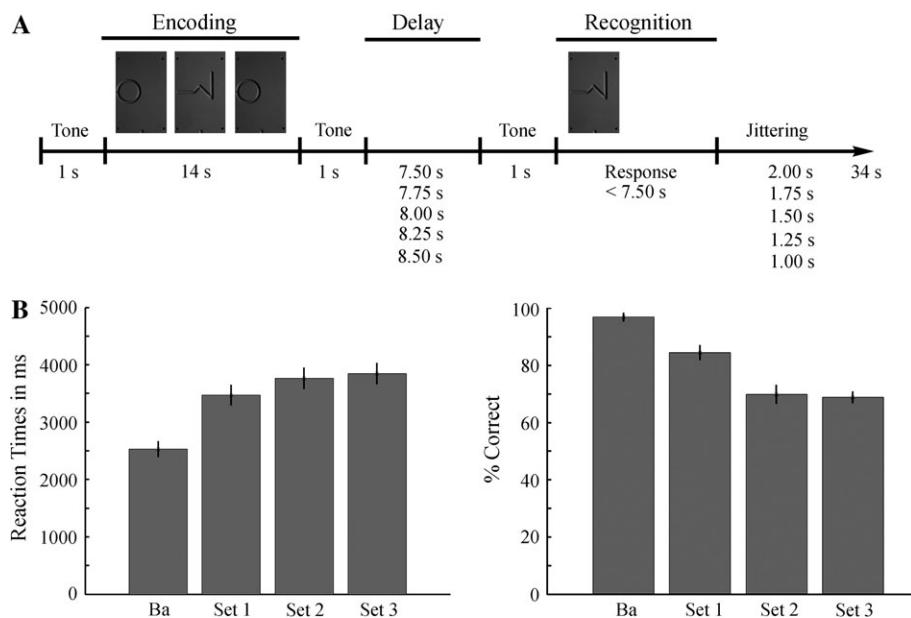
Imaging was performed on a 1.5 T GE Signa Scanner (GE Medical Systems, Milwaukee, WI) equipped with a standard quadrature birdcage

head coil. A high-resolution 3-dimensional set of anatomical images was acquired in the axial orientation for each participant using a  $T_1$ -weighted spoiled gradient echo sequence (field of view [FOV] =  $240 \times 180 \text{ mm}^2$ , matrix size  $256 \times 192$ , time echo [TE] = 6 ms, time repetition [TR] = 33 ms) covering the whole brain. Functional imaging was done with

a  $T_2^*$ -weighted gradient echo-planar imaging (EPI) sequence sensitive to blood oxygenation level-dependent (BOLD) contrasts (TR = 2000 ms; TE = 60 ms; flip angle =  $80^\circ$ ;  $64 \times 64$ -pixel matrix; voxel size =  $3.75 \times 3.75 \times 5 \text{ mm}$ ; FOV  $240 \times 240 \text{ mm}^2$ ), with each volume consisting of 19 axial slices (inter slice distance = 1 mm).



**Figure 1.** Experimental setup and task conditions. Left: The experimental setup shown as used in the training session outside the scanner. The same device was used in the scanner. Task stimuli were different line patterns engraved in plastic cards. The cards were attached to a triangular cardholder which could be turned such that one side was oriented toward the hand of the participant. Participants were blindfolded. They traced the line patterns with a stylus with their right hand and performed task-related button presses with their left hand. Right: Sample stimuli of the delayed-recognition task. Stimuli presented during encoding contained 0 (Ba, baseline), 1 (Set 1), 2 (Set 2), or 3 (Set 3) multisegment line patterns and 3, 2, 1, or 0 circular line patterns, respectively. An increasing number of multisegment line patterns reflects an increase in task difficulty. During recognition, one probe stimulus was presented which matched a stimulus from the memory set in 50% of the trials.



**Figure 2.** Schematic outline of the delayed-recognition task and behavioral results. (A) The task schedule is illustrated for a trial of the Set 1 condition. Three different line patterns had to be traced with a stylus and encoded. The hand movements had to be maintained in working memory for a variable delay of 7500–8500 ms. Then a probe stimulus had to be traced and a motor response had to be given indicating whether the probe matched one of the stimulus from the memory set. (B) Reaction times (left) and percent correct responses (right) for the 4 task conditions ( $N = 14$ ).

## Data Analysis

The statistic parametric mapping (SPM) package was used for image processing and statistical analyses (SPM2; <http://www.fil.ion.ucl.ac.uk/spm/>; Wellcome Department of Imaging Neuroscience, London, UK). The first 4 volumes of each fMRI run were discarded to allow for signal equilibration. Data preprocessing comprised the following steps: Images corrected for motion artifacts were normalized to a standard EPI template as defined by the Montreal Neurological Institute (MNI) closely approximate to the Talairach space (Talairach and Tournoux 1988). Spatial smoothing was applied by means of a Gaussian filter with 4 mm full width at half maximum. Functional data were corrected for slice-time acquisition differences using a sinc-interpolation algorithm.

The statistical analysis was based on a least-squares estimate using the general linear model for serially autocorrelated observations (Friston et al. 1995; Worsley and Friston 1995). Low-frequency signals were suppressed by applying 1/128 Hz highpass filter. An event-related design was implemented, and responses during each task period (encoding, maintenance, and recognition) were modeled separately for each condition (Set 1, Set 2, Set 3, baseline, and filler trials). Given estimates of the temporal smoothness of the hemodynamic response (Zarahn et al. 1997), the covariate modeling of the first seconds of the delay period would be contaminated by hemodynamic activity from the encoding period. The same problem concerns the recognition period that would be contaminated by hemodynamic activity of the delay period. To minimize this problem of multicollinearity, the first 3 s of the delay period were not considered in the analyses to temporally separate encoding from delay periods (cf., Postle et al. 2000). Additionally, we varied the length of the delay period from trial to trial; thus, our design allowed to deconvolve delay responses from recognition responses. The design matrix was generated by convolution of the respective predictor function of stimulus onsets with a synthetic hemodynamic response function based on a gamma variate (Friston et al. 1998). Additionally, the same predictor function of stimulus onsets was convolved with the first and second temporal derivative of the hemodynamic response to reveal 3 predictors in total for each experimental condition. The model includes an estimate of effective degrees of freedom (Worsley and Friston 1995).

Changes in BOLD signal associated with the encoding, delay and recognition periods of the behavioral task were assessed by the contrast Set 3 versus baseline, including both correct and erroneous trials. To examine brain regions that show an increased BOLD signal with task difficulty (Set 3 > Set 2 > Set 1 > baseline), a parametrical analysis was performed. For this purpose, the predictors were weighted by the logarithm of 2 (baseline), 3 (Set 1), 4 (Set 2), and 5 (Set 3). The resulting logarithmic function was a good estimate of the observed performance data (cf., Fig. 2B). The results of the parametrical analyses were then masked with the respective statistical parametric map of the direct contrast (Set 3 > baseline) using the MarsBar toolbox for SPM2 (Brett et al. 2002; <http://marsbar.sourceforge.net/>). Following first-level analyses, images of parameter estimates for each contrast of interest were entered into a second-level one-sample *t*-test, in which the mean estimate across participants at each voxel was tested against zero (random effects model). Significant regions of activation were identified using an uncorrected 2-tailed threshold of  $P < 0.001$  and a minimum cluster size of at least 10 adjacent voxels. All reported maxima of a cluster reached significance after correction for multiple comparisons by false discovery rate ( $P < 0.05$ ).

Anatomically distinct brain areas within volumes of interest (VOIs) were classified by means of the Anatomy toolbox for SPM2 (Eickhoff et al. 2005; [http://www.fz-juelich.de/ime/spm\\_anatomy\\_toolbox](http://www.fz-juelich.de/ime/spm_anatomy_toolbox)) that is based on histological processing and cytoarchitectonic analyses of 10 postmortem human brains. The resulting cytoarchitectural areas are probability maps. This means that VOIs are defined statistically, and therefore, they are not restricted to one cortical area only but do also extend into neighboring areas. However, the statistical probability for a specific VOI is always larger than for the neighboring VOIs. Weighted contrast values were calculated for selected VOIs using the MarsBar toolbox for SPM2 (Brett et al. 2002). For visualization purposes, thresholded statistical parametric maps were superimposed on a standard brain using MRICro (<http://www.sph.sc.edu/comd/rorden/mricro.html>) and Caret (Van Essen et al. 2001; <http://brainmap.wustl.edu/>

[resources/caretnew.html](http://resources/caretnew.html)) softwares. Trial-averaged event-related response time courses for various voxels of interest were calculated as the percent deviation from the mean fMRI signal measured across the participant's entire scanning session.

## Results

### Behavioral Data

Performance (Fig. 2B) was assessed by reaction times and percent correct rates (data are presented in Table 1). All participants performed significantly above chance (50%) in each task condition. A repeated-measures analysis of variance revealed a significant main effect of the 4-level factor task difficulty (baseline, Set 1, Set 2, and Set 3) for both reaction times ( $F_{3,39} = 65.62$ ,  $P < 0.0001$ ) and percent correct rates ( $F_{3,39} = 47.94$ ,  $P < 0.0001$ ). These main effects also reached statistical significance after exclusion of the baseline condition (Reaction times:  $F_{2,26} = 14.33$ ,  $P < 0.001$ ; correct response rates:  $F_{2,26} = 17.29$ ,  $P < 0.001$ ), although reaction times ( $F_{1,13} = 2.4$ ,  $P = 0.14$ ) and correct response rates ( $F_{1,13} = 0.42$ ,  $P = 0.53$ ) did not differ between Set 2 and Set 3 conditions.

### fMRI Data

Our first set of analyses identified brain areas generally engaged during encoding, maintenance, and recognition of kinesthetic information by contrasting the Set 3 versus the baseline condition (activated regions are listed in Table 2). In a second step, parametrical analyses were performed to reveal cortical regions where activity increased systematically with task difficulty.

### Encoding

Figure 3 (*I*: top row, ENC) shows cortical activation related to the encoding of hand movements. Frontal activation was found in bilateral dorsal and ventral premotor cortices, which was stronger in the left hemisphere. Additional activation occurred in ventrolateral prefrontal cortex (VLPFC) and right anterior medial frontal gyrus (MFG) in both hemispheres. Activation on the medial wall was located within presupplementary motor area (pre-SMA) and adjacent SMA proper (Picard and Strick 1996). Parietal activation was found along bilateral postcentral gyrus and adjoining anterior bank of postcentral sulcus that comprise Area 1 and Area 2 of the primary somatosensory cortex (SI), although the larger activation cluster was centered within Area 2 (cf., Fig. 4; for an anatomical description see Geyer et al. 1999, 2000; Grefkes et al. 2001). The time course of SI activity was tightly locked to the time window where hand movements were performed: SI activity peaked during the encoding period, declined during the delay period, and peaked again during the recognition period (cf., Fig. 4). The hemodynamic response within SI was modulated by task difficulty showing an increase with an increasing number of multisegment line patterns. An additional activation was found in

**Table 1**

Overview of the performance data for the 4 task conditions

	Baseline		Set 1		Set 2		Set 3	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
CR (%)	97.0	1.5	84.6	2.6	70.0	3.3	69.0	2.0
RT (ms)	2534.3	137.3	3476.2	178.8	3768.3	182.2	3849.5	183.0

Note: CR, correct responses; RT, reaction time; SEM standard error of the mean.

**Table 2**

Summary of the anatomical region, hemisphere, MNI coordinates ( $x, y, z$ ), and maximal  $Z$ -scores of significant activations of the direct contrast Set 3 > baseline for action encoding, maintenance, and recognition

Region	Encoding			$Z$ -scores	Maintenance			$Z$ -scores	Recognition			$Z$ -scores	
	$x$	$y$	$z$		$x$	$y$	$z$		$x$	$y$	$z$		
Frontal cortex													
Dorsal PM	L	-24	-12	60	3.99*	—	—	—	—	-30	-12	57	3.77
	R	18	3	69	4.40*	—	—	—	—	21	-12	54	3.92
Ventral PM	L	-51	12	33	4.57*	-42	6	39	4.19	-48	0	21	4.01
	R	57	12	33	3.79*	—	—	—	—	—	—	—	—
Pre-SMA		0	6	60	4.37*	-6	21	48	4.35	-6	3	57	3.67
VLPFC	L	-33	27	0	4.70*	-39	18	-6	3.83	-33	21	-3	3.89
	R	33	21	3	4.04*	—	—	—	—	33	24	-6	5.35*
Anterior MFG	L	-36	45	12	3.67	-42	48	9	3.82	—	—	—	—
	R	42	36	33	3.83	45	33	30	3.96	—	—	—	—
Parietal cortex													
Postcentral gyrus	SI-Area 1	L	-57	-24	51	4.38*	—	—	—	-57	-18	51	3.51
	SI-Area 2	L	-54	-30	51	4.39*	—	—	—	-57	-27	48	3.70
		R	54	-24	51	4.79*	—	—	—	—	—	—	—
Parietal operculum	SII-OP1/4	L	-63	-21	21	4.46	—	—	—	—	—	—	—
SPL	L	-12	-72	57	5.09*	—	—	—	—	-21	-75	51	4.09
	R	18	-66	60	4.66*	30	-63	60	4.29	27	-72	54	4.87*
aIPS(hIP1)/SPL	L	—	—	—	—	-39	-57	45	3.63*	—	—	—	—
aIPS(hIP2)/SMG	L	-45	-48	57	4.43*	-48	-45	42	3.56*	—	—	—	—
SMG	L	-42	-48	54	4.62*	-45	-57	54	4.33	-45	-42	48	3.89
Caudal IPS	L	-33	-81	33	4.87	-27	-84	27	4.19	—	—	—	—
	R	33	-84	39	4.42*	24	-90	33	3.96	—	—	—	—
Occipitotemporal cortex													
LOC	L	—	—	—	—	—	—	—	—	-45	-57	-6	4.09
	R	48	-57	-15	4.46*	—	—	—	—	—	—	—	—
Subcortical regions													
Thalamus	L	-15	-18	12	3.86*	—	—	—	—	-12	-12	12	3.85
Putamen	L	—	—	—	—	—	—	—	—	-24	9	3	4.21
Cerebellar regions													
Vermis_6		-3	-66	-27	3.52*	—	—	—	—	—	—	—	—

Note: L, left hemisphere; LOC, lateral occipital complex; OP, parietal operculum; PM, premotor cortex; R, right hemisphere; SMG, supramarginal gyrus; SPL, superior parietal lobe; MNI, montreal neurological institute. The asterisk indicates cortical regions that also show significant activation for the parametrical analysis reflecting task difficulty.

secondary somatosensory cortex (SII) located at the border between parietal operculum 1 (OP1) and 4 (OP4) (for an anatomical description see Eickhoff, Schleicher et al. 2006; Eickhoff, Amunts et al. 2006). In posterior parietal cortex, a widely distributed activation cluster was observed that captured anterior and posterior parts of the superior parietal lobe and the caudal descending branch of the IPS (cf., Fig. 3*I*: top row, ENC, right). Encoding of hand movements also activated right occipitotemporal cortex, partly overlapping with the lateral occipital complex (LOC, Malach et al. 1995; Grill-Spector et al. 1999). In addition to these neocortical areas, the left thalamus and the cerebellar vermis were recruited during the encoding period.

The majority of the observed cortical regions, except for anterior MFG, parietal operculum, and left caudal IPS, were also detected by the parametrical analysis reflecting a logarithmic increase in brain activity with increasing task difficulty. Because hand movements were performed during the encoding period, both sensorimotor and cognitive factors are potential contributors to this parametric modulation. An increase in the number of multisegment line patterns causes stronger tactile and kinesthetic input signals but imposes also higher mnemonic demands. To disentangle sensorimotor and mnemonic factors on the brain level, the results of the delay period have to be taken into account because of an exclusion from motor acts during this period.

### Maintenance

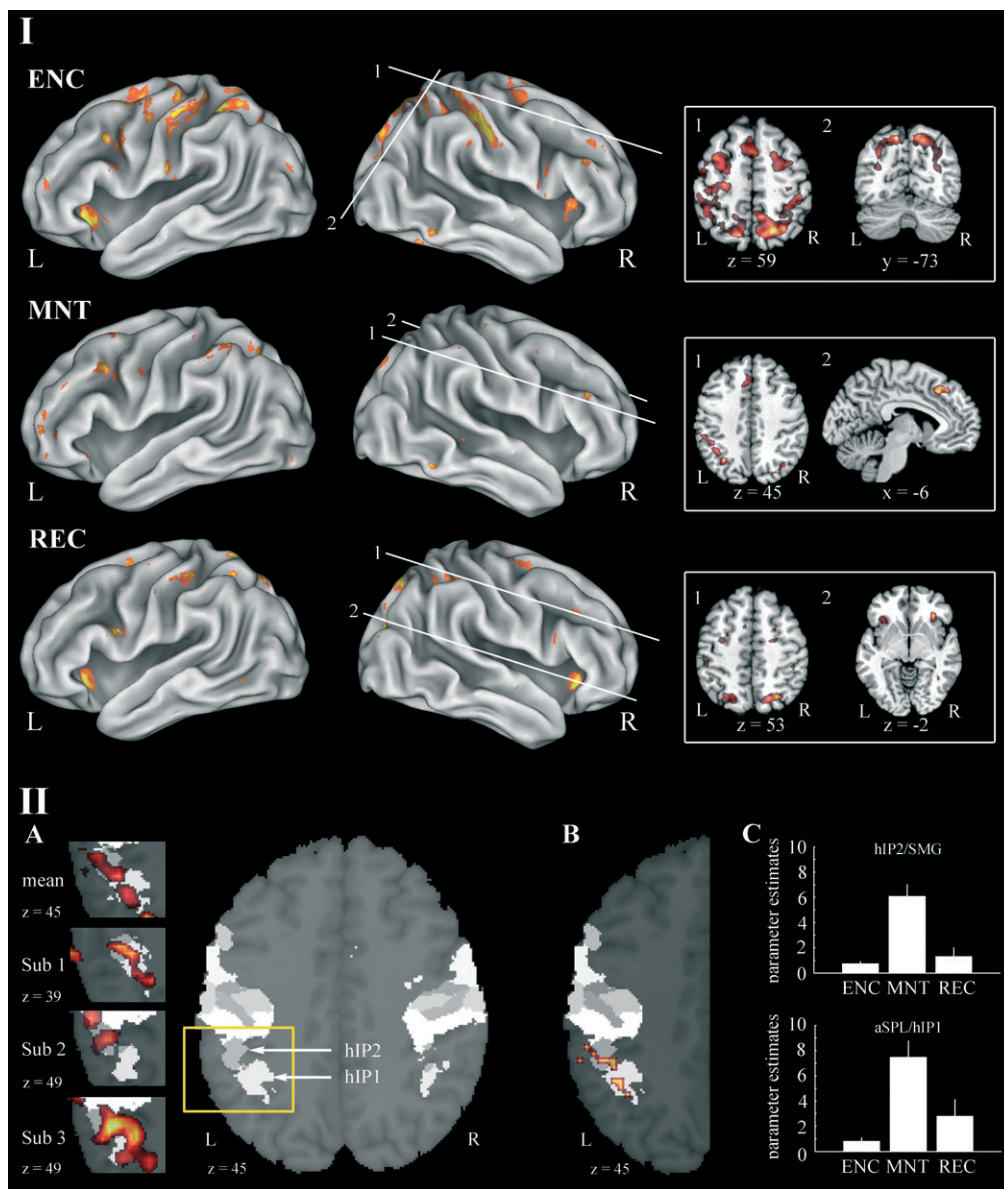
For maintenance of kinesthetic information, the most prominent activation occurred in left aIPS and closely adjacent areas

which showed 2 centers of activation: the first, located at human intraparietal Area 1 (hIP1; Choi et al. 2006) and adjoining aSPL (Stoekel et al. 2004), and the second, located anteriorly at human intraparietal Area 2 (hIP2; Choi et al. 2006) extending ventrally into the dorsorostral part of the supramarginal gyrus (cf., Fig. 3*I*: middle row, MNT, right). Figure 3*IIA* illustrates the anatomy of the intraparietal areas hIP1 and hIP2, the activation of group mean ( $N = 14$ ) within these 2 regions and 3 single-participant data exemplarily. A visual inspection of the single-participant data revealed that 14 participants showed a significant activation in hIP1 and 13 participants in hIP2 (minimum cluster size: 5 voxel;  $P < 0.05$ , uncorrected) leading to a reliable result in the group analysis. In addition, activation was found in left ventral premotor cortex, left VLPFC, bilateral anterior MFG, pre-SMA, right superior parietal lobe and bilateral caudal IPS (Fig. 3*I*: middle row, MNT).

To detect cortical regions modulated by memory load, a parametrical analysis was performed. The results revealed load-dependent activation in left aSPL ( $x/y/z$ , -45/-57/51;  $Z = 3.83$ ) and in left hIP2 ( $x/y/z$ , -48/-45/42;  $Z = 3.87$ ) (Fig. 3*II*B). Although the activation in aSPL extended ventrally into hIP1, hIP2 spread into the supramarginal gyrus. Comparing the parameter estimates across the 3 task periods, both regions elicited the strongest values for the maintenance period compared with the encoding and recognition periods (Fig. 3*II*C).

### Recognition

During the recognition period, activation was found in dorsal and ventral premotor cortex, bilateral VLPFC, pre-SMA, SI, left occipitotemporal cortex, and bilateral superior parietal lobe



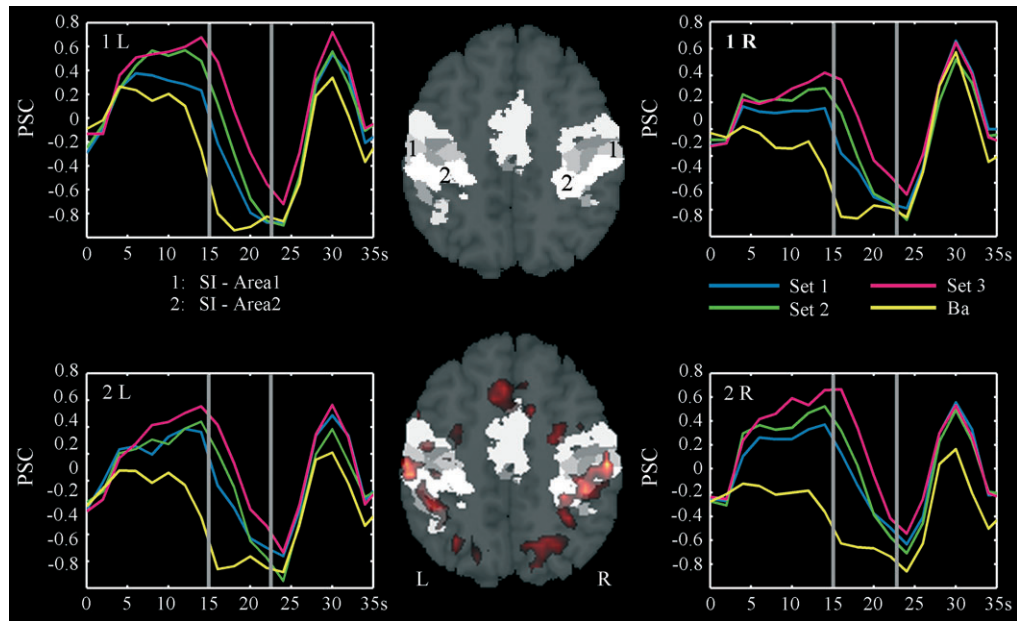
**Figure 3.** (I) BOLD responses in the delayed-recognition task during movement encoding (ENC) maintenance (MNT), and recognition (REC). Group-averaged ( $N = 14$ ) statistic maps of significantly activated areas are depicted for the contrast Set 3 versus baseline. Selected coronal axial and sagittal slices are shown on the right panel. Cluster size was set at 10 contiguous voxels and activation threshold was set at  $P < 0.001$ , uncorrected. Figures were created with the software packages Caret (<http://brainmap.wustl.edu/resources/caretnew.html>) and MRIcro (<http://www.sph.sc.edu/comd/rorden/micro.html>). L, left; R, right. (II) Activation within the aIPS. (A) Maximum probability map (MPM) on axial section at  $z = 45$ . hIP1 and hIP2 of the aIPS are coded by different gray levels. The left panel shows neural activation of the contrast Set 3 versus baseline during the delay period for group-averaged data (mean  $N = 14$ ) and for 3 participants (sub 1, sub 2, and sub 3). BOLD effects are superimposed on a section view zoomed into the region around the aIPS as indicated by the yellow box. (B) Activation within hIP1 and hIP2 as revealed by the parametrical analysis is overlaid on axial section at  $z = 45$  of the MPM. The illustration is restricted to the left hemisphere because no significant activation occurred in the right IPS. (C) Bar plots show parameter estimates of the contrast Set 3 versus baseline for areas aSPL/hIP1 and hIP2/SMG for the encoding (ENC), maintenance (MNT), and recognition (REC) periods.

extending into supramarginal gyrus (Fig. 3*F* bottom row, REC). Subcortical activation was elicited in left thalamus and putamen. The results of the parametrical analysis showed significant activation in right VLPFC ( $x/y/z$ , 33/21/-9;  $Z = 5.08$ ) and right superior parietal lobe ( $x/y/z$ , 30/-72/48;  $Z = 4.18$ ).

## Discussion

In this experiment, we investigated with fMRI the functional significance of the dorsal stream in kinesthetic-motor control and working memory maintenance of action-related kinesthetic information. Participants performed a modified version of

a delayed-recognition task, in which they encoded, shortly maintained, and recognized hand movements without visual guidance. Task difficulty was systematically manipulated by the number of complex hand movement sequences per trial leading to increased response errors and latencies with increasing difficulty. Kinesthetic encoding of hand movements activated SI and SII, posterior parietal cortex (d-d stream and v-d stream), premotor areas, anterior MFG, VLPFC, and right occipitotemporal cortex (ventral stream). The majority of the observed regions responded to task difficulty reflecting an increase in cognitive or sensorimotor demands. Activity in posterior



**Figure 4.** Cortical activity and its trial-averaged time courses in SI. Brain activation of the contrast Set 3 versus baseline during the encoding period is superimposed on the maximum probability map (MPM) for primary somatosensory cortex on axial section at  $z = 51$ . The numbers of the MPM indicate the anatomical locations of Area 1 and Area 2 of the coded by different gray levels. Percent signal change (PSC) of selected voxels within Area 1 and Area 2 of SI are depicted for the 4 task conditions. The first and second vertical gray lines mark the end of the encoding period and the beginning of the recognition period respectively. L, left; R, right. Figures were created with the software packages Anatomy toolbox (Eickhoff et al. 2005; [http://www.fz-juelich.de/ime/spm\\_anatomy\\_toolbox](http://www.fz-juelich.de/ime/spm_anatomy_toolbox)) and MRlcro (<http://www.sph.sc.edu/cmd/rorden/micro.html>).

parietal cortex, premotor regions, and anterior MFG largely overlapped between encoding and maintenance of kinesthetic information. However, only activity in left aIPS and adjacent aSPL (v-d stream) was affected by memory load during the delay period. Movement recognition elicited a similar activation cluster as observed during encoding, but in this period, only the right superior parietal lobe and the right VLPFC were sensitive to task difficulty.

The present findings suggest that the action representation system of the dorsal stream is recruited for kinesthetic action control, indicating close somatosensory-motor coupling within these areas. This function, however, seems to be under influence of the ventral stream. In accordance with the proposed account by Rizzolatti and Matelli (2003), the networks within the v-d stream seem to play a crucial role in working memory maintenance of action-related kinesthetic information. Our results nicely complement and extend a recent model by Dijkerman and de Haan (forthcoming) in which distinct processing streams subserving action and perception in the tactile system are proposed (see also Fiehler et al. forthcoming). In the following, we will first review the functional properties of the areas involved in kinesthetic guidance of hand actions and will then discuss the role of the v-d stream in action-related mnemonic processes based on kinesthetic information.

#### ***Kinesthetic-Motor Control System within the Dorsal Stream***

A broad range of evidence, including neurophysiological and anatomical studies in monkeys and neuropsychological and neuroimaging studies in humans, suggests that the dorsal stream plays a key role in visually guided online action control (e.g., Goodale and Milner 1992). Here, we show that the action representation systems of the dorsal stream are also utilized for kinesthetically guided actions. Thus, the present results to-

gether with previous findings on tactile object exploration (e.g., Binkofski et al. 1999; Jäncke et al. 2001) point to a common neural substrate for visual and haptic action control.

In the present task, complex hand actions were substantially guided by kinesthetic input signals from the hand and fingers. Tactile feedback from the fingertips holding the stylus, however, could also be used, but to a low degree. In line with previous imaging studies on tactile object exploration (Amedi et al. 2001; Jäncke et al. 2001; James et al. 2002; Stoeckel et al. 2003, 2004), we observed a clear activation cluster in SI for kinesthetically guided hand movements. We found activation in Area 1 and Area 2 extending into adjacent Area 3b, whereas activity was most pronounced in Area 2. This finding agrees with previous observations showing that Area 2 processes primarily kinesthetic information (Burton 2002). Although neurons in Area 3b and 1 respond to a variety of different mechanical stimuli, neurons in Area 2 are activated by more complex cutaneous stimuli (e.g., object shape and curvature) or by active tactile tasks, suggesting an involvement of Area 2 in higher order somatosensory processing (Bodegard et al. 2001, 2003; Ruben et al. 2006).

Area 2 activation occurred bilaterally with larger clusters in the right hemisphere, whereas Area 1 was activated only in the left hemisphere, contralateral to the moving hand. This is in accord with anatomical findings in monkeys demonstrating that transcallosal connections of Area 3a, 3b, and 1 are sparse for the hand region but more abundant in Area 2 (Killackey et al. 1983). Recent brain-imaging studies in humans also observed bilateral activation in Area 2 during kinesthetic discrimination (Bodegard et al. 2003) and kinesthetic illusions (Naito et al. 2005) with a right hemispheric dominance irrespective of the hand used. These results suggest an important engagement of right Area 2 in limb movement control and the representation of kinesthetic information about limb positioning.

Interestingly, in the present study, task difficulty modulated SI activity, that is, activity increased with a rising number of complex hand movement sequences. Consistent findings were observed in an electrophysiological study in which participants performed sequential finger movements of different complexity and sequence length (Hummel et al. 2003). The results showed a complexity-dependent modulation of sensorimotor activity, mainly ipsilateral, but no effect of sequence length (motor memory load). The authors concluded that increasing sensorimotor activation reflects increasing processing load due to more difficult movement transitions independent from motor memory load. Following this view, the observed parametrical modulation of SI activity can be attributed to an increase in sensorimotor processing demands rather than an increase in motor memory load. As sequential complexity of movements is known to positively correlate with premotor activity (cf., Harrington et al. 2000), we also found a parametrical modulation in the lateral premotor cortex and in the pre-SMA.

Results from primate research demonstrate an elaborative processing of kinesthetic information by the superior parietal lobe. Monkey area PE, the area forming most of the superior parietal lobe convexity, has been shown to be active during passive joint rotation, deep tissue pressure, and active arm movements (Sakata et al. 1973; Mountcastle et al. 1975; Lacquaniti et al. 1995). Neurons in superior parietal lobe differ from those in SI by several response characteristics. Only neurons in superior parietal lobe responded to multiple joint interactions and integrated both tactile and joint information (Sakata et al. 1973), suggesting that this region is involved in higher order processing of somatosensory input. However, there are dense corticocortical connections (Jones and Powell 1969; Pandya and Kuypers 1969) and similar receptor distributions (Scheperjans et al. 2005) in SI and superior parietal lobe providing intense mutual interaction. In accordance with the monkey data, the human superior parietal lobe has been observed to be active during hand and finger movements that require kinesthetic control processes (e.g., Seitz et al. 1991; Gerardin et al. 2000). Moreover, lesions in the posterior parietal cortex were shown to produce tactile apraxia, a severe impairment of exploratory hand movements in the absence of elementary sensory or motor deficits, associated with tactile agnosia (Binkofski et al. 2001).

Our data are in line with previous findings by demonstrating a substantial engagement of the superior parietal lobe during hand and finger movements guided by kinesthetic signals. This result indicates a role of the d-d stream in kinesthetic-motor coupling, a result previously shown for the visual (e.g., Goodale and Milner 1992) and tactile (e.g., Binkofski et al. 1999) domain. The observed bilateral activation is consistent with the response characteristics of monkey superior parietal lobe neurons that fire in the contra- and ipsilateral receptive fields (Sakata et al. 1973). We further found that activity in superior parietal lobe significantly increased with task difficulty, indicating that this area is sensitive to higher computational demands.

Activity in the superior parietal lobe extended into the aIPS and adjacent supramarginal gyrus. Primate studies showed that most of the neurons located in the aIPS, basically area PEip, respond to somatosensory stimuli and become active in association with arm movements, probably representing the hand orientation or shape of the handgrip (Rizzolatti et al. 1998; Murata et al. 2000). A recent study by Naito and Ehrsson (2006) revealed supportive results in humans. Kinesthetic hand-object

illusions elicited by vibrating the tendon of a limb activated aIPS (i.e., hIP1 and hIP2), ventrally adjacent supramarginal gyrus, and parietal operculum in the left hemisphere. The authors proposed that the left inferior parietal lobe is involved in sensorimotor transformations, that is, a direct transmission of kinesthetic and tactile information from the hand into motor commands. In particular, the aIPS has been discussed as a flexible dynamic area capable of goal-dependent updating of actions in order to establish an internal action representation (cf., Desmurget and Grafton 2000). This updating process is based on iterative comparisons during an ongoing movement between an efference copy of the motor command and incoming sensory information, either for detecting or correcting errors between the current action plan and the current sensorimotor state (Tunik et al. 2005; Rice et al. 2006). The involvement of aIPS in dynamic action control is supported by the recent proposal that human aIPS is an evolutionary newer area than its putative monkey homologue area AIP. Consequentially, aIPS is assumed to function on a complex integrative level providing very sophisticated control of action (Orban et al. 2006).

The observed activity in the left aIPS and contiguous supramarginal gyrus during execution of hand movements on the basis of kinesthetic and tactile information is compatible with the role of the v-d stream in action organization (Rizzolatti and Matelli 2003). Given the conglomeration of both visual and somatosensory neurons within aIPS (Sakata et al. 1995), we assume that the proposed function of aIPS in dynamic, goal-dependent online control of actions is not only restricted to the visual domain (Tunik et al. 2005) but can also be assumed for the somatosensory domain.

In contrast to previous results on exploratory movements (Binkofski et al. 1999; Jäncke et al. 2001), we observed activation in the right occipitotemporal cortex, that is, in an area located within the ventral stream and known to be involved in multimodal object perception and recognition (Malach et al. 1995; Grill-Spector et al. 1999; Amedi et al. 2001). Tracer injection studies in monkeys found reciprocal connections of area AIP with the inferiotemporal cortex, suggesting an interaction between the dorsal and the ventral stream (Andersen et al. 1990; Lewis and van Essen 2000). This idea is also substantiated by a clinical study showing that a patient with bilateral lesions in posterior parietal cortex was severely impaired in grasping new objects but could significantly improve her performance when grasping familiar objects (Jeannerod et al. 1994; see also, Himmelbach and Karnath 2005). This indicates that information about object identity provided by the intact ventral stream is conveyed to the aIPS for action control. Thus, the aIPS might represent a convergence zone that integrates information from both the ventral and the dorsal stream.

To conclude, the results of the present study provide strong support for the idea that networks of the dorsal stream, including the d-d and v-d streams, are utilized for online action control on the basis of kinesthetic information. Based on results from previous studies reviewed above (e.g., Bodegard et al. 2001), one might assume a hierarchical mode of haptic information processing for action control as follows. Kinesthetic (and to a low-degree tactile) input signals from the hand and the fingers are processed in SI, especially in Area 2, and are then conveyed to the posterior parietal cortex. The posterior parietal cortex, in particular the left aIPS, converts kinesthetic input



signals into motor commands and rapidly adjusts the ongoing movements. Due to strong cortical connections of aIPS with ventral premotor cortex, the information is further transferred to the ventral premotor cortex important for the performance of precise hand movements (for evidence in monkeys see, e.g., Luppino et al. 1999; for recent evidence in humans see, Rushworth et al. 2006). This transmission process, however, seems to be (at least in part) under the influence of ventral stream networks (cf., Goodale and Westwood 2004).

### ***Kinesthetic Working Memory within the Ventrodorsal Stream***

Maintenance of kinesthetic information activated posterior parietal regions, left ventral premotor cortex, and anterior MFG. This is in agreement with earlier studies on tactile working memory (cf., Stoeckel et al. 2003, 2004; Kaas et al. 2006). An additional activation occurred in the pre-SMA that was located rostrally ( $y = 21$ ) to the activation foci elicited during the encoding ( $y = 6$ ) and recognition ( $y = 3$ ) periods. The functional role of the pre-SMA has been discussed in the framework of higher order aspects of motor control, that is, updating of motor plans (Shima et al. 1996), control of complex movements sequences (Picard and Strick 1996), and processing of sequential information independent of further motor intentions (Schubotz and von Cramon 2002). Comparing the coordinates of the different studies, one might consider a rostral-caudal anatomical gradient within the pre-SMA, whereas the rostral part of the pre-SMA is more involved in controlling complex sequential processes irrespective of a motor component and the caudal part of the pre-SMA is more engaged in abstract motor functions. Consistent with this idea, Gerardin et al. (2000) found a stronger activation in the rostral pre-SMA ( $y = 18$ ) when contrasting imagined sequential hand movements with executed ones and a larger activation on the border of caudal pre-SMA and SMA proper ( $y = 0$ ) for executed compared with imagined movements. Similar functional rostral-caudal distinctions were proposed for the medial (pre-SMA vs. SMA proper, Picard and Strick 1996) and the dorsolateral (dorsolateral pre-premotor cortex vs. dorsolateral premotor cortex; Picard and Strick 2001) premotor cortex.

Although several cortical areas were active during short-term maintenance of kinesthetic information, only 2 left posterior parietal activation cluster, aIPS and adjacent aSPL, responded systematically to memory load, that is, an increase of activity with increasing mnemonic demands. According to the cytoarchitecturally defined parcellation of aIPS in the areas hIP1 and hIP2 (Choi et al. 2006), the first activation cluster belongs to area hIP2 extending into the supramarginal gyrus, whereas the second activation cluster partially covers area hIP1 with the center of activation in aSPL (Stoeckel et al. 2004). The present data strongly suggest that aIPS and adjacent posterior parietal areas play a key role in human working memory of action-related kinesthetic information necessary for prospective motor acts. Given that the observed cortical regions are nodal points of the v-d stream, our findings reveal further evidence for its role on action recognition (cf., Rizzolatti and Matelli 2003).

The present results on kinesthetic working memory are in accordance with lately published fMRI studies on tactile working memory (Stoeckel et al. 2003, 2004; Kaas et al. 2006; Preuschhof et al. 2006). Stoeckel et al. (2003) reported delay-related activity in the left aIPS for tactile object discrimination.

In a later study using a similar paradigm, an area located more dorsocaudally, termed aSPL, was observed which partly overlapped with the aIPS (Stoeckel et al. 2004). The authors suggest that aSPL activity is related to the maintenance of shape information triggered by kinesthetic signals. Activity in areas of the v-d stream was also reported by Kaas et al. (2006) applying a tactile orientation-matching task. However, activation of the inferior parietal lobe predominantly occurred during an early delay period ranging from 2 to 4 s, whereas prefrontal and parieto-occipital activity dominated during later delay periods (4–8 s). These findings are supported by recent results on vibrotactile working memory showing inferior parietal activation during a short (0.1 s) and a longer (4.1 s) delay interval (Preuschhof et al. 2006).

As pointed out above, aIPS seem to play a crucial role in the transformation of somatosensory information into motor commands (Naito and Ehrsson 2006). In particular, the aIPS is supposed to perform dynamic, goal-dependent, sensorimotor transformations in order to establish an internal representation of the action (Tunik et al. 2005; Rice et al. 2006). This process requires the integration of a variety of action-related information provided by sensory input signals, e.g., shape, size, orientation, or location (Orban et al. 2006). The task used here does require a precise encoding of different movement parameters mainly derived from kinesthetic input signals in egocentric coordinates, that is, in a frame of reference centered on the agent's body (e.g., hand and finger orientation, start direction, changes in movement course, length of the movement segments, and end position). It seems possible that the overall shape of the movement path was extracted additionally (cf., Bodegard et al. 2001). On the basis of the incoming kinesthetic information, the aIPS establishes an internal representation of the action, which must be maintained precisely over the delay period in order to enable successful recognition. The load-dependent modulation of activity in aIPS and closely adjoining areas observed during the delay period suggests their decisive role in working memory maintenance of kinesthetic information necessary for prospective motor acts. This function, however, seems to be implemented in the left hemisphere. Based on previous findings in nonhuman primates (Murata et al. 1996), one can speculate that the aIPS shows similar mnemonic functions in both humans and monkeys.

Action recognition activated similar brain regions as encoding comprising frontal and parietal areas. However, only the right superior parietal lobe and right VLPFC were sensitive to task difficulty. Because exactly one stimulus was presented for recognition, the parametric modulation of brain activity should rather reflect load-dependent cognitive demands than sensorimotor complexity. Our findings agree with other recent imaging studies indicating a contribution of posterior parietal regions to recognition processes (for a review see, Wagner et al. 2005). The present findings, however, extend previous results by showing that posterior parietal regions also contribute to the recognition of action information on the basis of kinesthetic input only. A study by Bledowski et al. (2006) also reported activation in posterior parietal cortex and VLPFC during the recognition phase in a visual delayed-matching task. The authors interpreted their results in the framework of the output buffer hypothesis (cf., Wagner et al. 2005). They proposed that the posterior parietal cortex operates continuously on the storage buffer necessary for stimulus evaluation and memory search, whereas the VLPFC is involved in controlled memory

search that takes place only when a stimulus evaluation in posterior parietal areas is not sufficient.

In sum, we show that the action representation systems of the d-d and v-d streams are utilized not only for visual but also for kinesthetic action control. Moreover, networks within the v-d stream, in particular the left aIPS and closely adjacent areas, are also engaged in working memory maintenance of kinesthetic information. These results are in accordance with the proposed functions of the dorsal stream (cf., Goodale and Milner 1992; Rizzolatti and Matelli 2003) and extend these to the somatosensory domain.

## Notes

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