

# Passive somatosensory discrimination tasks in healthy volunteers: Differential networks involved in familiar versus unfamiliar shape and length discrimination

Ann Van de Winckel,<sup>a,\*</sup> Stefan Sunaert,<sup>b</sup> Nicole Wenderoth,<sup>c</sup> Ron Peeters,<sup>b</sup>  
Paul Van Hecke,<sup>b</sup> Hilde Feys,<sup>a</sup> Els Horemans,<sup>a</sup> Guy Marchal,<sup>b</sup>  
Stephan P. Swinnen,<sup>c</sup> Carlo Perfetti,<sup>d</sup> and Willy De Weerd<sup>d</sup>

<sup>a</sup>Department of Rehabilitation Sciences, Faculty of Kinesiology and Rehabilitation Sciences, Katholieke Universiteit Leuven, Tervuursevest 101, B-3001 Heverlee (Leuven), Belgium

<sup>b</sup>Department of Radiology, Faculty of Medicine, University Hospitals, K.U. Leuven, Belgium

<sup>c</sup>Department of Kinesiology, Faculty of Kinesiology and Rehabilitation Sciences, K.U. Leuven, Belgium

<sup>d</sup>Centro studi di Villa Miari, Riabilitazione Neurocognitiva, Santorso, Italy

Received 16 July 2004; revised 28 January 2005; accepted 28 January 2005  
Available online 24 March 2005

Somatosensory discrimination of unseen objects relies on processing of proprioceptive and tactile information to detect spatial features, such as shape or length, as acquired by exploratory finger movements. This ability can be impaired after stroke, because of somatosensory-motor deficits. Passive somatosensory discrimination tasks are therefore used in therapy to improve motor function. Whereas the neural correlates of active discrimination have been addressed repeatedly, little is known about the neural networks activated during passive discrimination of somatosensory information. In the present study, we applied functional magnetic resonance imaging (fMRI) while the right index finger of ten healthy subjects was passively moved along various shapes and lengths by an fMRI compatible robot.

Comparing discriminating versus non-discriminating passive movements, we identified a bilateral parieto-frontal network, including the precuneus, superior parietal gyrus, rostral intraparietal sulcus, and supramarginal gyrus as well as the supplementary motor area (SMA), dorsal premotor (PMd), and ventral premotor (PMv) areas. Additionally, we compared the discrimination of different spatial features, i.e., discrimination of length versus familiar (rectangles or triangles) and unfamiliar geometric shapes (arbitrary quadrilaterals). Length discrimination activated mainly medially located superior parietal and PMd circuits whereas discrimination of familiar geometric shapes activated more laterally located inferior parietal and PMv regions. These differential parieto-frontal circuits provide new insights into the neural basis of extracting spatial features from somatosensory input

and suggest that different passive discrimination tasks could be used for lesion-specific training following stroke.

© 2005 Elsevier Inc. All rights reserved.

**Keywords:** fMRI; Somatosensory discrimination; Tactile; Parietal cortex; Precuneus

---

## Introduction

Deriving tactile-kinesthetic information from exploratory finger movements forms the basis of discrimination of unseen objects. Recent functional imaging studies have shown that the discrimination of macrogeometric object features, such as shape or length by active exploration, predominantly engages frontoparietal circuits including ventral and dorsal premotor cortex, secondary somatosensory area (SII), superior parietal lobe, anterior part of the intraparietal sulcus (AIP), and supramarginal gyrus (Binkofski et al., 1999; Bodegård et al., 2000, 2001; Hadjikhani and Roland, 1998; Kawashima et al., 1994; O'Sullivan et al., 1994; Roland et al., 1998; Servos et al., 2001; Stoeckel et al., 2003, 2004; Stoesz et al., 2003). Moreover, Bodegård et al. (2001) proposed a hierarchy in these frontoparietal areas related to discrimination tests: areas 3b and 1 are engaged in all types of microgeometric and macrogeometric stimulation, area 2 is preferentially activated for curvature changes, whereas AIP and supramarginal gyrus are more involved in shape and full object discrimination than discrimination of curvature or edges alone. The same frontoparietal areas, however, are also activated during object exploration and manipulation, not involving object discrimination (Binkofski

---

\* Corresponding author. Fax: +32 16 32 91 92.

E-mail address: Ann.VandeWinckel@faber.kuleuven.be  
(A. Van de Winckel).

Available online on ScienceDirect ([www.sciencedirect.com](http://www.sciencedirect.com)).

et al., 1999; Gitelman et al., 1996; Jäncke et al., 2001) as well as in passive arm movements without discrimination (Nelles et al., 1999).

Accordingly, it is a matter of debate whether the observed activation mainly reflects the processing of somatosensory information to perceive macrogeometry of objects, or the control of motor actions, necessary to explore the object. To our knowledge, only one study used passive touch discrimination tasks, in which the experimenter moved the object across the distal phalanx of the right index finger such that no motor actions of the subject were required (Bodegård et al., 2001). Passive touch discrimination activated parieto-frontal networks similar to those observed during active touch discrimination. The right anterior part of the cerebellum additionally responded significantly to active compared to passive discrimination. Whereas Bodegård et al. (2001) stimulated cutaneous receptors related to touch, little is known about the discrimination of proprioceptive information arising from passively moving a finger. Such passive, somatosensory discrimination tasks are used during the rehabilitation of stroke patients, suffering from hemiplegia (Perfetti, 1997; Perfetti, 2001). Since active movements are hampered in these patients, passive somatosensory discrimination exercises can be applied to stimulate the sensorimotor system, and thus to improve motor outcome (Perfetti, 1997, 2001). The neural networks which are activated by these passive discrimination tasks are still unknown.

In the present study, we explored which brain areas are concerned with the processing of proprioceptive information in a purely somatosensory context. We specifically designed a functional magnetic resonance imaging (fMRI) experiment, in which subjects were required to discriminate passive movements of different shapes and length, as imposed by an MRI compatible robot. More specifically, in all conditions, subjects were simultaneously exposed to passive movements of the finger as well as to music fragments. Before each trial, they were instructed to discriminate either the passive finger movements (experimental condition) or the music fragments (control condition). A sufficiently high difficulty level was chosen for both discrimination tasks, such that subjects had to attend maximally to either one of both modalities. This procedure prevented subjects from covertly discriminating somatosensory information during the control condition. With this unique setup, we examined, first, which brain areas were involved in the passive discrimination of spatial features and, second, whether the passive discrimination of shape versus length activated distinct neural networks.

## Materials and methods

### Subjects

Ten healthy volunteers (6 men, 4 women) with a mean age of 56.8 years (range 44–77 years) gave their written informed consent to participate in this study. No subject exhibited overt neurological or musculoskeletal deficits. All subjects except one were right-handed as tested by the Edinburgh Handedness Inventory (Oldfield, 1971) and all had a normal cognitive performance (8 persons scored 30/30, 2 persons scored 29/30) as indicated by the “Mini-Mental State Examination” (Folstein et al., 1975). The study was approved by the ethical committee of the Faculty of Medicine of K.U. Leuven.

### Experimental setup

During the fMRI scanning session, the distal interphalangeal joint of the right index finger was fixed with sensitive tape and Velcro to a plastic platelet of an fMRI compatible robot (developed by “Optidrive”, Leuven, Belgium) (Fig. 1). The robot consisted of two stepping motor modules that moved the platelet along the horizontal and vertical axis in the transversal plane within a maximum range of motion of 8 cm. The onset of these passive movements was pseudo-randomized such that the finger movement could start at any Cartesian coordinate within this 8-cm square. The plastic platelet could also move backward and forward over 3 cm, and rotate over 180° within the transversal plane (Fig. 1) to enhance comfort when the finger was guided along shapes in the air. The finger was moved in such a way that participants could feel the outline of different shapes in the air, as well as over a variable distance along a horizontal wooden bar. All movements were primarily felt in the metacarpophalangeal joint of the right index finger and, for larger movements, also in the wrist. During the experiment, the participants adopted a supine position with the right arm and the legs supported by cushions to enhance comfort. They held a response button in their left hand, and wore headphones. Head movements were restricted by a bite bar and eyes were closed.

### Discrimination task

Discrimination was performed with eyes closed and required participants to decide whether the passive movement or music fragments were the same or not. In all discrimination conditions, passive movements were provided together with music fragments. Subjects were instructed before each trial whether they had to discriminate either the passive movements or the music fragments. For the discrimination of passive movements, three different tasks were used (Fig. 2): (1) the robot generated movements with the finger across a variable horizontal distance [LENGTH(mus)]. In this condition only, the right index finger touched the horizontal cross bar and length was the only discriminative feature; (2) the

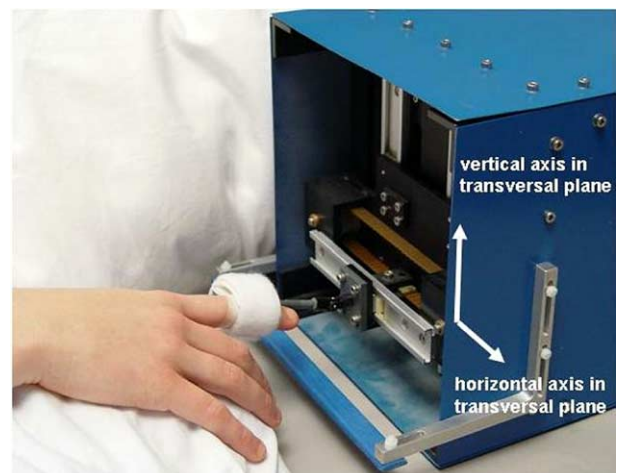


Fig. 1. fMRI compatible robot which moves the right index finger to produce various familiar shapes [F-SHAPE(mus)] and unfamiliar shapes [UF-SHAPE(mus)] in the air for the shape discrimination tasks, and across the wooden crossbar for length discrimination [LENGTH(mus)]. The robot allows movements in the transversal plane.

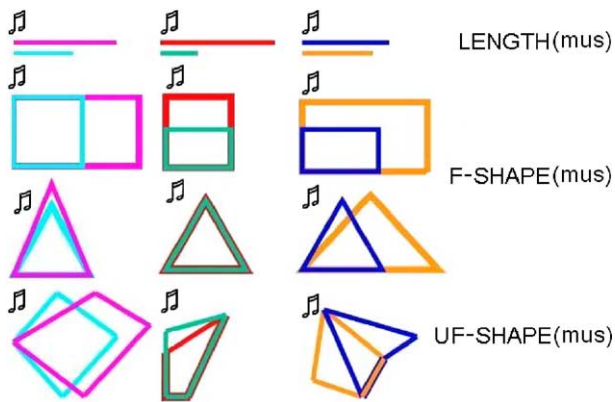


Fig. 2. Somatosensory discrimination tasks used in the experiment: LENGTH(mus): attention to line discrimination. F-SHAPE(mus): attention to discrimination of familiar geometrical shapes. UF-SHAPE(mus): attention to discrimination of unfamiliar geometrical shapes. Simultaneously, music stimulation was offered.

robot generated familiar geometric shapes in the air [F-SHAPE(-mus)] such as triangles, squares, and rectangles. These could differ with respect to height or width or to angle in triangles; (3) the robot generated unfamiliar geometric shapes in the air [UF-SHAPE(mus)] such as quadrilateral shapes with unparallelled and unequal sides. The shapes could differ with respect to height, width, angles, and could have one or two different sides, or totally different shapes. The minimal difference for lengths, widths, or heights in the three conditions was 2 cm. The shapes and lines had to be exactly the same in length, orientation, form, and size, to be defined as equal.

During each of the 3 somatosensory discrimination conditions, a matched music discrimination condition was presented (control), i.e., subjects had to discriminate the music fragments, while the finger was passively moved (4) over a variable horizontal distance [(length)MUS], (5) along a familiar geometric shape [(f-shape)MUS], or (6) an unfamiliar geometric shape [(uf-shape)MUS].

Music fragments were considered different if the melody changed, even for a few notes, an instrument was added or omitted, the same tune started with another note, or the rhythm was changed. The music fragments contained no human voice, to exclude interference with activated language areas. The fragments were selected and cut using the software “Cool Edit” (Adobe Systems Incorporated, USA). Performance of both music and somatosensory discrimination tasks were assessed beforehand to define task difficulty. In agreement with other studies (O’Sullivan et al., 1994; Roland and Mortensen, 1987; Seitz et al., 1991; Stoeckel et al., 2003), a score of at least 75% correct was reached on the answers for all tasks. This percentage was considered to motivate the participants and to preserve attentional focus onto the task. Participants did not receive feedback on their performance at any time. The pilot studies confirmed also that the percentage correct answers on both passive movement discrimination and music discrimination remained stable, regardless of the number of training sessions performed.

Note that, although both stimuli were offered at the same time, subjects were instructed prior to each condition whether they had to discriminate either the passive movements or the music fragments and also which type of movement task would be presented, i.e., familiar geometric shape, unfamiliar geometric shape, or length discrimination. At all times, participants were

asked to focus on only one stimulus and discard the other stimulus. Due to the complexity of the requested discrimination task, none of the participants experienced either problems discarding the other stimulus or confusion associated with choosing between the two stimuli. In many cases, participants reported that they were not aware of the other stimulus while concentrating on performing the requested discrimination task. Thus, the participants did not need to shift attention during the trials. Accordingly, the present task did not comply with the typical definition of a ‘dual-task’ design, as commonly used in the behavioral literature (Cockburn et al., 2003; Haggard et al., 2000), whereby participants have to process two tasks at the same time.

Each discrimination trial started with the instruction “triangle”, “square”, “tactile”, “music”, or “rest”. In all but the rest condition, the first of a pair of somatosensory and music stimuli was presented after command “one”. This lasted 30–45 s, then the subjects heard “two” and the second movement/music fragment was offered. Immediately following the second stimulus, subjects had 1 s to decide whether the stimuli were equal or different with respect to a specific feature. Participants answered according to a two alternative forced-choice paradigm (Seitz et al., 1991; Stoeckel et al., 2003). The participants squeezed the response button once when the movements or music fragments were the same, did nothing when the two stimuli were different and squeezed twice when they wanted to correct their answer.

The stimuli were presented in a three by two design where the participants were asked to discriminate, i.e., three times two passive somatosensory stimuli (experimental condition), then three times a discrimination of two music fragments (control condition) and so on.

Prior to the fMRI scanning session, three training sessions were held to familiarize the volunteers with the test procedure. During these training sessions, nine different exercise trials in total were offered, comparable to the runs in the scanner. The setup during the training sessions was similar to the scan session.

#### Scanning procedure and scanning conditions

fMRI was performed on a 1.5-T Philips Intera scanner equipped with an 8 channel phased array head coil (MRI Devices Corporation, WI, USA). High-resolution anatomical images of each subject were acquired using a T1-weighted gradient echo pulse sequence (3D-TFE, magnetization prepared with a 180° IR pulse), consisting of 190 axial slices (0.86 × 0.86 mm in-plane resolution, 1 mm slice thickness).

Functional images were acquired using a gradient-echo EPI-scanning sequence (TR = 2.350 s; TE = 50 ms; flip angle = 90°). Volumes consisted of 32 axial slices covering the whole brain. Slices were oriented parallel to the AC–PC line (in-plane resolution of 3 × 3 mm, 4.85 mm slice thickness). Each run lasted for 9 min and 20 s during which 238 dynamic scans were acquired. These functional scans were preceded by four dummy scans, which were not used in the analysis. Both response button registration and robot performance were synchronized to the scan sequence.

Seven conditions were presented. The first three conditions involved the three somatosensory discriminations, named F-SHAPE(mus), UF-SHAPE(mus), and LENGTH(mus), during which no attention was given to the music fragments (experimental conditions). The three music discrimination tasks, during which no attention was given to somatosensory stimulation, are

referred to as (f-shape)MUS, (uf-shape)MUS, and (length)MUS (control conditions). The abbreviations indicate the condition which has to be discriminated in capital letters and the stimulus which was not attended to between brackets. REST was the seventh condition, where neither movement, nor music was presented. UF-SHAPE(mus) and (uf-shape)MUS represented a pair of the same movements and the same melody, but the order of appearance was altered. This was also the case for F-SHAPE(mus), (f-shape)MUS, and for LENGTH(mus) versus (length)MUS. All seven conditions were presented twice, i.e., six pairs of movement-music stimuli, along with a rest condition twice. In this way, tasks were perfectly matched and could be subtracted from each other with confidence. In all conditions, the difficult and easy tasks were both present in a random order and the exercises were different in each run. The conditions F-SHAPE(mus), (f-shape)MUS, UF-SHAPE(mus), and (uf-shape)MUS lasted approximately 45 s and LENGTH(mus), (length)MUS, and REST lasted approximately 30 s. Eight subjects performed five and two subjects performed six runs.

#### *Data processing and analysis*

Data were analyzed using MATLAB (Mathworks, Natick, MA) and SPM99 software (Wellcome Department of Cognitive Neurology, London, UK, <http://www.fil.ion.ucl.ac.uk/spm>). Images were realigned, co-registered to the anatomical T1 weighted image, and normalized to a standard reference frame (Talairach and Tournoux, 1988), using a representative brain template (MNI, Montreal Neurological Institute). During normalization, images were re-sampled to a voxel size of  $2 \times 2 \times 2$  mm and spatially smoothed with a 6-mm full-width-at-half-maximum (FWHM) Gaussian kernel.

A general linear model was used in which for each condition a boxcar function was convolved with the standard SPM99 hemodynamic response function. The subjects' movement parameters, obtained during the image realignment step, were inserted as covariates of no interest to reduce movement-related artifacts. For the statistical analysis, the time series were high-pass filtered with a filter width of 560 s to remove slow signal drift and low-pass filtered with a Gaussian kernel of 3 s to remove high-frequency noise.

More precise anatomical localizations of the primary somatosensory cortex (SI) and AIP were obtained through cytoarchitectonic probabilistic maps of these areas. The activations found in this study were compared to the probability maps within the MNI-space (<http://www.bic.mni.mcgill.ca/cytoarchitectonics/>, Geyer et al., 1996, 1999, 2000a,b; Grefkes et al., 2001).

The present study aimed to identify brain areas involved in the discrimination of spatial features, as extracted from somatosensory information during passive movements. For this purpose, we compared discrimination of somatosensory stimuli to “distractor” music discrimination as control condition. We added this music discrimination to make sure that participants would not discriminate the simultaneously added passive movements during the control condition. We hypothesized that music discrimination would not activate any areas, which are specifically related to somatosensory discrimination, but only those areas related to general discrimination processes. Using this procedure, only those brain areas specific to somatosensory discrimination were presumably detected, whereas activation related to passive movements per se or to general discrimination processes were excluded. Contrasts of interest were calculated for each subject and run individually. For

the group statistics, these contrasts were entered into a second-level mixed effects analysis. This consisted of several comparisons. First, brain areas which were more strongly activated for somatosensory discriminations than for music discriminations were identified by comparing the activations of all three somatosensory discriminations [F-SHAPE(mus) + UF-SHAPE(mus) + LENGTH(mus)] versus all three music discriminations [(f-shape)MUS + (uf-shape)MUS + (length)MUS]. The results were thresholded at  $P < 0.05$ , corrected for multiple comparisons, and were reported for clusters larger than 10 voxels. Second, we identified brain areas concerned with the discrimination processes, related to a specific discrimination type. Therefore, each somatosensory discrimination condition was compared to its respective partner in music discrimination, i.e., F-SHAPE(mus) versus (f-shape)MUS, etc. Results were also thresholded at  $P < 0.05$ , corrected for multiple comparisons, and were reported for clusters larger than 10 voxels. Third, our interest was directed to detecting differences in brain activation between the three somatosensory discrimination tasks. Therefore, we calculated three interactions (i.e., [(UF-SHAPE(mus) – (uf-shape)MUS) versus (F-SHAPE(mus) – (f-shape)MUS)], etc.).

Subsequently, we performed a region of interest (ROI, sphere with 8 mm radius) analysis, for areas that have previously been identified in active discrimination tasks (Binkofski et al., 1999; Bodegård et al., 2000, 2001; Hadjikhani and Roland, 1998; Kawashima et al., 1994; O'Sullivan et al., 1994; Roland et al., 1998; Servos et al., 2001; Stoekel et al., 2003, 2004; Stoesz et al., 2003) and were significantly activated in our main contrasts as derived in step 2. The interaction was considered to be significant when  $P < 0.05$  was reached, after correction for multiple comparisons.

## **Results**

### *Discrimination performance*

In both training and scanning sessions, all participants obtained at least the required 75% correct answers for all tasks. In the training sessions, the ten subjects reached a mean score of, respectively, 86% for F-SHAPE(mus); 88% for (f-shape)MUS; 78% for UF-SHAPE(mus); 89% for (uf-shape)MUS; 80% for LENGTH(mus); and 91% for (length)MUS. In the scanning sessions, the performance rate could not be recorded for four participants because of technical problems. However, the mean performances of the remaining six participants were comparable to those of the training sessions: 84% for F-SHAPE(mus); 94% for (f-shape)MUS; 80% for UF-SHAPE(mus); 87% for (uf-shape)MUS; 75% for LENGTH(mus); and 90% for (length)MUS.

### *Imaging data*

#### *Main effect of SOMATOSENSORY versus AUDITORY discrimination*

To determine which areas were generally activated by the discrimination of passive movements, we calculated which regions responded more strongly to the somatosensory discrimination tasks than to the music discrimination tasks (Table 1, Fig. 3A). We identified a bilateral parietal–premotor network including the precuneus, the superior parietal gyrus, the intraparietal sulcus (located dorsally to the 50% probability map of area 2b; the right

Table 1  
Main contrast SOMATOSENSORY > AUDITORY

Brain area (hemisphere)	MNI coordinates			Z value
	x	y	z	
<b>SOMATOSENSORY &gt; AUDITORY</b>				
Precuneus				
(R)*	6	-60	64	6.41
(L)	-6	-58	64	6.74
Superior parietal gyrus				
(R)	18	-60	66	6.74
(L)	-28	-54	66	7.26
Horizontal part of intraparietal sulcus (rostral part of AIP)				
(R)	42	-44	52	6.74
(L)	-42	-40	48	6.63
Ascending part of intraparietal sulcus (rostral part of AIP)				
(R)	52	-32	56	7.33
(L)	-36	-38	40	6.92
Supramarginal gyrus				
(R)	60	-26	38	7.72
(L)	-54	-30	42	6.76
Superior frontal gyrus (SMA)	0	-8	54	5.60
Superior frontal gyrus (PMd)				
(R)	28	-2	66	7.58
(L)	-30	-6	68	7.47
Inferior frontal gyrus (pars opercularis) (PMv) (R)	56	10	24	7.08
Middle frontal gyrus (superior part) (PMv) (L)	-54	6	38	5.60

Note. Z scores and localizations (MNI coordinates) for all significantly activated voxels ( $P < 0.05$ , corrected for multiple comparisons) located within a cluster larger than 10 voxels for the contrast SOMATOSENSORY > AUDITORY, representing “all somatosensory discrimination with unattended music stimulation > all music discrimination with unattended somatosensory stimulation”. Additionally, we report areas tending to be bilaterally activated ( $*P < 0.001$ , uncorrected for multiple comparisons).

side of the ascending part however showed in one cluster [ $x = 52$ ;  $y = -32$ ;  $z = 56$ ] 4/13 overlap with the probability map of area 2b), the supramarginal gyrus, the supplementary motor area (SMA) as well as both dorsal (PMd) and ventral premotor cortex (PMv). Cerebellar activation was found on individual, but not on group level when somatosensory discrimination was subtracted

Table 2  
Main contrast UNFAM SHAPE > UNFAM SHAPEMUS

Brain area (hemisphere)	MNI coordinates			Z value
	x	y	z	
<b>UF-SHAPE(mus) &gt; (uf-shape)MUS</b>				
Precuneus				
(R)	6	-62	62	7.32
(L)	-6	-56	66	6.82
Superior parietal gyrus				
(R)	28	-54	64	6.39
(L)	-26	-54	66	6.98
Horizontal part of intraparietal sulcus (L)	-42	-40	48	6.16
Supramarginal gyrus (R)	52	-34	56	6.32
Superior frontal gyrus (SMA)	0	-12	54	4.99
Superior frontal gyrus (PMd)				
(R)	28	0	64	6.43
(L)	-28	-4	68	6.21
Inferior frontal gyrus (pars opercularis) (PMv)				
(R)	58	12	24	6.01
(L)	-48	8	26	4.96

Note. Z scores and localizations (MNI coordinates) for all significantly activated voxels ( $P < 0.05$ , corrected for multiple comparisons) located within a cluster larger than 10 voxels for the contrast UF-SHAPE(mus) > (uf-shape)MUS, representing “unfamiliar shape discrimination with unattended music stimulation > music discrimination with unattended unfamiliar shape stimulation”.

from music discrimination. Conversely, music discrimination elicited only activation in the superior temporal gyrus (secondary auditory cortex) at the right side when compared to all passive somatosensory discriminations. No other areas, found in the somatosensory discrimination task, activated specifically for music discrimination.

#### Main effect for discriminating unfamiliar shapes (UF-SHAPE(mus) > (uf-shape)MUS)

Comparing UF-SHAPE(mus) to (uf-shape)MUS (Table 2, Fig. 3B), we found significant activation of bilateral precuneus, right and left superior parietal gyrus, right supramarginal gyrus, and left anterior part of the horizontal intraparietal sulcus (located dorsally to the 50% probability map of area 2b). Within the premotor cortex, significant activation was yielded for the SMA, and bilaterally in PMd and PMv. Particularly for PMv, the right hemisphere was more activated than the left hemisphere.

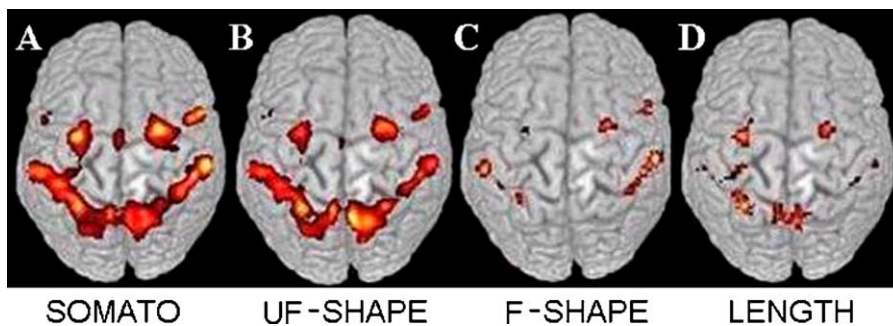


Fig. 3. Brain activation as revealed by the four main contrasts. (A) SOMATO: somatosensory discrimination > auditory discrimination; (B) UF-SHAPE: unfamiliar geometrical shape discrimination [UF-SHAPE(mus)] > music discrimination [(uf-shape)MUS]; (C) F-SHAPE: familiar geometrical shape discrimination [F-SHAPE(mus)] > music discrimination [(f-shape)MUS]; (D) LENGTH: length discrimination of horizontal lines [LENGTH(mus)] > music discrimination [(length)MUS].

*Main effect for discriminating familiar shapes (F-SHAPE(mus) > (f-shape)MUS)*

F-SHAPE(mus) contrasted with (f-shape)MUS activated less midline areas but a more laterally located parietal–premotor network that tended to be bilaterally activated (Table 3, Fig. 3C). It included the superior parietal gyrus, the ascending part of the intraparietal sulcus (located dorsally to the 50% probability map of area 2b), and the supramarginal gyrus as well as PMd and PMv.

*Main effect for discriminating length (LENGTH(mus) > (length)MUS)*

Contrasting the LENGTH(mus) and the (length)MUS condition, a network containing mainly medial parietal as well as dorsal premotor areas were identified (Table 4, Fig. 3D). It encompassed a bilateral activation of the precuneus and activation of the superior parietal gyrus, the supramarginal gyrus, as well as the horizontal part of the intraparietal sulcus. PMd was activated bilaterally. Although tactile input was present in both LENGTH(mus) and (length)MUS condition, left primary somatosensory cortex (SI, 40% overlap with probability map of area 3b) activation was seen when attention was drawn to the somatosensory discrimination.

*Interaction of discriminating unfamiliar shapes versus familiar shapes [UF-SHAPE(mus) – (uf-shape)MUS] > [F-SHAPE(mus) – (f-shape)MUS]*

Within the network, identified for the UF-SHAPE(mus) main effect, we tested which areas responded significantly more strongly to the discrimination of unfamiliar shapes than to the discrimination of familiar shapes (Table 5, Fig. 4). Significant differences were found for the right supramarginal gyrus, right and left superior parietal gyrus, left horizontal intraparietal sulcus and

Table 3  
Main contrast FAM SHAPE > FAM SHAPEMUS

Brain area (hemisphere)	MNI coordinates			Z value
	x	y	z	
F-SHAPE(mus) > (f-shape)MUS				
Superior parietal gyrus				
(R)*	34	–56	60	3.23
(L)	–32	–50	64	5.17
Ascending part of intraparietal sulcus				
(R)*	32	–42	42	4.01
(L)	–36	–40	40	5.64
Supramarginal gyrus				
(R)	58	–26	38	6.28
(L)	–54	–32	40	5.87
Superior frontal gyrus (PMd)				
(R)	26	–2	66	5.55
(L)*	–26	–6	70	4.66
Inferior frontal gyrus (pars opercularis) (PMv)				
(R)	56	10	24	5.91
(L)*	–50	10	32	3.25

*Note.* Z scores and localizations (MNI coordinates) for all significantly activated voxels ( $P < 0.05$ , corrected for multiple comparisons) located within a cluster larger than 10 voxels for the contrast F-SHAPE(mus) > (f-shape)MUS, representing “familiar shape discrimination with unattended music stimulation > music discrimination with unattended familiar shape stimulation”. Additionally, we report areas tending to be bilaterally activated ( $*P < 0.001$ , uncorrected for multiple comparisons).

Table 4  
Main contrast LENGTH(mus) > (length)MUS

Brain area (hemisphere)	MNI coordinates			Z value
	x	y	z	
LENGTH(mus) > (length)MUS				
Precuneus				
(R)	6	–64	60	5.53
(L)	–6	–62	62	5.54
Superior parietal gyrus				
(R)*	28	–54	58	4.27
(L)	–30	–56	64	6.05
Horizontal part of intraparietal sulcus				
(R)*	44	–40	54	4.62
(L)	–42	–38	48	5.10
Supramarginal gyrus				
(R)	60	–26	38	4.77
(L)*	–60	–30	32	4.53
Around central sulcus (SI) (L)				
(L)	–30	–28	62	4.92
Superior frontal gyrus (PMd)				
(R)	28	–2	68	5.47
(L)	–30	–8	68	5.70

*Note.* Z scores and localizations (MNI coordinates) for all significantly activated voxels ( $P < 0.05$ , corrected for multiple comparisons) located within a cluster larger than 10 voxels for the contrast LENGTH(mus) > (length)MUS, representing “length discrimination with unattended music stimulation > music discrimination with unattended length stimulation”. Additionally, we report areas tending to be bilaterally activated ( $*P < 0.001$ , uncorrected for multiple comparisons).

bilateral precuneus, as well as for SMA, bilateral PMd, and left PMv. The converse interaction did not elicit any significant activation differences.

Table 5  
Interactions between [UF-SHAPE(mus) > (uf-shape)MUS] > [F-SHAPE(mus) > (f-shape)MUS]

Brain area (hemisphere)	MNI coordinates			Z value
	x	y	z	
[UF-SHAPE] > [F-SHAPE]				
Precuneus				
(R)	12	–60	66	4.68
(L)	–8	–52	68	4.13
Superior parietal gyrus				
(R)	22	–58	66	4.06
(L)	–28	–58	62	4.66
Horizontal part of intraparietal sulcus (L)				
(L)	–44	–36	44	4.28
Supramarginal gyrus (R)				
(R)	46	–30	56	3.46
Superior frontal gyrus (SMA)				
(R)	4	–18	56	3.10
Superior frontal gyrus (PMd)				
(R)	34	–2	60	3.90
(L)	–24	–6	62	3.84
Inferior frontal gyrus (pars opercularis) (PMv) (L)				
(L)	–48	8	18	4.14

*Note.* Z scores and localizations (MNI coordinates) of peaks of significantly ( $P < 0.05$ , corrected for multiple comparisons, areas with >10 significant voxels) activated regions for interactions between the contrast [UF-SHAPE] (representing the contrast “unfamiliar shape discrimination with unattended music stimulation > music discrimination with unattended unfamiliar shape stimulation”) compared to [F-SHAPE] (representing the contrast “familiar shape discrimination with unattended music stimulation > music discrimination with unattended familiar shape stimulation”).

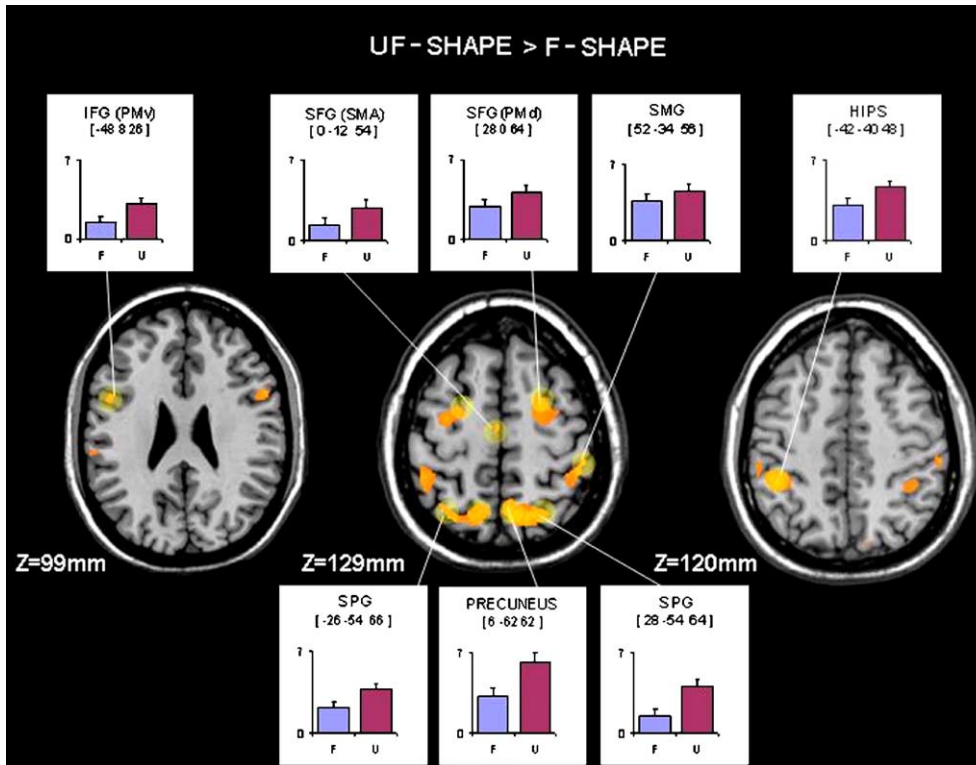


Fig. 4. Brain activation as revealed by the UF-SHAPE > F-SHAPE interaction. The orange cluster indicates the network as revealed by the UF-SHAPE main contrast [i.e., UF-SHAPE(mus) > (uf-shape)MUS]. Yellow areas mark regions that differ significantly ( $P < 0.05$ ) from the F-SHAPE contrast. For these regions, bar plots display the estimated blood oxygenation level dependent (BOLD) response (arbitrary units on the ordinate) for the contrasts UF-SHAPE(mus) > (uf-shape)MUS (U) and F-SHAPE(mus) > (f-shape)MUS (F). Legend: IFG (inferior frontal gyrus); SFG (superior frontal gyrus); SMG (supramarginal gyrus); HIPS (horizontal part of intraparietal sulcus); SPG (superior parietal gyrus).

*Interaction of discriminating unfamiliar shapes versus length [UF-SHAPE(mus) – (uf-shape)MUS] > [LENGTH(mus) – (length)MUS]*

Within the network identified for the UF-SHAPE(mus) main contrast, only the right superior parietal gyrus was more activated in the UF-SHAPE(mus) discrimination compared to the LENGTH(mus) discrimination (Table 6, Fig. 5A). Note that the

same area was also identified by the above UF-SHAPE(mus) > F-SHAPE(mus) contrast. Thus, the right superior parietal gyrus appears to become specifically activated during the discrimination of unfamiliar shapes.

The converse interaction revealed that LENGTH(mus) discrimination elicited a significantly higher response than UF-SHAPE(mus) discrimination in the left horizontal intraparietal sulcus and in the left SI (Table 6, Fig. 5B).

Table 6  
Interactions between [UF-SHAPE(mus) > (uf-shape)MUS] and [LENGTH(mus) > (length)MUS]

Brain area (hemisphere)	MNI coordinates			Z value
	x	y	z	
[UF-SHAPE] > [LENGTH]				
Superior parietal gyrus (R)	32	-56	58	3.66
[LENGTH] > [UF-SHAPE]				
Horizontal part of intraparietal sulcus (L)	-44	-36	44	2.82
Around central sulcus (SI) (L)	-36	-28	58	4.15

Note. Z scores and localizations (MNI coordinates) of peaks of significantly ( $P < 0.05$ , corrected for multiple comparisons, areas with >10 significant voxels) activated regions for interactions between the contrast [UF-SHAPE] (representing the contrast “unfamiliar shape discrimination with unattended music stimulation > music discrimination with unattended unfamiliar shape stimulation”) compared to [LENGTH] (representing the contrast “length discrimination with unattended music stimulation > music discrimination with unattended length stimulation”) and vice versa.

*Interaction of discriminating length versus familiar shapes [LENGTH(mus) – (length)MUS] > [F-SHAPE(mus) – (f-shape)MUS]*

Within the areas determined by the LENGTH(mus) main effect, bilateral precuneus, left superior parietal gyrus, left horizontal intraparietal sulcus, left SI and bilateral PMd were significantly more strongly activated during LENGTH(mus) than during F-SHAPE(mus) discrimination (Table 7, Fig. 6). Importantly, the left horizontal intraparietal sulcus as well as the left SI were previously also identified in the LENGTH(mus) > UF-SHAPE(mus) comparison and seem, therefore, to be specifically related to the functional requirements of LENGTH(mus) discrimination.

The converse interaction did not reveal any significant differences.

To summarize, the interaction analysis confirmed that the different somatosensory discrimination tasks activated distinct parieto-premotor networks. In particular, the superior parietal gyrus appeared to be specifically involved in the kinesthetic discrimination of unfamiliar shapes, while the left horizontal

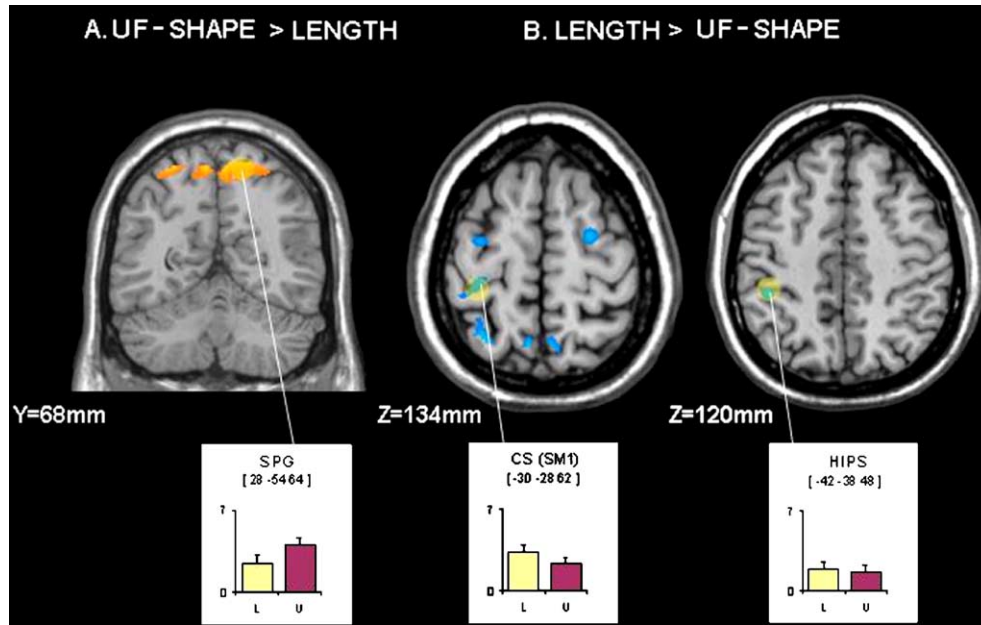


Fig. 5. Brain activation as revealed by the UF-SHAPE versus LENGTH interaction. The orange cluster indicates the network as revealed by the UF-SHAPE main contrast [i.e., UF-SHAPE(mus) > (uf-shape)MUS]. The blue cluster indicates the network as revealed by the LENGTH main contrast. Yellow areas mark regions that differ significantly ( $P < 0.05$ ) from the LENGTH contrast. For these regions, bar plots display the estimated blood oxygenation level dependent (BOLD) response (arbitrary units on the ordinate) for the contrasts UF-SHAPE(mus) > (uf-shape)MUS (U) and LENGTH(mus) > (length)MUS (L). Legend: SPG (superior parietal gyrus); CS (around central sulcus); HIPS (horizontal part of intraparietal sulcus).

intraparietal sulcus and left SI were activated during tactile-kinesthetic discrimination of length.

## Discussion

In the present study, we investigated which brain areas were involved in the discrimination of spatial features when the index finger of the right hand was passively moved by a robot. In

Table 7

Interactions between [LENGTH(mus) > (length)MUS] > [F-SHAPE(mus) > (f-shape)MUS]

Brain area (hemisphere)	MNI coordinates			Z value
	x	y	z	
[LENGTH] > [F-SHAPE]				
Precuneus				
(R)	10	-60	62	3.45
(L)	-6	-56	66	4.41
Superior parietal gyrus (L)	-24	-52	66	2.77
Horizontal part of intraparietal sulcus (L)	-44	-36	44	4.44
Around central sulcus (SI) (L)	-34	-28	56	4.58
Superior frontal gyrus (PMD)				
(R)	26	4	64	3.15
(L)	-36	-6	64	4.02

Note. Z scores and localizations (MNI coordinates) of peaks of significantly ( $P < 0.05$ , corrected for multiple comparisons, areas with >10 significant voxels) activated regions for interactions between the contrast [LENGTH] (representing the contrast “length discrimination with unattended music stimulation > music discrimination with unattended length stimulation”) compared to [F-SHAPE] (representing the contrast “familiar shape discrimination with unattended music stimulation > music discrimination with unattended familiar shape stimulation”).

particular, we tested whether the passive discrimination of shape with different geometrical features versus length discrimination activated distinct neural networks. To address this issue, shape and length discrimination were contrasted to music discrimination. Both tasks differed only with respect to the processed modality, but not to the stimuli presented or the higher cognitive functions involved in discrimination tasks in general. The percentage of correct answers varied between 75% and 100% for all conditions, indicating that subjects solved the discrimination tasks with a high degree of success. In particular, the percentage of correct answers across the three somatosensory discrimination tasks varied only slightly (78–86% in the training session), indicating that the difficulty of the three tasks was reasonably matched. Accordingly, changes in brain activation can be interpreted as a unique index of processing somatosensory information during spatial discrimination.

The general comparison of somatosensory versus music discrimination revealed a bilateral frontoparietal network, including the precuneus, superior parietal gyrus, horizontal and anterior intraparietal sulcus, the supramarginal gyrus, as well as PMv, PMd, and SMA. This is in concordance with earlier findings on active discrimination (Bodegård et al., 2001; Deiber et al., 1996; Hadjikhani and Roland, 1998; O’Sullivan et al., 1994; Roland et al., 1998; Seitz et al., 1991). Previous results suggest that the cerebellum plays an important role in discrimination (Bodegård et al., 2001; Hadjikhani and Roland, 1998; Seitz et al., 1991; Stoeckel et al., 2003; Stoesz et al., 2003). However, in our study, comparing somatosensory to music discrimination, cerebellar activity did not reach significance, indicating that the cerebellum is probably involved in various types of discrimination.

Contrasting each somatosensory discrimination condition to its music discrimination counterpart revealed separate networks



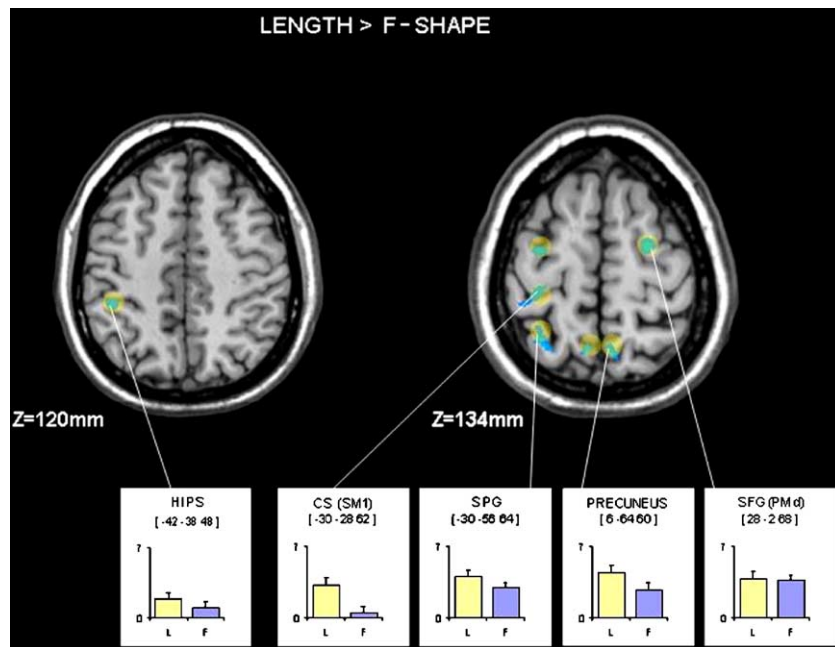


Fig. 6. Brain activation as revealed by the LENGTH > F-SHAPE interaction. Blue cluster indicates the network as revealed by the LENGTH main contrast [i.e., LENGTH(mus) > (length)MUS]. Yellow areas mark regions that differ significantly ( $P < 0.05$ ) from the F-SHAPE contrast. For these regions, bar plots display the estimated blood oxygenation level dependent (BOLD) response (arbitrary units on the ordinate) for the contrasts LENGTH(mus) > (length)MUS (L) and F-SHAPE(mus) > (f-shape)MUS (F). Legend: HIPS (horizontal part of intraparietal sulcus); CS (around central sulcus); SPG (superior parietal gyrus); SFG (superior frontal gyrus).

involved in different types of passive somatosensory discrimination. In general, unfamiliar shape discrimination yielded the largest frontoparietal network among all three conditions, whereas familiar shape and length discrimination were each associated with subdivisions of the latter network. The larger network observed during unfamiliar shape discrimination is presumably associated with higher task demands for processing spatial information. More specifically, the shapes of the quadrilaterals were not known in advance such that no prior mental image of the geometric features could be formed. By contrast, subjects knew in advance that they had to discriminate lines, squares, rectangles, or triangles during the remaining discrimination conditions. The identified areas involved in passive movement discrimination exhibited task-specific differences in the BOLD response as indicated by the interaction, whereas such modulations were not observed across the music discrimination control conditions.

The function of the activated parietal and premotor areas will be discussed in more detail next.

#### Superior parietal gyrus

Although the superior parietal gyrus was activated during all discrimination tasks, it was most significantly active during the unfamiliar shape condition. Studies examining active discrimination revealed that the superior parietal cortex is involved in kinesthesia (Binkofski et al., 1999) and the discrimination of tactile objects which differed in length or shape (Hadjikhani and Roland, 1998; Seitz et al., 1991; Stoeckel et al., 2004). Previous patient studies have also provided evidence that lesions in the posterior parietal lobe hamper adequate processing of somatosensory information and spatiotemporal movement patterns (Binkofski et

al., 2001; Pause et al., 1989), as well as discriminative sensation (stereognosis, graphesthesia, position sense) (Bassetti et al., 1993). Interestingly, unfamiliar shape discrimination required right superior parietal gyrus involvement. This confirms recent findings of Stoeckel et al. (2004) who contrasted active discrimination of distinguishable against undistinguishable objects with an event-related fMRI design. These authors suggested that conscious attention for tactile object shape discrimination of distinguishable objects activated preferentially the right hemisphere (Stoeckel et al., 2004). Although we used a block-design, thus highlighting the spatial distribution of the general activation pattern instead of the different phases of somatosensory discrimination across time, our results seem to confirm and extend these observations. Our results indicated that the right superior parietal cortex specifically covered kinesthetic discrimination processing, even when no active movement or tactile contact was present. Furthermore, the interaction analysis revealed that the right superior parietal gyrus was significantly more solicited during unfamiliar shape discrimination than during the remaining two types of somatosensory discrimination, i.e., when shape complexity was high. This is in good agreement with the general notion that perceptual processing of spatial information displays a right hemispheric dominance (de Jong et al., 2001; Galati et al., 2000; Stephan et al., 2003; Vallar, 1997).

Moreover, the left superior parietal gyrus became more strongly activated during the discrimination of unfamiliar shapes and length than during the discrimination of familiar shapes, as revealed by the interaction analyses. In accordance to previous studies, this left hemisphere activation could be related to maintaining somatosensory information in working memory (Stoeckel et al., 2004). Note that familiar shapes such as triangles, squares, and rectangles can be discriminated relatively

early during the trial (i.e., often already when the second or third corner is reached), whereas for both length as well as unfamiliar shapes, discrimination is carried out later in the trial. Accordingly, more information has to be maintained such that the working memory demands are higher during the latter two conditions.

#### *Precuneus*

The precuneus was activated bilaterally in unfamiliar shape and in length discrimination, but not in familiar shape discrimination. To the best of our knowledge, this is the first study identifying precuneus activation in discrimination tasks. We hypothesize that this medially located activation is associated with attentional deployment to the movement trajectory, and/or involvement in complex mental imagery, as required for solving the task. This interpretation is based upon previous studies accrediting precuneus involvement in spatial response selection (Schumacher et al., 2003), tactile motion (Hagen et al., 2002), visual shape and size retrieval (Oliver and Thompson-Schill, 2003), mental imagery dealing with spatial components (Sathian et al., 1997; Vanlierde et al., 2003), and memory recall (Mellet et al., 1998). Both retrieval of spatial information and setting up spatial attributes have been ascribed to precuneus activity during motor imagery (Malouin et al., 2003). Other studies reported that both superior parietal gyrus and precuneus responded to preparatory pointing activity as well as directing attention to a peripheral visual location (Astafiev et al., 2003). Additionally, the left anterior precuneus locus, as identified with the interaction analysis of length versus familiar shape discrimination ( $x, y, z = -6, -56, 66$ ), is comparable to the region attributed to shifting attention in space, as identified by Astafiev et al. (2003) ( $x, y, z = -3, -56, 60$ ) and Simon et al. (2002) ( $x, y, z = -4, -56, 54$ ).

#### *Anterior intraparietal sulcus*

Both the horizontal and ascending part of the intraparietal sulcus were close (<7.3 mm and <6.2 mm, respectively) to an area supposed to represent the human analogue of monkey's anterior intraparietal area (AIP), as defined by Grefkes et al. (2002). This area was shown to be involved in macrogeometric somatosensory discrimination studies (Bodegård et al., 2001; Grefkes et al., 2002; O'Sullivan et al., 1994; Roland and Zilles, 1998; Roland et al., 1998; Seitz et al., 1991; Stoeckel et al., 2003; Stoesz et al., 2003). Our results are in line with the findings of Roland et al. (1998) that the AIP is active during discrimination of rectangular parallelepipeds when effects of motor activity are filtered out. According to lesion studies, AIP plays an important role in processing sensorimotor information during finger movements (Binkofski et al., 1998). Binkofski et al. (2000) also demonstrated AIP activation during imagery of finger movements. On the other hand, axis orientation discrimination seems to be segregated in AIP. According to Taira et al. (1998), one area in the left AIP was found to be responsive to hand movements, whereas another area in the right intraparietal sulcus related to perception.

The findings in the present study extend these observations: although the left AIP combined all types of shape and length discrimination, different areas within the left AIP seemed to become activated, depending on the predictability of the movement outcome. Activation in the left horizontal intraparietal

sulcus (posterior to area 2) was observed in unfamiliar shape and length discrimination, suggesting its increased attentional involvement when the outcome of the final movement is less predictable. Indeed, the volunteers could not predict the end of the line [in LENGTH(mus)] or the fourth side of the quadrilateral [in UF-SHAPE(mus)], whereas they could predict the third or fourth line when feeling a triangle or square/rectangle [in F-SHAPE(mus)]. The intraparietal sulcus seems to reflect preparation of higher-level processing and attention, required for the performance of motion-processing tasks (Luks and Simpson, 2004). Differential attentional demands could therefore have been inherent to our paradigm and can, partly, account for the difference in activation modulation of the intraparietal sulcus. On the other hand, the left ascending part of the intraparietal sulcus (dorsal to area 2b) has been related to familiar shape discrimination. Judging from the interaction analysis, the left horizontal part of the intraparietal sulcus appeared to be specifically sensitive to length discrimination, since it was significantly more strongly activated during length discrimination than during the other two somatosensory discrimination tasks. Note that only the length discrimination task contained a tactile component. However, for all main contrasts as well as the interaction analyses, the somatosensory discrimination was compared to a stimulus-matched control condition. Therefore, this additional activation does probably not arise from tactile touch per se, but rather from using tactile together with somatosensory information to solve the length discrimination task.

#### *Supramarginal gyrus*

The right supramarginal gyrus was involved in all passive somatosensory discrimination tasks. Several studies have confirmed this area to be related to both passive and active discrimination of shape, length, edge, and curvature (Bodegård et al., 2001; Hadjikhani and Roland, 1998; O'Sullivan et al., 1994; Roland et al., 1998). Focal lesions in the supramarginal gyrus impaired tactile object recognition even though normal sensation was spared (Caselli, 1993; Reed et al., 1996). Only Stoeckel et al. (2003) stated that the supramarginal gyrus participates in exploration of shape and not in the discrimination itself. However, consistent with the majority of the studies, our findings also identify the supramarginal gyrus as an important locus for processing somatosensory discrimination of length and shape.

#### *Supplementary motor area*

The SMA was only significantly activated during unfamiliar shape discrimination, suggesting a relation with task complexity, especially when complex motor imagery is required. So far, SMA activation did not appear in other studies examining somatosensory discrimination of shapes (Bodegård et al., 2001; Hadjikhani and Roland, 1998; O'Sullivan et al., 1994; Roland et al., 1980, 1998), presumably because these objects or shapes always carried a familiar geometric component, comparable to familiar shape discrimination in the present study. This suggests that a certain task complexity threshold has to be exceeded before SMA is activated. This hypothesis is further backed up by the findings that SMA is activated during motor imagery and programming (Deiber et al., 1996; Mellet et al., 1998; Rao et al., 1993; Remy et al., 1994; Richter et al., 1997; Roland et al., 1980; Stefan et al., 1995), as

well as complex finger movements without discrimination task (Shibasaki et al., 1993).

#### *Ventral premotor cortex*

PMv was inactive during length discrimination but was activated on the right side during familiar shape discrimination, and bilaterally during unfamiliar shape discrimination. PMv is highly involved in motor imagery (Binkofski et al., 2000; Decety et al., 1994; Hanakawa et al., 2003; Stefan et al., 1995) as well as imagining the construction of three-dimensional objects (Jäncke et al., 2001), which all require preparation for complex motor performance with considerable sensorimotor control (Binkofski and Buccino, 2004). The observed bilateral PMv activation during unfamiliar shape discrimination may therefore imply that more complex spatial features derived from passive movements also required more complex mental imagery of unfamiliar shapes, as compared to familiar shape or length discrimination. Furthermore, PMv is also activated during object manipulation (Binkofski et al., 1999), higher-order forearm/finger motor control (Binkofski and Buccino, 2004; Binkofski et al., 2000), mental rotation necessary for hand recognition (Parsons et al., 1995), sensorimotor integration, and associative sensorimotor learning (Halsband and Freund, 1990). Interestingly, the left ventral premotor cortex seems to be involved in kinesthetic motor imagery of one's own movement (Binkofski and Buccino, 2004; Porro et al., 2000), whereas right ventral premotor cortex activation is more apparent during imagery of spatial target motion in extrapersonal space (Binkofski and Buccino, 2004). This latter finding can be linked with our study. In the bilateral PMv activation seen during unfamiliar shape discrimination, the right hemisphere was more activated than the left. Thus, the results in both unfamiliar and familiar shape discrimination show that this lateral area was also activated when motion features were actually perceived within a discrimination setting.

#### *Dorsal premotor cortex*

During familiar shape discrimination, PMd activation was detected in the right hemisphere only whereas length and unfamiliar shape discrimination revealed bilateral activation. In analogy with the findings in AIP, we speculate that the shapes of triangles, squares, and rectangles could be predicted after at most two line trajectories, thereby requiring less complex motor imagery to solve the task. PMd activation was previously revealed in tactile form discrimination and praxic function (Sadato et al., 2000; Seitz et al., 1991). Furthermore, various aspects of movement generation and control recruit PMd (Picard and Strick, 2001). In monkeys, PMd acquires target and arm position information, depending on the context in which movement is performed (Wise et al., 1997). Because of its connection with area 7b in the posterior parietal lobe, PMd may encode the spatial environment, based on exploratory finger movements (Mellet et al., 1996). In the present study, however, such processing even occurred without active movement. Therefore, as in monkeys (Geyer et al., 2000a,b), PMd in humans appears to be relying upon proprioceptive information in the generation of output. Perhaps this area is triggered more when either complex visualization of the movement trajectories is needed (in unfamiliar shape discrimination) or when the unpredictability of the

movement outcome is enhanced (in both unfamiliar shape and length discrimination).

#### *Primary somatosensory area*

In this study, area 3b was significantly more activated during length as compared to the remaining discrimination tasks. The tip of the right index finger touched the wooden crossbar in both the LENGTH(mus) and (length)MUS conditions. This indicates that allocating attention to tactile length discrimination produced an additional activation in area 3b. This is consistent with previous findings suggesting that SI exhibits an attention-related increase in somatosensory stimulation (Waberski et al., 2002), in tactile attention tasks (Burton et al., 1999), and attention to touch (Johansen-Berg et al., 2000). SI activity is also evident during passive movements of the metacarpophalangeal joint with minimal tactile contact (Mima et al., 1999), in all kinds of microgeometric and macrogeometric stimuli with touch (Bodegård et al., 2001), and during imagination of tactile stimulation (Hodge et al., 1996).

### **Conclusion**

Brain activation during passive somatosensory discrimination tasks was studied in healthy elderly subjects. To the best of our knowledge, this is the first fMRI study examining 'passive' somatosensory discrimination imposed by an fMRI compatible robot. By comparing stimulus-matched conditions of somatosensory to music discrimination, we were able to highlight those areas that were specifically sensitive to passive discrimination of familiar and unfamiliar shape and to tactile length discrimination, after ruling out activations related to general discrimination processes or to passive movement. This study extends previously obtained knowledge, gained by 'active' discrimination studies in healthy volunteers. Our results suggest that familiar shape and length discrimination bear on different neuronal networks. Length discrimination required more medially located superior parietal and dorsal premotor circuits, which was associated with increased attentional demands to track relevant proprioceptive information when spatial information was sparse. The primary somatosensory cortex was specifically involved in focused attention to tactile length discrimination. Familiar shape discrimination exhibited a more laterally located network, including inferior parietal and ventral premotor regions, related to processing of familiar uncomplicated shapes. However, these shapes also required enhanced attention to keep track of the movement trajectory. Unfamiliar shape discrimination encompassed both networks, which may be explained by the unpredictability of the shape associated with more complex mental imagery required to solve the task. Based on the present findings, we encourage the use of different passive discrimination tasks for lesion-specific training in the rehabilitation of stroke patients.

### **Acknowledgments**

We wish to thank all subjects who participated in the study. Our gratitude goes to Pascal Hamaekers and Guido Putzeys for their assistance and teaching in scanning. Many thanks go to the firm OPTIDRIVE and especially to Jan Van Elsacker and Koen

Rowies for their customer service. We appreciate the help of Wim Machiels and Liesbet De Wit for the picture of the fMRI robot. A special word of gratitude is expressed to Marc Noël for his critical review of the manuscript. We also wish to thank the anonymous referees for their useful contribution to a previous version of the article.

## References

- Astafiev, S.V., Shulman, G.L., Stanley, C.M., Snyder, A.Z., Van Essen, D.C., Corbetta, M., 2003. Functional organization of human intraparietal and frontal cortex for attending, looking, and pointing. *J. Neurosci.* 23, 4689–4699.
- Bassetti, C., Bogousslavsky, J., Regli, F., 1993. Sensory syndromes in parietal stroke. *Neurology* 43, 1942–1949.
- Binkofski, F., Buccino, G., 2004. Motor functions of the Broca's region. *Brain Lang.* 89, 362–369.
- Binkofski, F., Dohle, C., Posse, S., Stephan, K.M., Hefter, H., Seitz, R.J., Freund, H.J., 1998. Human anterior intraparietal area subserves prehension: a combined lesion and functional MRI activation study. *Neurology* 50, 1253–1259.
- Binkofski, F., Buccino, G., Posse, S., Seitz, R.J., Rizzolatti, G., Freund, H., 1999. A fronto-parietal circuit for object manipulation in man: evidence from an fMRI-study. *Eur. J. Neurosci.* 11, 3276–3286.
- Binkofski, F., Amunts, K., Stephan, K.M., Posse, S., Schormann, T., Freund, H.J., Zilles, K., Seitz, R.J., 2000. Broca's region subserves imagery of motion: a combined cytoarchitectonic and fMRI study. *Hum. Brain Mapp.* 11, 273–285.
- Binkofski, F., Kunesch, E., Classen, J., Seitz, R.J., Freund, H.J., 2001. Tactile apraxia: unimodal apractic disorder of tactile object exploration associated with parietal lobe lesions. *Brain* 124, 132–144.
- Bodegård, A., Ledberg, A., Geyer, S., Naito, E., Zilles, K., Roland, P.E., 2000. Object shape differences reflected by somatosensory cortical activation. *J. Neurosci.* 20, RC51.
- Bodegård, A., Geyer, S., Grefkes, C., Zilles, K., Roland, P.E., 2001. Hierarchical processing of tactile shape in the human brain. *Neuron* 31, 317–328.
- Burton, H., Abend, N.S., MacLeod, A.M., Sinclair, R.J., Snyder, A.Z., Raichle, M.E., 1999. Tactile attention tasks enhance activation in somatosensory regions of parietal cortex: a positron emission tomography study. *Cereb. Cortex* 9, 662–674.
- Caselli, R.J., 1993. Ventrolateral and dorsomedial somatosensory association cortex damage produces distinct somesthetic syndromes in humans. *Neurology* 43, 762–771.
- Cockburn, J., Haggard, P., Cock, J., Fordham, C., 2003. Changing patterns of cognitive–motor interference (CMI) over time during recovery from stroke. *Clin. Rehabil.* 17, 167–173.
- Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., Mazziotta, J.C., Fazio, F., 1994. Mapping motor representations with positron emission tomography. *Nature* 371, 600–602.
- Deiber, M.P., Ibañez, V., Sadato, N., Hallett, M., 1996. Cerebral structures participating in motor preparation in humans: a positron emission tomography study. *J. Neurophysiol.* 75, 233–247.
- de Jong, B.M., van der Graaf, F.H., Paans, A.M., 2001. Brain activation related to the representations of external space and body scheme in visuomotor control. *NeuroImage* 14, 1128–1135.
- Folstein, M.F., Folstein, S.E., McHugh, P.R., 1975. "Mini-mental state". A practical method for grading the cognitive state of patients for the clinician. *J. Psychiatr. Res.* 12, 189–198.
- Galati, G., Lobel, E., Vallar, G., Berthoz, A., Pizzamiglio, L., Le Bihan, D., 2000. The neural basis of egocentric and allocentric coding of space in humans: a functional magnetic resonance study. *Exp. Brain Res.* 133, 156–164.
- Geyer, S., Ledberg, A., Schleicher, A., Kinomura, S., Schormann, T., Buegel, U., Klingberg, T., Larsson, J., Zilles, K., Roland, P.E., 1996. Two different areas within the primary motor cortex of man. *Nature* 382, 805–807.
- Geyer, S., Schleicher, A., Zilles, K., 1999. Area 3a, 3b, and 1 of human primary somatosensory cortex: 1. Microstructural organization and interindividual variability. *NeuroImage* 10, 63–83.
- Geyer, S., Matelli, M., Luppino, G., Zilles, K., 2000. Functional neuroanatomy of the primate isocortical motor system. *Anat. Embryol. (Berl.)* 202, 443–474.
- Geyer, S., Schormann, T., Mohlberg, H., Zilles, K., 2000. Areas 3a, 3b, and 1 of human primary somatosensory cortex: 2. Spatial normalization to standard anatomical space. *NeuroImage* 11, 684–696.
- Gitelman, D.R., Alpert, N.M., Kosslyn, S., Daffner, K., Scinto, L., Thompson, W., Mesulam, M.M., 1996. Functional imaging of human right hemispheric activation for exploratory movements. *Ann. Neurol.* 39, 174–179.
- Grefkes, C., Geyer, S., Schormann, T., Roland, P., Zilles, K., 2001. Human somatosensory area 2: observer-independent cytoarchitectonic mapping, interindividual variability, and population map. *NeuroImage* 14, 617–631.
- Grefkes, C., Weiss, P.H., Zilles, K., Fink, G.R., 2002. Crossmodal processing of object features in human anterior intraparietal cortex: an fMRI study implies equivalencies between humans and monkeys. *Neuron* 35, 173–184.
- Hadjikhani, N., Roland, P.E., 1998. Cross-modal transfer of information between the tactile and the visual representations in the human brain: a positron emission tomographic study. *J. Neurosci.* 18, 1072–1084.
- Hagen, M.C., Franzen, O., McGlone, F., Essick, G., Dancer, C., Pardo, J.V., 2002. Tactile motion activates the human middle temporal/V5 (MT/V5) complex. *Eur. J. Neurosci.* 6, 957–964.
- Haggard, P., Cockburn, J., Cock, J., Fordham, C., Wade, D., 2000. Interference between gait and cognitive tasks in a rehabilitating neurological population. *J. Neurol., Neurosurg. Psychiatry* 69, 479–486.
- Halsband, U., Freund, H.J., 1990. Premotor cortex and conditional motor learning in man. *Brain* 113, 207–222.
- Hanakawa, T., Immisch, I., Toma, K., Dimyan, M.A., Van Gelderen, P., Hallett, M., 2003. Functional properties of brain areas associated with motor execution and imagery. *J. Neurophysiol.* 89, 989–1002.
- Hodge, C., Dubroff, J., Huckins, S., Szeverinyi, N., 1996. Somatosensory imagery activates primary sensory cortex in humans: a functional MRI study. *NeuroImage* 3, S209.
- Jäncke, L., Kleinschmidt, A., Mirzazade, S., Shah, N.J., Freund, H.-J., 2001. The role of the inferior parietal cortex in linking the tactile perception and manual construction of object shapes. *Cereb. Cortex* 11, 114–121.
- Johansen-Berg, H., Christensen, V., Woolrich, M., Matthews, P.M., 2000. Attention to touch modulates activity in both primary and secondary somatosensory areas. *NeuroReport* 11, 1237–1241.
- Kawashima, R., Roland, P.E., O'Sullivan, B.T., 1994. Activity in the human primary motor cortex related to ipsilateral hand movements. *Brain Res.* 663, 251–256.
- Luks, T.L., Simpson, G.V., 2004. Preparatory deployment of attention to motion activates higher-order motion-processing brain regions. *NeuroImage* 22, 1515–1522.
- Malouin, F., Richards, C.L., Jackson, P.L., Dumas, F., Doyon, J., 2003. Brain activations during motor imagery of locomotor-related tasks: a PET study. *Hum. Brain Mapp.* 19, 47–62.
- Mellet, E., Tzourio, N., Crivello, F., Joliot, M., Denis, M., Mazoyer, B., 1996. Functional anatomy of spatial mental imagery generated from verbal instructions. *J. Neurosci.* 16, 6504–6512.
- Mellet, E., Petit, L., Mazoyer, B., Denis, M., Tzourio, N., 1998. Reopening the mental imagery debate: lessons from functional anatomy. *NeuroImage* 8, 129–139.
- Mima, T., Sadato, N., Yazawa, S., Hanakawa, T., Fukuyama, H., Yonekura, Y., Shibasaki, H., 1999. Brain structures related to active and passive finger movements in man. *Brain* 122, 1989–1997.
- Nelles, G., Spiekramann, G., Jueptner, M., Leonhardt, G., Müller, S., Gerhard, H., Diener, H.C., 1999. Evolution of functional reorganization

- in hemiplegic stroke: a serial positron emission tomographic activation study. *Ann. Neurol.* 46, 901–909.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9, 97–113.
- Oliver, R.T., Thompson-Schill, S.L., 2003. Dorsal stream activation during the retrieval of object size and shape. *Cogn. Affect. Behav. Neurosci.* 3, 309–322.
- O'Sullivan, B.T., Roland, P.E., Kawashima, R., 1994. A PET study of somatosensory discrimination in man. Microgeometry versus macrogeometry. *J. Neurosci.* 6, 137–148.
- Parsons, L.M., Fox, P.T., Downs, J.H., Glass, T., Hirsch, T.B., Martin, C.C., Jerabek, P.A., Lancaster, J.L., 1995. Use of implicit motor imagery for visual shape discrimination as revealed by PET. *Nature* 375, 54–58.
- Pause, M., Kunesch, E., Binkofski, F., Freund, H.J., 1989. Sensorimotor disturbances in patients with lesions of the parietal cortex. *Brain* 112, 1599–1625.
- Perfetti, C., 1997. *Der hemiplegische Patient- Kognitiv-therapeutische Übungen*. Pflaum Physiotherapie. Richard Pflaum Verlag GmbH and Co. KG, München.
- Perfetti, C., 2001. *L'exercice thérapeutique cognitif pour la rééducation du patient hémiparétique*. Masson, Paris.
- Picard, N., Strick, P.L., 2001. Imaging the premotor areas. *Curr. Opin. Neurobiol.* 11, 663–672.
- Porro, C.A., Cettolo, V., Francescato, M.P., Baraldi, P., 2000. Ipsilateral involvement of primary motor cortex during motor imagery. *Eur. J. Neurosci.* 12, 3059–3063.
- Rao, S.M., Binder, J.R., Bandettini, P.A., Hammeke, T.A., Yetkin, F.Z., Jesmanowicz, A., Lisk, L.M., Morris, G.L., Mueller, W.M., Estkowski, L.D., Wong, E.C., Haughton, V.M., Hyde, J.S., 1993. Functional magnetic resonance imaging of complex human movements. *Neurology* 43, 2311–2318.
- Reed, C.L., Caselli, R.J., Farah, M.J., 1996. Tactile agnosia. Underlying impairment and implications for normal tactile object recognition. *Brain* 119, 875–888.
- Remy, P., Zilbovicius, M., Leroy-Willig, A., Syrota, A., Samson, Y., 1994. Movement- and task-related activations of motor cortical areas: a positron emission tomographic study. *Ann. Neurol.* 36, 19–26.
- Richter, W., Andersen, P.M., Georgopoulos, A.P., Kim, S.G., 1997. Sequential activity in human motor areas during a delayed cued finger movement task studied by time-resolved fMRI. *NeuroReport* 8, 1257–1261.
- Roland, P.E., Mortensen, E., 1987. Somatosensory detection of microgeometry, macrogeometry and kinaesthesia in man. *Brain Res. Rev.* 434, 1–42.
- Roland, P.E., Zilles, K., 1998. Structural divisions and functional fields in the human cerebral cortex. *Brain Res. Brain Res. Rev.* 26, 87–105.
- Roland, P.E., Larsen, B., Lassen, N.A., Skinhoj, E., 1980. Supplementary motor area and other cortical areas in organization of voluntary movements in man. *J. Neurophysiol.* 43, 118–136.
- Roland, P.E., O'Sullivan, B., Kawashima, R., 1998. Shape and roughness activate different somatosensory areas in the human brain. *Proc. Natl. Acad. Sci.* 95, 3295–3300.
- Sadato, N., Ibanez, V., Deiber, M.P., Hallett, M., 2000. Gender difference in premotor activity during active tactile discrimination. *NeuroImage* 11, 532–540.
- Sathian, K., Zangaladze, A., Hoffman, J.M., Grafton, S.T., 1997. Feeling with the mind's eye. *NeuroReport* 8, 3877–3881.
- Schumacher, E.H., Elston, P.A., D'Esposito, M., 2003. Neural evidence for representation-specific response selection. *J. Cogn. Neurosci.* 15, 1111–1121.
- Seitz, R.J., Roland, P.E., Bohm, C., Greitz, T., Elander, S.S., 1991. Somatosensory discrimination of shape: tactile exploration and cerebral activation. *Eur. J. Neurosci.* 3, 481–492.
- Servos, P., Lederman, S., Wilson, D., Gati, J., 2001. fMRI-derived cortical maps for haptic shape, texture, and hardness. *Brain Res. Cogn. Brain Res.* 12, 307–313.
- Shibasaki, H., Sadato, N., Lyshkow, H., Yonekura, Y., Honda, M., Nagamine, T., Suwazono, S., Magata, Y., Ikeda, A., Miyazaki, M., et al., 1993. Both primary motor cortex and supplementary motor area play an important role in complex finger movement. *Brain* 166, 1387–1398.
- Simon, O., Mangin, J.F., Cohen, L., Le Bihan, D., Dehaene, S., 2002. Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. *Neuron* 33, 475–487.
- Stefan, K.M., Fink, G.R., Passingham, R.E., Silbersweig, D., Ceballos-Baumann, A.O., Frith, C.D., Frackowiak, R.S., 1995. Functional anatomy of the mental representation of upper extremity movements in healthy subjects. *J. Neurophysiol.* 73, 373–386.
- Stephan, K.E., Marshall, J.C., Friston, K.J., Rowe, J.B., Ritzl, A., Zilles, K., Fink, G.R., 2003. Lateralized cognitive processes and lateralized task control in the human brain. *Science* 301, 384–386.
- Stoeckel, M.C., Weder, B., Binkofski, F., Buccino, G., Jon Shah, N., Seitz, R.J., 2003. A fronto-parietal circuit for tactile object discrimination: an event-related fMRI study. *NeuroImage* 19, 1103–1114.
- Stoeckel, M.C., Weder, B., Binkofski, F., Choi, H.J., Amunts, K., Pieperhoff, P., Shah, N.J., Seitz, R.J., 2004. Left and right superior parietal lobule in tactile object discrimination. *Eur. J. Neurosci.* 19, 1067–1072.
- Stoesz, M.R., Zhang, M., Weisser, V.D., Prather, S.C., Mao, H., Sathian, K., 2003. Neural networks active during tactile form perception: common and differential activity during macrospatial and microspatial tasks. *Int. J. Psychophysiol.* 50, 41–49.
- Taira, M., Kawashima, R., Inoue, K., Fukuda, H., 1998. A PET study of axis orientation discrimination. *NeuroReport* 9, 283–288.
- Talairach, J., Tournoux, P., 1988. *Co-Planar Stereotaxic Atlas of the Brain*. Thieme Medical Publishers, New York.
- Vallar, G., 1997. Spatial frames of reference and somatosensory processing: a neuropsychological perspective. *Philos. Trans. R. Soc. Lond., B Biol. Sci.* 352, 1401–1409.
- Vanlierde, A., De Volder, A.G., Wanet-Defalque, M.C., Veraart, C., 2003. Occipito-parietal cortex activation during visuo-spatial imagery in early blind humans. *NeuroImage* 19, 698–709.
- Waberski, T.D., Gobbele, R., Darvas, F., Schmitz, S., Buchner, H., 2002. Spatiotemporal imaging of electrical activity related to attention to somatosensory stimulation. *NeuroImage* 17, 1347–1357.
- Wise, S.P., Boussaoud, D., Johnson, P.B., Caminiti, R., 1997. Premotor and parietal cortex: corticocortical connectivity and combinatorial computations. *Annu. Rev. Neurosci.* 20, 25–42.