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Functional properties and interaction of the anterior and posterior intraparietal areas in humans

Elisa Shikata,[1,2,4] Farsin Hamzei,[1] Volkmar Glauche,[1] Martin Koch,[1] Cornelius Weiller,[1] Ferdinand Binkofski[3] and Christian Büchel[1]
[1]Cognitive Neuroscience Laboratory, Department of Neurology, Hamburg University School of Medicine, Martinstrasse 52, D-20246 Hamburg, Germany
[2]Department of Neurology, Nihon University School of Medicine, Tokyo, Japan
[3]Department of Neurology, Lübeck University School of Medicine, Germany
[4]Division of Applied System Neuroscience, Nihon University School of Medicine, Tokyo, Japan

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Abstract

In the monkey the lateral bank of the anterior part of the intraparietal sulcus (area AIP), contains neurons that are involved in visually guided, object-related hand movements. It has also been shown that neurons in the caudal part of the intraparietal sulcus (area CIP) preferentially respond to 3D surface orientation. According to these results, it has been hypothesized that neurons in area CIP primarily encode the 3D features of an object and forwards this information to area AIP. AIP then utilizes this information for appropriate hand actions towards the object. Based on analogies to these primate studies, recent neuroimaging studies have suggested human homologues of areas AIP and CIP, however, the functional interaction between these areas remains unclear. Our event related fMRI study was designed to address specifically the question, how CIP and AIP interact in the process of adjustment of hand orientation towards objects. Volunteers were asked to perform three tasks: discrimination of surface orientation, imaging of visually guided hand movements and execution of visually guided hand movements. Our data show that the human AIP was activated both during discrimination of surface orientation and during the subsequent spatial adjustment of the thumb and index finger position towards the surface orientation. In contrast, human CIP was activated by the surface orientation but not by spatial adjustment of finger position. These data clearly indicate that the function of human CIP is more involved in coding 3D features of the objects, whereas human AIP is more involved in visually guided hand movements, similar to its role in the monkey.

Introduction

In order to grasp and manipulate objects in space it is necessary to match the hand and finger configuration with 3D features of an object (preshaping) (Jeannerod, 1986). The building of a central representation of visual geometrical 3D features in this context is of foremost importance. Patients with parieto-occipital lesions for example, exhibit deficits in the matching of hand and fingers to the shape, size and orientation of objects (Jeannerod *et al*., 1994).

Through neurophysiological studies in alert monkeys, Sakata and colleagues have demonstrated that posterior parietal areas within the intraparietal sulcus (IPS) play a crucial a role in the reconstruction of 3D objects to be manipulated by the hand (Sakata *et al*., 1998). It has also been shown that neurons in the anterior part of the IPS (area AIP) are related to visually guided hand movements (Taira *et al*., 1990; Sakata *et al*., 1995) and some AIP neurons respond to the sight of 3D object features (Murata *et al*., 2000). Furthermore, it has been reported that neurons in the caudal part of the IPS (area CIP) show selectivity for the 3D axis or surface orientation (Kusunoki *et al*., 1993; Shikata *et al*., 1996; Taira *et al*., 2000; Tsutsui *et al*., 2001, 2002). Based on these findings it has been speculated, that the CIP area is involved in coding 3D features of objects. Since AIP has no direct access to information about spatial object features, it has been further speculated that area CIP could be the source of this information for AIP that is essential for grasping (Sakata *et al*., 1998).

Recently, neuroimaging studies which have focused on the discrimination of axis and surface orientation in space and crossmodal object features have demonstrated increased neural activation in the anterior part of the intraparietal sulcus, the putative human homologue of primate area AIP (Faillenot *et al*., 1997, 1999; Binkofski *et al*., 1998, 1999; Taira *et al*., 1998; Shikata *et al*., 2001; Grefkes *et al*., 2002). In our previous study using texture gradients for the investigation of pure surface orientation discrimination, we also observed increased neural activation in this putative AIP area and as well as in the caudal part of the IPS, which might resemble the human homologue of area CIP (Shikata *et al*., 2001). In analogy to nonhuman primate data, it may be speculated that human CIP is directly related to surface orientation discrimination and that activation of area AIP is related to the visual representation of 3D features of objects for grasping (Shikata *et al*., 2001). To confirm the hypothesis that human CIP mainly processes visual information about 3D features of objects, whereas human AIP is more involved in visually guided hand movements, we designed an fMRI study in which subjects were required to adjust their hand orientation to the orientation of a surface presented as a texture gradient. In particular it was hoped we would be able to identify which cortical areas responded to the surface orientation and

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Correspondence: Dr Christian Büchel, as above.
E-mail: buechel@uke.uni-hamburg.de

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to the according hand adjustment and which responded to surface orientation alone.

Materials and methods

Nine healthy volunteers (mean age 26.6 ± 4.5 years, 4 females and 5 males, all right-handed) with normal visual function gave their written informed consent to participate in this study. The protocol of the study was approved by the Hamburg University School of Medicine Ethics Committee.

Stimuli

The stimuli used in this experiment consisted of the same texture elements as were used in a previous study (Shikata *et al*., 2001), but which were 80% of the diameter of the original set. Instead of a colour axis from red to yellow we used an axis of blue to yellow to avoid problems with deuteranopia (Fig. 1). In brief, texture elements consisted of coloured dots with a diameter of 0.26 degrees in the fronto-parallel plane assembled into a perspective array. This plane was slanted at 30- and 45-degrees creating a pair of stimuli. This pair was then rotated around the horizontal plane in 45-degree steps, resulting in 16 different orientations. The background of the texture was black. These texture stimuli had 6.3-degrees aperture and appeared as a round disc (Fig. 1). All visual stimuli were presented on a screen positioned on top of the MR scanner head coil, which was viewed by the subjects through a 45° mirror. The effective field of view was $10 \times 15^\circ$ of visual angle. The sequence of visual stimuli was controlled by a PC running the ‘Presentations’ package version 0.42 (Neurobehavioural systems; http://www.neurobehaviouralsystems.com).

Subjects performed a delayed matching-to-sample task with 4 different tasks organized in 3 sessions. In the first two tasks subjects were required to discriminate either orientation or colour; orientation discrimination (task O) or colour discrimination (task C), respectively. In the third task, volunteers were asked to imagine grasping the visual stimulus with the right hand in addition to performing a subsequent orientation discrimination. They were asked to imagine grasping as if the grasping a slanted round disc, adapting the index finger and thumb to the orientation of the surface (task OI). In the fourth task, volunteers were asked to pantomime grasping movements with no real objects as if they were grasping a slanted round disc with their right index finger and thumb, taking into account the surface orientation of the disc (task OM).

Each trial began with a cue letter, which indicated the trial type. The letter ‘O’,‘C’,‘OI’ and ‘OM’ indicated a task O, task C, task OI and task OM, respectively. Figure 1 shows the task procedure. The cue was followed by a sample stimulus. After the sample stimulus, a single matching stimulus was presented. Subjects were instructed to press the right button with their left index finger when the stimulus showed the same orientation (task O, task OI, task OM) or the same colour (task C) as the sample, respectively, and the left button with the middle finger when the matching stimulus was different. Stimuli were presented for 1000 ms with a stimulus onset asynchrony randomized between 2500 and 4000 ms in Sessions 1 and 2 and 3000 and 4500 ms in Session 3. Subjects were also instructed to pantomime a grasping movement (task OM) or to imagine a grasping movement (task OI) after sample stimuli in OI and OM trials, respectively. During the inter-stimulus interval, a white dot was presented as a fixation point (diameter 0.6°) at the centre of the screen. Volunteers were instructed to fixate on this spot throughout all trials.

All tasks were performed in three separate sessions. In the first session only tasks O and C were performed, in order to avoid implicit movement components. The second session included three tasks: O, C and OI to conform without real movement. The third session included all of four trial types. Before fMRI scanning volunteers were introduced to the stimuli and trained on all tasks.

Image acquisition

MR scanning was performed on a 1.5 T MRI scanner (Siemens Vision). A fast imaging sequence was employed (32 slices with a TR of 2.6 s (TE = 40 ms, FA 90 degrees, matrix 64^*64, field of view 210^*210 mm) using a gradient echo, echo-planar (EPI) $T2^*$-sensitive sequence. The slices were centred on the parietal lobe but covered most of the brain. We acquired 158 volumes in the first session, 227 in session 2 and 395 in session 3.

Image processing and statistical analysis

Image processing and statistical analyses were carried out using SPM99 (Friston *et al*., 1995b; Worsley & Friston, 1995). All volumes were realigned to the fist volume (Friston *et al*., 1995a), spatially normalized to a standard EPI template (Talairach & Tournoux, 1988; Evans *et al*., 1994) and finally smoothed using a 6-mm full-width at half-maximum (FWHM) isotropic Gaussian kernel for individual analyses. A wider filter of 9 mm FWHM was used for the group analysis.

Data analysis was performed by modelling the visual stimuli and the motor responses presented during each trial (task O, C, OI and OM) as delta functions convolved with a haemodynamic response function (HRF). In a separate analysis whole trials were modelled by a Fourier set in order to investigate the overall pattern of the BOLD signal.

Specific effects were tested with appropriate linear contrasts of the parameter estimates, resulting in a t-statistic for each and every voxel. These *t*-statistics constituted a statistical parametric map (SPM). SPMs are interpreted by referring to the probabilistic behaviour of Gaussian random fields. Data were analysed for each subject individually and at the group level using a random effects analysis.

TABLE 1. Group analysis (nine subjects)

		Foci significantly* activated by orientation discrimination vs. colour				
Area		*x*	*y*	*z*	*Z*-score	(*n*)
Parietal						
Left anterior IPS	(a)	−36	−39	39	3.88	9
Right anterior IPS		39	−39	39	3.51	8
Left posterior IPS	(b)	−9	−75	54	4.33	8
Right posterior IPS		21	−66	60	4.07	8
Left middle IPS	(c)	−30	−69	54	3.32	3
Right middle IPS		33	−69	51	3.11	2
Left supramarginal gyrus		−54	−42	45	4.05	3
Right supramarginal gyrus		51	−36	48	3.25	2
Right postcentral sulcus		45	−24	36	4.26	0
Occipital						
Left interoccipital sulcus		−27	−75	33	3.75	1
Right interoccipital sulcus		36	−75	36	3.42	1
Left middle occipital gyrus		−54	−60	−18	3.38	2
Right middle occipital gyrus		51	−66	−12	3.69	1
Frontal						
Left superior frontal sulcus	(h)	−30	−12	57	4.14	7
Right superior frontal sulcus		36	0	60	3.87	4
Left inferior frontal gyrus					n.s	4
Right inferior frontal gyrus		51	9	27	3.78	1

$^*P < 0.001$, uncorrected; *n*, number of subjects who showed the activation sites in that area (masked OI and OM condition); n.s. not significant. (a, b, c and h) Areas indicated in Fig 2.

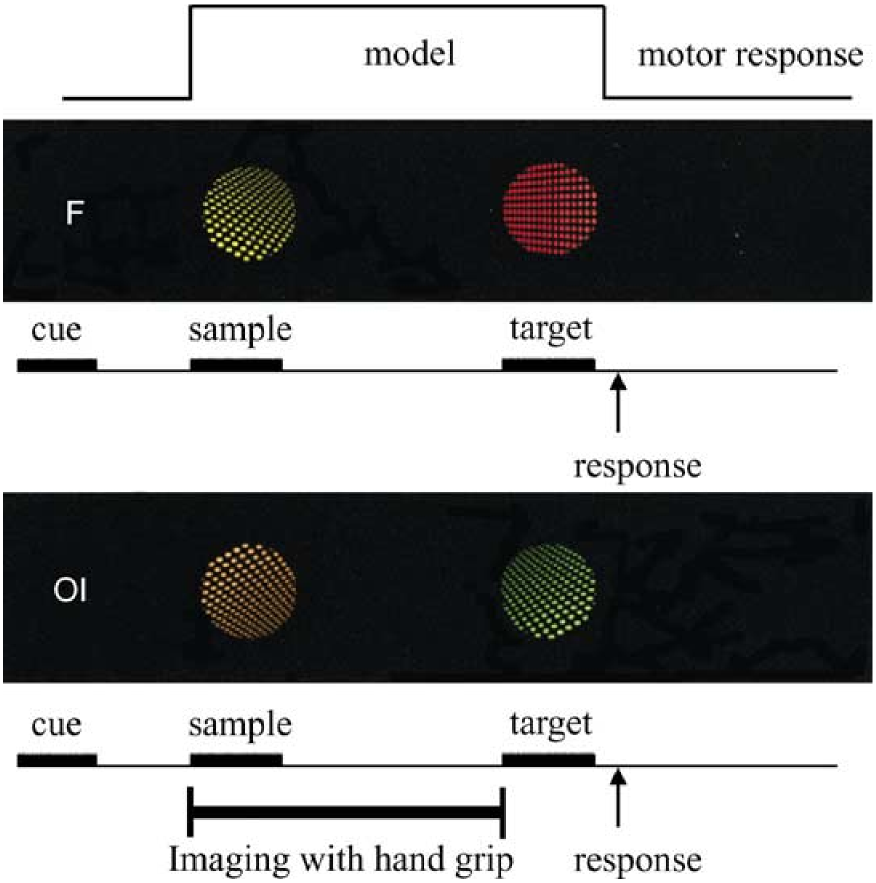

FIG. 1. Paradigm as employed in the study. Stimuli were presented at the centre of the screen. The task was a delayed matching-to-sample task. After a cue stimulus, sample and matching stimuli were presented sequentially. Subjects were instructed to press a different button for matching and nonmatching stimuli. In the OI and OM conditions, subjects were instructed to perform the imagery of a grasping movement after the sample stimuli in OI and OM trials, respectively.

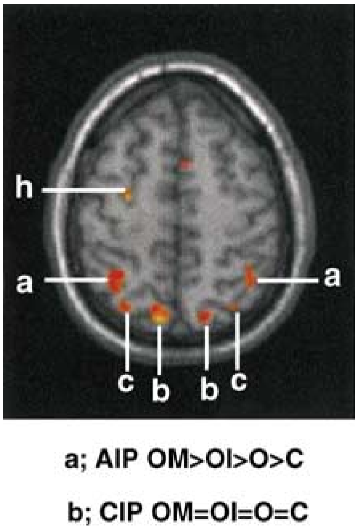

FIG. 2. Activated region in the group analysis (random effects model) for surface orientation discrimination vs. colour discrimination ($P < 0.001$ uncorrected). The z-coordinate of the axial slice is 54 mm (a) Anterior part of IPS ($x = -36$, $y = -39$, $z = 39$ mm and $x = 39$, $y = -39$, $z = 39$ mm). (b) Posterior part of IPS ($x = -9$, $y = -75$, $z = 54$ mm and $x = 24$, $y = -66$, $z = 60$ mm). (c) Middle part of IPS ($x = -30$, $y = -69$, $z = 54$ mm and $x = 33$, $y = -69$, $z = 54$ mm). (h) Superior frontal sulcus ($x = -30$, $y = -12$, $z = 57$ mm and $x = 36$, $y = -0$, $z = 60$ mm). The functional regions are listed in Table 1.

Results

Activation related to orientation discrimination in parietal cortex

Table 1 shows the location of the peak activations from the analysis of the group data (random effects model). Identical letters indicate identical location as in Fig. 2. In the group analysis, the comparison between orientation and colour discrimination revealed significant activations in the anterior and posterior part of IPS in each hemisphere. The activity in the anterior part of the IPS covered the lateral and bottom part of the sulcus (continuously on the left side, intermittently on the right side: $x = -36$, $y = -39$, $z = 39$ mm and $x = 39$, $y = -39$, $z = 39$ mm; Table 1, Fig. 2, arrow a), and there were separate foci of

TABLE 2. Z-score of AIP and CIP (random effects model)

	OM > OI	OI > O	O > C
AIP (a)†			
Left	4.73*	4.19*	3.88*
Right	3.42*	4.44*	3.51*
CIP (b)†			
Left	2.31	1.02	4.33*
Right	1.43	0.78	4.07*

$^{*}P < 0.001$, uncorrected (otherwise not significant). †Locations (a and b) as indicated in Fig. 2.

activation on both sides of the posterior part of the IPS ($x = -9$, $y = -75$, $z = 54$ mm and $x = 24$, $y = -66$, $z = 60$ mm; Table 1, Fig. 2, arrow b). The locations of the significant activations were similar to those from previous experiments.

It was also found that there was another significant activation site in a more superior part of the IPS (middle part of IPS) covering the superior parietal lobule ($x = -30$, $y = -69$, $z = 54$ mm and $x = 33$, $y = -69$, $z = 54$ mm; Table 1, Fig. 2, arrow c). Table 1 also shows the number of subjects who showed these significant activations in each location. Most of the subjects revealed significant activation in anterior (left, 9/9; right, 8/9) and posterior part of IPS (left, 8/9; right, 8/9), whereas fewer subjects revealed significant activation in the middle part of IPS (left, 3/9; right, 2/9). In our previous experiment using only individual subject data, a few subjects also revealed activation in middle part of IPS, but with a lower threshold. Furthermore, activations in bilateral frontal lobes, at the posterior end of the superior frontal sulcus (left; $x = -30$, $y = -12$, $z = 57$ mm; Table 1, Fig. 2, arrow h) and in bilateral occipital lobes at the middle occipital gyrus and in interoccipital sulcus, the boundary with the IPS were found in this random effect analysis.

Activation related to imagination or execution of visually guided hand movement

In the tasks OI and OM, the components of both surface orientation discrimination and movement were included. To dissociate these two components, we first performed a comparison between OI and O (Table 3; left column) and between OM and O, and then also between OM and OI (Table 3; right column). The comparison between OI and O in the group analysis (Table 3; left) revealed significant activations in the IPS only in bilateral anterior parts but not in the middle and posterior part. The differential activation between OM and OI (Table 3; right) also revealed significant activations in bilateral anterior part, but not in the middle and posterior part of IPS. Bilateral superior parietal and left postcentral gyrus was activated differentially in the OM vs. OI, while not in the OI *vs.* O comparison. Bilateral inferior parietal lobe activations were also shown in the OM *vs.* OI, whereas only right inferior parietal one was shown in the OI *vs.* O comparison. Proprioceptive and efference copy may be contained in OM activation.

Table 2 shows the *Z*-scores from the significant activations in the anterior and posterior part of the IPS in each condition. The activation in the anterior part of IPS clearly shows a condition dependent modulation (OM > OI > O > C) in both hemispheres. On the other side, the *Z*-score in the posterior part of IPS shows no such condition related modulation including surface orientation discrimination task (OM = OI = O > C).

Table 4 shows the number of subjects who showed significant activation in the anterior and posterior part of IPS. The activation in the anterior part of IPS shows a modulation by the condition (OM > OI = O > C) in individual subjects. On the contrary, the activation in the posterior part of IPS in five individual shows no modulation by condition. In any individual subject, the activation in the right posterior part of IPS was not modulated by hand orientation movements. Although, two of 9 subjects showed a significant activation modulated by condition (OM > OI > O > C) in the left posterior part of IPS only.

TABLE 3. Group analysis of nine subjects: the significantly* activated foci in the parietal area

	Imagining vs. orientation only				Grasping vs. imagining			
	x	*y*	*z*	*Z*-score	*x*	*y*	*z*	*Z*-score
Left anterior IPS	−39	−39	51	3.88	−30	−45	45	3.42
Right anterior IPS	45	−39	39	3.37	45	−30	39	4.73
Left posterior IPS	–	–	–	n.s.	–	–	–	n.s.
Right posterior IPS	–	–	–	n.s.	–	–	–	n.s.
Left middle IPS	–	–	–	n.s.	–	–	–	n.s.
Right middle IPS	–	–	–	n.s.	–	–	–	n.s.
Left inferior parietal gyrus	–	–	–	n.s.	−51	−33	45	4.96
Right inferior parietal gyrus	57	−48	33	3.62	63	−27	21	5.01
Left superior parietal gyrus	–	–	–	n.s.	−30	−54	60	4.67
Right superior parietal gyrus	–	–	–	n.s.	27	−45	60	3.89
Left postcentral gyrus	–	–	–	n.s.	−42	−27	63	3.79

*$P < 0.001$, uncorrected.

TABLE 4. Numbers of subjects, out of nine, who showed significant* activation in the anterior and posterior parts of IPS

	Anterior IPS				Posterior IPS			
Comparison	Bilateral activation	Left activation	Right activation	No activation	Bilateral activation	Left activation	Right activation	No activation
O > C	8	1	–	–	7	1	1	–
OI > C	6	2	1	–	7	1	1	–
OM > C	6	1	2	–	7	1	1	–
OI > O	–	4	3	2	–	3	1	5
OM > OI	5	2	2	–	3	1	–	5
OM > O	7	1	1	–	2	1	1	5

*$P < 0.001$, uncorrected.

Discussion

Our results clearly show, that activation related to actual hand movements in the anterior part of IPS in the both hemispheres was found to be much higher than in other imagery and surface orientation conditions (OM > OI > O). On the other hand, in the posterior part of IPS (CIP), no significant difference in the activation between the tasks, including a surface orientation component (OM = OI = O) was found. The CIP activation was also not related to the hand movement component.

In our previous neuroimaging study, in which subjects were required to discriminate surface orientation without any hand movements, we found activation in both, the posterior (CIP) and the anterior part of the IPS (AIP). Based on neurophysiological data in primates we speculated that area CIP is primarily related to coding of 3D orientation discrimination and sends this information on to AIP. AIP is utilizing this information to create appropriate visually guided hand movements (Shikata *et al*., 2001). The present study was explicitly designed to test this hypothesis. We sought to disentangle the functional differences between area AIP and CIP by employing additional tasks containing imagery and execution of visually guided hand movements. As hypothesized, our data clearly indicate that the function of the human area CIP is more concerned with coding of 3D features of the objects, whereas human AIP is more involved in visually guided hand movements.

Area AIP

In accord with our previous data AIP was activated during orientation discrimination. As predicted, this activation was significantly weaker than that observed during imagery or actual performance of movements. Neurons in area AIP in the monkey, which is known to be related to visually guided hand manipulation, can also be activated by the sight of 3D objects (Taira *et al*., 1990; Sakata *et al*., 1995). Many of these neurons had motor components with visual input, showing less activation during manipulation in the dark than in the light, and some of them were activated during fixation of a particular object for manipulation. Therefore, these neurons were classified as visuo-motor neurons (Sakata *et al*., 1995). Other neurons in AIP (motor-dominant neurons) were activated by movements in the dark, without any visual or tactile component. Since activity in these motor-related neurons showed selectivity for particular patterns of hand movement (Murata *et al*., 2000), it was suggested that this activity might be related to the efference copy of the motor programs that are received from the motor association cortex (Jeannerod *et al*., 1995). Area F5 in the ventral premotor cortex, is related to precise hand movements and has strong reciprocal connections with area AIP (Matelli *et al*., 1986; Luppino *et al*., 1999).

Area CIP

Several neuroimaging studies have revealed a hemispheric lateralization of activation during axis orientation and surface orientation discrimination tasks in humans. In a PET study of size and orientation discrimination, activation was evoked in the posterior part of the right IPS (Faillenot *et al*., 1999). Another fMRI study, using visual object and grating discrimination, activated the caudal part of the left IPS (Faillenot *et al*., 2001), whereas perception of the structure of a surface based on shading, activated the caudal part of the right IPS (Taira *et al*., 2001). In our previous study of surface orientation discrimination, we found significant CIP activation in both hemispheres (Shikata *et al*., 2001). However, it is also known that the right parietal cortex is more involved in visuo-spatial information processing, whereas the left parietal cortex plays a greater role in visuo-motor integration. Activation of left CIP has also been reported for 3D object discrimination by tactile manipulation in the absence of visual guidance (Jäncke *et al*., 2001). Therefore, it is possible that human CIP shows a hemispheric specialization.

Other imaging studies have reported motion and direction sensitivity of areas in the posterior part of the IPS (Shulman *et al*., 1999; Sunaert *et al*., 1999) and activation of the posterior part of the IPS in the context of visuo-spatial attention (Vandenberghe *et al*., 1996; Nobre *et al*., 1997, 2000; Corbetta *et al*., 1998, 2000; Gitelman *et al*., 1999; Hopfinger *et al*., 2000). However, it remains unclear whether all these activations include area CIP. Our visual stimulus was identical in all four conditions, therefore in the orientation discrimination task and colour discrimination conditions, we can exclude the possibility that motion sensitivity or motor components activated CIP. With respect to attention, some studies have reported activation close to CIP (Corbetta *et al*., 1998, 2000; Vandenberghe *et al*., 1996; Gitelman *et al*., 1999; Hopfinger *et al*., 2000; Nobre *et al*., 2000). It is possible that attention can modulate activation in the posterior part of IPS. However, it is unlikely, that spatial attentional shifts are different in the four conditions used here.

Similar activation patterns for all four conditions (three tasks including surface orientation discrimination component and even in colour discrimination task) were observed in the middle part of the IPS. The obvious difference is seen in the activation patterns between posterior part of IPS and middle part of IPS. It is thus possible that the middle part of the IPS is related to spatial attention more than the posterior part, where we suspected the homologue of CIP in humans.

In general

Concerning the functional relationship between AIP and CIP in humans, Faillenot *et al*. (2001) postulated that the anterior part of the IPS might be more important for performing orientation discrimination than the more posterior regions from lesion reviews. In contrary to their suggestion, our previous study suggested that it is the posterior part of IPS that is primarily involved in orientation discrimination (Shikata *et al*., 2001). In this study on surface orientation discrimination we observed a strong modulation of CIP by performance, i.e. a stronger activation in those trials in which the subject performed correctly. Only a weak modulation by performance was observed in the anterior part of the right IPS. Using surface discrimination from shading (which is one of depth cue in the perception of surface orientation) task, Taira *et al*. (2001) also reported that the activation in right posterior part of IPS was specific for this task not in anterior part of IPS.

We conclude therefore that the function of human area CIP is more involved in coding 3D features of the objects, whereas human AIP is more involved in visually guided hand movements, similar as in the monkey.

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Abbreviations

AIP, anterior part of the intraparietal sulcus; CIP, caudal part of the intraparietal sulcus; IPS, intraparietal sulcus.

References

Binkofski, F., Buccino, G., Posse, S., Seitz, R.J., Rizzolatti, G. & Freund, H.-J. (1999) A fronto-parietal circuit for object manipulation in man: evidence from an fMRI study. *Eur. J. Neurosci.*, **11**, 3276–3286.

Binkofski, F., Dohle, C., Posse, S., Stephan, K.M., Hefter, H., Seitz, R.J. & Freund, H.-J. (1998) Human anterior intraparietal area subserves prehension. *Neurology*, **50**, 1253–1259.

Corbetta, M., Akvudak, E., Conturo, T.E., Snyder, A.Z., Ollinger, J.M., Drury, H.A., Linenweber, M.R., Petersen, S.E., Raichle, M.E., Van Essen, D.C. & Shulman, G.L. (1998) A common network of functional areas for attention and eye movements. *Neuron*, **21**, 761–773.

Corbetta, M., Kincade, J.M., Ollinger, J.M., McAvoy, M.P. & Shulman, G.L. (2000) Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neurosci.*, **3**, 292–297.

Evans, A.C., Kambar, M., Collins, D.L. & MacDonald, D. (1994) An MRI-based probabilistic atlas of neuroanatomy. In Shorvon, S., Fish, D., Anermann, H., Bydder, G.M. & Stafan, H. (eds), *Magnetic Resonance Scanning and Epilepsy*. Plenum, New York, pp. 263–274.

Faillenot, I., Decety, J. & Jeannerod, M. (1999) Human brain activity related to the perception of spatial features of objects. *Neuroimage*, **10**, 114–124.

Faillenot, I., Sunaert, S., Van Hecke, P. & Orban, G.A. (2001) Orientation discrimination of objects and gratings compared: an fMRI study. *Eur. J. Neurosci.*, **13**, 585–596.

Faillenot, I., Toni, I., Decety, J., Grégoire, M.C. & Jeannerod, M. (1997) Visual pathways for object-oriented action and object recognition. Functional anatomy with PET. *Cereb. Cortex*, **7**, 77–85.

Friston, K.J., Ashburner, J., Frith, C.D., Poline, J.-B., Heather, J.D. & Frackowiak, R.S.J. (1995a) Spatial registration and normalization of images. *Hum. Brain Map.*, **2**, 1–25.

Friston, K.J., Holmes, A.P., Worsley, K.P., Poline, J.-B., Frith, C.D. & Frackowiak, R.S.J. (1995b) Statistical parametric maps in functional imaging: a general linear approach. *Hum. Brain Map.*, **2**, 189–210.

Gitelman, D.R., Nobre, A.C., Parrish, T.B., LaBar, K.S., Kim, Y.-H., Meyer, J.R. & Mesulam, M.-M. (1999) A large-scale distributed network for covert spatial attention. *Brain*, **122**, 1093–1106.

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.

Hopfinger, J.B., Buonovore, M.H. & Mangun, G.R. (2000) The neural mechanisms of top-down attentional control. *Nature Neurosci.*, **3**, 284–291.

Jäncke, L., Kleinschmidt, A., Mirzazade, S., Shah, N.J. & Freund, H.-J. (2001) The rule of the inferior parietal cortex in linking the tactile perception and manual construction of object shapes. *Cereb. Cortex*, **11**, 114–121.

Jeannerod, M. (1986) The formation of finger grip during prehension. A cortically mediated visuomotor pattern. *Behav. Brain Res.*, **19**, 99–116.

Jeannerod, M., Arbib, M.A., Rizzolatti, G. & Sakata, H. (1995) Grasping objects the cortical mechanisms of visuomotor transformation. *Trends Neurosci.*, **18**, 314–320.

Jeannerod, M., Decety, J. & Michel, F. (1994) Impairment of grasping movements following a bilateral posterior parietal lesion. *Neuropsychologia*, **32**, 369–380.

Kusunoki, M., Tanaka, Y., Ohtsuka, H., Ishiyama, K. & Sakata, H. (1993) Selectivity of the parietal visual neurons in the axis orientation of objects in space. *Soc. Neurosci. Abstr.*, **19**, 770.

Luppino, G., Murata, A., Govoni, P. & Matelli, M. (1999) Largely segregated parietofrontal connections linking rostral intraparietal cortex (area AIP and VIP) and the ventral premotor cortex (areas F5 and F4). *Exp. Brain Res.*, **128**, 181–187.

Matelli, M., Camarda, R., Glickstein, M. & Rizzolatti, G. (1986) Afferent and efferent projections of the inferior area 6 in the macaque monkey. *J. Comp. Neurol.*, **251**, 281–298.

Murata, A., Gallese, V., Luppino, G., Kaseda, M. & Sakata, H. (2000) Selectivity for the shape, size, and orientation of objects for grasping in neurons of monkey parietal area AIP. *J. Neurophysiol.*, **83**, 2580–2601.

Nobre, A.C., Gitelman, D.R., Dias, E.C. & Mesulam, M.M. (2000) Covert visual spatial orienting and saccades: overlapping neural systems. *Neuroimge*, **11**, 210–216.

Nobre, A.C., Sebestyen, G.N., Gitelman, D.R., Mesulam, M.M., Frackowiak, R.S.J. & Frith, C.D. (1997) Functional localization of the system for visuospatial attention using positron emission tomography. *Brain*, **120**, 515–533.

Sakata, H., Taira, M., Kusunoki, M., Murata, A., Tanaka, Y. & Tsutsui, K. (1998) Neural coding of 3D features of objects for hand action in the parietal cortex of the monkey. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, **353**, 1363–1373.

Sakata, H., Taira, M., Murata, A. & Mine, S. (1995) Neural mechanisms of visual guidance of hand action in the parietal cortex of the monkey. *Cereb. Cortex*, **5**, 429–438.

Shikata, E., Hanzei, F., Glauche, V., Knab, R., Dettmers, C., Weiller, C. & Büchel, C. (2001) Surface orientation discrimination activated caudal and anterior intraparietal sulcus in humans: an event-related fMRI study. *J. Neurophysiol.*, **85**, 1309–1313.

Shikata, E., Tanaka, Y., Nakamura, H., Taira, M. & Sakata, H. (1996) Selectivity of the parietal visual neurons in 3D orientation of surface of stereoscopic stimuli. *Neuroreport*, **7**, 2385–2394.

Shulman, G.L., Ollinger, J.M., Akbudak, E., Conturo, T.E., Snyder, A.Z., Petersen, S.E. & Corbetta, M. (1999) Areas involved in encoding and applying directional expectations to moving objects. *J. Neurosci.*, **19**, 9480–9496.

Sunaert, S., Van Hecke, P., Marchal, G. & Orban, G.A. (1999) Motion-responsive regions of the human brain. *Exp. Brain Res.*, **127**, 355–370.

Taira, M., Kawashima, R., Inoue, K. & Fukuda, H. (1998) A PET study for axis orientation discrimination. *Neuroreport*, **9**, 283–288.

Taira, M., Mine, S., Georgopoulos, A.P., Murata, A. & Sakata, H. (1990) Parietal cortex neurons of the monkey related to the visual guidance of hand movement. *Exp. Brain Res.*, **83**, 29–36.

Taira, M., Nose, I., Inoue, K. & Tsutusi, K. (2001) Cortical areas related to attention to 3D surface structures based on shading: an fMRI study. *Neuroimage*, **14**, 959–956.

Taira, M., Tsutsui, K.I., Jiang, M., Yara, K. & Sakata, H. (2000) Parietal neurons represent surface orientation from the gradient of binocular disparity. *J. Neurophysiol.*, **83**, 3140–3146.

Talairach, P. & Tournoux, J.A. (1988) *Stereotactic Coplanar Atlas of the Human Brain*. Thieme Stuttgart.

Tsutsui, K., Jiang, M., Yara, K., Sakata, H. & Taira, M. (2001) Integration of Perspective and Disparity Cues in Surface-Orientation-Selective Neurons of Area CIP. *J. Neurophysiol.*, **86**, 2856–2867.

Tsutsui, K.I., Sakata, H., Naganuma, T. & Taira, M. (2002) Neural correlates for perception of 3D surface orientation from texture gradient. *Science*, **298**, 409–412.

Vandenberghe, R., Dupont, P., De Bruyn, B., Bormans, G., Michiels, J., Mortelmans, L. & Orban, G.A. (1996) The influence of stimulus location on the brain activation pattern in detection and orientation discrimination. A PET study of visual attention. *Brain.*, **119** (4), 1263–1276.

Worsley, K.J. & Friston, K.J. (1995) Analysis of fMRI time series revisited-again. *Neuroimage*, **2**, 173–181.