Surface Orientation Discrimination Activates Caudal and Anterior Intraparietal Sulcus in Humans: An Event-Related fMRI Study

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Shikata, Elisa, Farsin Hamzei, Volkmar Glauche, René Knab, Christian Dettmers, Cornelius Weiller, and Christian Büchel. Surface orientation discrimination activates caudal and anterior intraparietal sulcus in humans: an event-related fMRI study. *J Neurophysiol* 85: 1309–1314, 2001. Perception of surface orientation is an essential step for the reconstruction of the three-dimensional (3D) structure of an object. Human lesion and functional neuroimaging studies have demonstrated the importance of the parietal lobe in this task. In primate single-unit studies, neurons in the caudal part of the intraparietal sulcus (CIP) were found to be active during the extraction of surface orientation through monocular (two-dimensional) cues such as texture gradients and linear perspective as well as binocular (3D) cues such as disparity gradient and orientation disparity. We used event-related fMRI to study the functional neuroanatomy of surface orientation discrimination using stimuli with monocular depth cues in six volunteers. Both posterior (CIP) and anterior (AIP) areas within the intraparietal sulcus showed a stronger activation during surface orientation as compared with a control (color discrimination) task using identical stimuli. Furthermore, the signal changes in CIP showed a greater performance effect than those in AIP, suggesting that CIP is tightly linked to the discrimination task.

INTRODUCTION

For the perception of a three-dimensional shape of an object, it is necessary to represent the geometry of its surface (Gibson 1950; Marr 1982). There are several cues to discriminate surface orientation in depth, such as disparity gradient, velocity gradient, texture gradient, and linear perspective (Johnston and Passmor 1994). Cues for surface orientation discrimination are subdivided into binocular and monocular cues. Among different binocular cues for the representation of surface orientation, disparity gradient is the most crucial one (Howard and Rogers 1995). On the other hand, most important monocular cues for the three-dimensional orientation of a surface are texture gradients and linear perspectives (Gibson 1950).

In recent neurophysiological studies in the alert monkey, Shikata et al. (1996) found surface-orientation selective (SOS) neurons in the lateral bank of the caudal part of the intraparietal sulcus (area CIP). Most of them were found to be sensitive to binocular disparity gradients (Taira et al. 2000b). There are also studies demonstrating populations of neurons within CIP that responded to monocular texture gradient cues as well as to binocular disparity cues (Tsutsui et al. 1998).

Faillenot et al. (1999) investigated the functional neuroanatomy of three-dimensional (3D) surface orientation processing using positron emission tomography (PET) in humans. The stimuli used were flat polygons with binocular disparity and perspective cues. In that study, the right intraparietal sulcus and occipito-temporal junction were significantly activated by the 3D surface orientation and two-dimensional (2D) axis orientation discrimination task. Unfortunately, the coarse spatial resolution of PET group studies did not allow a finer anatomical characterization of the areas within the intraparietal sulcus. Taira et al. (1998) investigated the discrimination of 2D axis in a fronto-parallel plane with a reaching task. This study also included an orientation discrimination task, showing an increase of activation in the right intraparietal sulcus. Again the spatial resolution was limited in this PET study. Only recently a functional MRI study suggested that bilateral areas of the intraparietal sulcus are activated during the discrimination of convex and concave surfaces from shading cues without disparity (Taira et al. 2000a). This is one of the few studies employing monocular cues for surface orientation discrimination in depth.

In summary, it is still unclear which areas of the human parietal cortex are involved in the perception of surface orientation with monocular depth cues such as texture gradients. For this purpose, we designed an event-related fMRI study to investigate surface orientation discrimination in depth using texture gradients as monocular cues. In accord with our previous work in primates, we hypothesized the involvement of regions within the intraparietal sulcus in this task. We further tested the hypothesis that signal changes in these areas are correlated with performance.

METHODS

Subjects and visual stimuli

Six healthy, male volunteers (aged 29.5 ± 3.64) with normal visual function gave written informed consent to participate in this study. The texture elements consisted of black dots with a diameter of 0.33°

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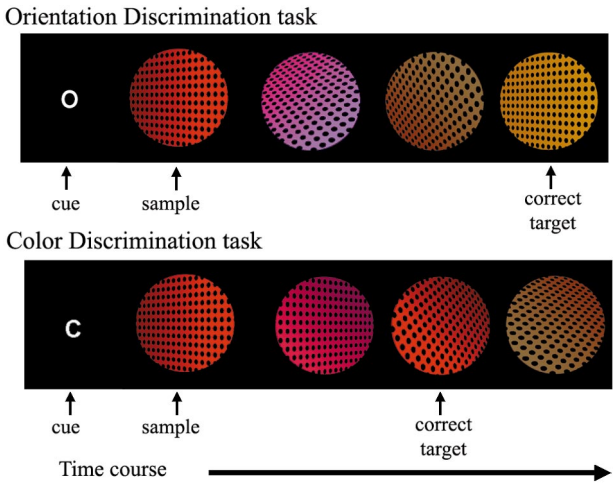

FIG. 1. Timeline of visual stimuli used in the study. Stimuli were presented in the center of the screen. The task was a delayed matching to sample task. After a cue stimulus, sample and test stimuli composed of dot textures were presented sequentially. Subjects were instructed to press a button as soon as the test stimulus with the required feature appeared.

in the fronto-parallel plane assembled into a perspective array. This plane was slanted 30 and 45°, creating a pair of stimuli. This pair was then rotated around the horizontal plane in 45° steps, resulting in 16 different orientations. The background of the texture was filled with nine different colors ranging from red to yellow. These texture stimuli were presented inside an 8°-diam aperture and appeared as if viewed through a round window. The combination of nine colors with 16 orientations resulted in 144 stimuli. A liquid crystal display video-projector back-projected the stimuli on a screen positioned on top of the head coil which was viewed by the subjects through a 45° mirror (10 × 15° field of view).

Task

Two different trial types, orientation and color discrimination, were tested in a delayed matching to sample task. Stimuli were identical for both trial types. Each trial began with a cue letter, indicating the type of the next trial. The letter 'O' indicated an orientation trial, the letter 'C' indicated a color trial. The cue was followed by a sample stimulus. After the sample stimulus, one to four test stimuli were presented. Subjects were instructed to fixate the cue stimulus in the center of the screen and hold their gaze in that position throughout the trial. They pressed a button when the test stimulus showed the same orientation or the same color as the sample stimulus. We were mainly interested in evoked hemodynamic responses during the period before subjects made a button press response indicating the correct test stimulus (Fig. 1). Therefore we presented more long trials in which the third or fourth sample stimulus was the target (2, 4, 13, and 16 trials of length 1–4 test stimuli). The short trials (1st or 2nd test stimulus correct) were used to deter subjects from adopting a strategy of ignoring the first few test stimuli. A total of 70 stimuli were presented.

The stimulus presentation time was 500 ms with a stimulus onset asynchrony randomized between 1,500 and 2,500 ms. The task sequence was controlled by a PC running the "Presentations" package (Neurobehavioral systems; http://www.neurobehavioralsystems.com).

Image acquisition

MR scanning was performed on a 1.5 T MRI scanner (Siemens Vision); 340 volumes (25 contiguous, axial, 3 mm thick slices each, 1 mm gap) were acquired using a gradient echo echo-planar (EPI) T2*-sensitive sequence (TR 2800 ms, TE 60 ms, FA 90 degrees, matrix 64*64, field of view 210*210 mm). The slices were oriented to cover the parietal cortex.

Image processing and statistical analysis

Image processing and statistical analysis were carried out using SPM99 (Friston et al. 1995c; Worsley and Friston 1995). All volumes were realigned to the first volume (Friston et al. 1995a), spatially normalized (Friston et al. 1995a) to a standard EPI template (Evans et al. 1994; Talairach and Tournoux 1988) and finally smoothed using a 6-mm full-width at half-maximum isotropic Gaussian kernel. Data analysis was performed by modeling the different trials ("color" and "orientation") as trains of delta functions convolved with a hemody-

TABLE 1. *Location and magnitude of activations*

	R				L			
Subject	Coordinate			*z* value	Coordinate			*z* value
Anterior part of IPS								
	x	*y*	*z*		*x*	*y*	*z*	
S1	58	−22	44	5.8*	−30	−40	50	6.9*
S2	40	−42	62	5.9*	−52	−30	50	5.8*
S3	50	−24	40	4.6†	−34	−50	48	6.7*
S4	46	−32	50	6.4*	−40	−34	42	6.4*
S5	42	−30	62	3.7†	−32	−42	50	5.8*
S6	36	−42	51	4.1†	−36	−42	42	5.0*
Mean location ± SD	45.3 ± 7.2	−32.0 ± 7.8	51.5 ± 8.3		−37.3 ± 7.3	−39.6 ± 6.4	47.0 ± 3.6	
Group modulation	36	−33	39	2.4	—	—	—	—
Posterior part of IPS								
	x	*y*	*z*		*x*	*y*	*z*	
S1	10	−72	58	7.8*	−8	−62	62	7.5*
S2	20	−74	60	5.8*	−12	−76	56	6.0*
S3	26	−66	56	4.8*	−20	−70	62	5.9*
S4	20	−66	56	5.5*	−20	−62	54	7.8*
S5	22	−56	60	3.1†	−16	−62	56	4.6†
S6	—	—	—	—	−18	−75	51	4.7†
Mean location ± SD	19.6 ± 5.3	−66.8 ± 6.3	58 ± 1.8		−15.7 ± 4.43	−67.8 ± 6.1	56.8 ± 4.0	
Group modulation	6	−60	63	3.0†	−12	−57	60	3.0†

z values are given for the maxima. Group modulation indicates the location in which a significantly higher signal was observed when a trial was performed correctly. IPS, intraparietal sulcus; R, right; L, left. * $P < 0.05$, corrected. † $P < 0.001$, uncorrected.

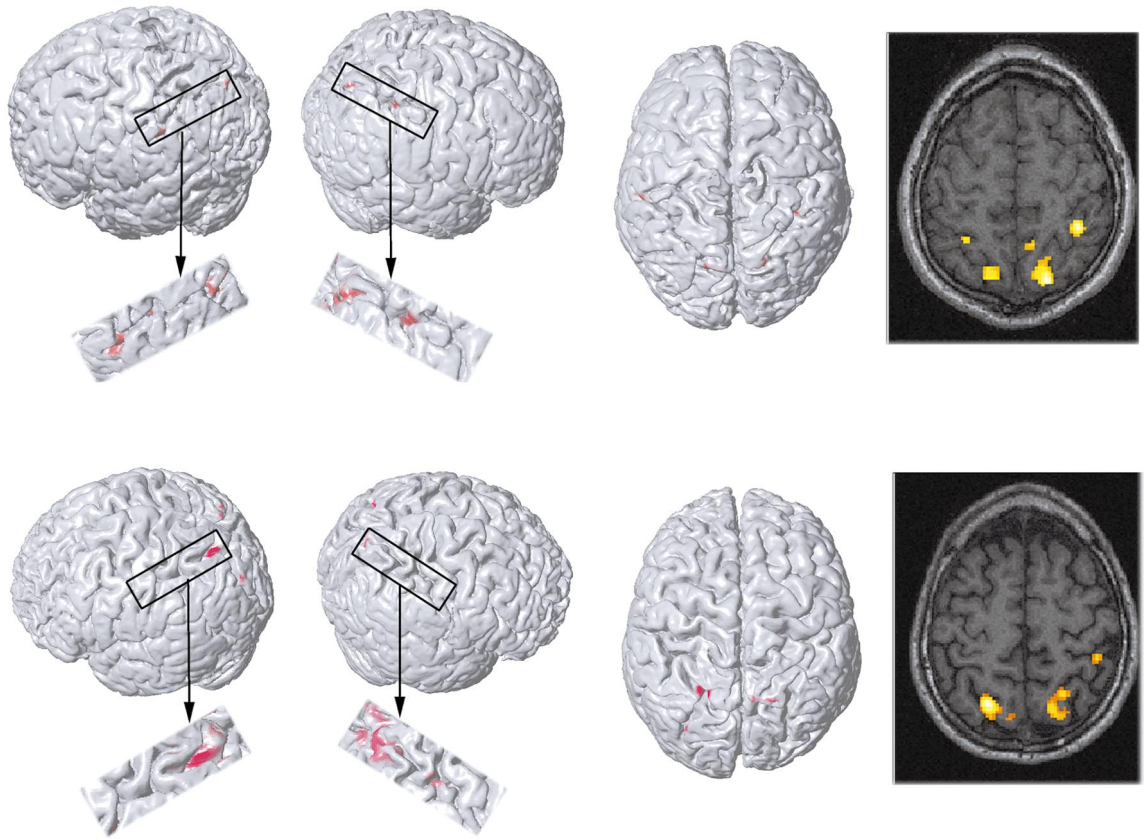

FIG. 2. Activated regions in 2 individual subjects for surface orientation vs. color discrimination. Significant activations ($P < 0.05$ corrected) are rendered on individual brain surfaces. Activations were confined to the intraparietal sulcus (IPS). The detailed image shows an enlargement of the IPS with activations thresholded at $P < 0.001$, uncorrected. On the right, activations of posterior and anterior IPS are overlayed on an axial slice ($P < 0.05$, corrected). Slices are at $z = 60$ and $z = 54$ mm. No activation was seen between these 2 areas.

namic response function (HRF). An event-related approach was necessary because the stimulus onset asynchrony was randomized and not constant. Furthermore the event-related approach allowed us to model the motor responses (i.e., button presses) that served as a control for stimulus timing accuracy. To account for residual onset latency differences, an additional regressor was created by convolving the same delta functions with the partial derivative of the HRF with respect to time. Regression coefficients for all regressors were estimated using least squares within SPM99 (Friston et al. 1995b).

Specific effects were tested with appropriate linear contrasts of the parameter estimates for the HRF regressor of both trial types, resulting in a *t*-statistic for each and every voxel. These *t*-statistics constitute a statistical parametric map (SPM). SPMs are interpreted by referring to the probabilistic behavior of Gaussian random fields. Data were analyzed for each subject individually and for the group. The threshold adopted was $P < 0.05$ (corrected for multiple comparisons). However, we also report weaker activations where appropriate. The color discrimination task served as a control for visual input and task difficulty. In a group analysis, we tested the hypothesis that the level of activity in areas defined by the contrast of interest is related to task performance. We therefore split up the "discrimination" trials into trials with correct and incorrect responses and compared the evoked signals.

For display purposes, a high-resolution ($1 \times 1 \times 1$ mm voxel size) structural MRI was acquired for each volunteer using a standard 3-D T1 weighted FLASH sequence. This structural volume was coregistered to the functional scans by normalizing it to a T1 template in the same space as the template used to normalize the functional data set. After co-registration with the functional data, the brain surface was triangularized to display activations of each individual subject on the individual 3D rendered brain.

RESULTS

Task performance

The rate of correct responses was higher (mean 78.15%; range 61.9–88.1%) for surface orientation discrimination than for color discrimination (mean 66.9%; range 54.2–79.1%). The average reaction time (RT) for both trial types was 664 ± 178 ms. RTs for orientation discrimination were slower (696 ± 178 ms) than for color discrimination trials (632 ± 172 ms).

Neuroimaging

Activations due to the motor response were confined to sensorimotor cortex and SMA, showing a peak at around 5 s after the button press. Our hypothesis mainly concerned areas within the intraparietal sulcus, which varies in size and position among volunteers. The full spatial resolution of fMRI can thus only be explored on the basis of single subject analyses.

Comparison of orientation vs. color discrimination

The comparison of orientation with color discrimination revealed significant areas of signal increases (activations) in the medial posterior part of the parietal cortex. Individual

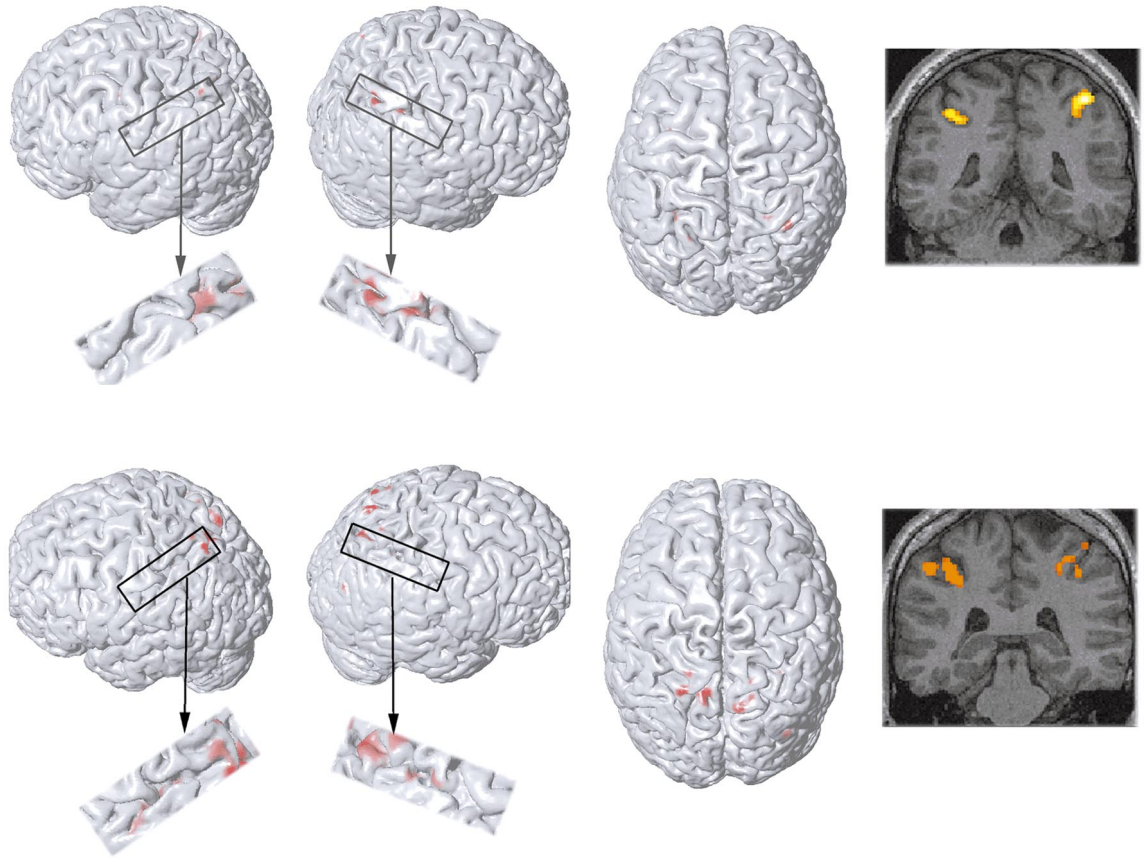

FIG. 3. Activated regions in 2 other subjects for surface orientation vs. color discrimination. Significant activations ($P < 0.05$, corrected) are rendered on individual brain surfaces. Activations were confined to the IPS. The detailed image shows an enlargement of the IPS with activations thresholded at $P < 0.001$, uncorrected. On the *right*, activations of the anterior IPS are overlayed on a coronal slice ($P < 0.05$, corrected). Coronal slices are at $y = -45$ and $y = -40$ mm.

analyses precisely located those activations to the posterior part of the intraparietal sulcus (IPS). Five of six subjects showed a bilateral activation in this region. One subject only showed activation in the left hemisphere. Table 1 shows the location according to the MNI template brain, the z statistic and P values.

All six subjects showed bilateral activations in the anterior part of the intraparietal sulcus. This activation was more medial and posterior-inferior to sensorimotor cortex (SMC; coordinate in mean ± SD: $x = -45.3 \pm 5.7$, $y = -29.3 \pm 5.1$, $z = 58.8 \pm 5.3$), as revealed by the single trial analysis of all button presses made by the subject during the experiment. The location and statistics are also summarized in Table 1. Notably, we found no activation in an area within the IPS between the described anterior and posterior activations. This area might correspond to the parietal eye field (PEF) involved in visually guided saccades and pursuit eye movement as described by Petit and Haxby in fMRI (1999).

Figure 2 shows the result of two subjects (*subjects S2* and *S4*). Significant activations ($P < 0.05$ corrected) are rendered on individual brain surfaces. The detailed image shows an enlargement of the IPS with activations thresholded at $P < 0.001$ uncorrected. On the right side of the figure, we overlaid activations on an axial slice showing activations of the posterior and anterior part of IPS ($P < 0.05$ corrected). Figure 3 shows the result of two other subjects (*subjects S3* and *S1*). Activation of the anterior part of the IPS ($P < 0.05$ corrected) are shown on the *right* side of the figure.

We also observed inconsistent activations outside the parietal cortex. One subject (*S1*) showed bilateral activations in bilateral inferior occipital gyri. In the temporal lobe, one subject (*S6*) showed activation in the left inferior temporal gyrus. Two subjects (*S1* and *S4*) showed activations in the precentral gyrus. One of them (*S1*) had bilateral activations, the other showed activation only on the right side.

Comparison of color vs. orientation discrimination

Two subjects revealed areas of significant signal increases (activations) in the left frontal cortex ($P < 0.05$ corrected). The other subjects showed no significant activations in the areas sampled.

Group analysis

The group analysis was used to determine whether areas showing an orientation discrimination-related activity show significantly more signal during correct trials when compared with incorrect trials. The most significant performance effect ($P < 0.05$, corrected for volume of main effect) was seen in the posterior intraparietal area. A weaker modulation was also observed in the anterior intraparietal region on the right (Table 1).

DISCUSSION

We have shown that surface orientation discrimination in depth with monocular cues activates circumscribed structures in the parietal cortex in humans. Using single-subject analyses, we were able to precisely locate these activations to a posterior and anterior region within the intraparietal sulcus. Furthermore, we found a significantly higher activation of bilateral posterior region and to a lesser degree of right anterior region in trials in which subjects performed the task correctly.

Performance in the control task (color discrimination) was less accurate than in the experimental task of orientation discrimination. When designing the stimuli, we had to take care that the experimental task was no more difficult than the control task. This is because several neuroimaging studies have shown activations related to task difficulty, which would be a confounding factor (Fiez et al. 1995). One possible explanation for the less accurate performance during the control task is the distracting brightness variation due to shading.

In area CIP, SOS neurons have been identified in the monkey (Shikata et al. 1996). These neurons responded preferentially to flat stimuli (square or disk) in a particular orientation defined by binocular disparity and perspective cues. Recently Taira et al. (2000b) reported that many SOS neurons were sensitive to the surface orientation defined by binocular disparity cues without perspective cues. There are also studies demonstrating populations of neurons within CIP that responded to monocular cues of texture gradient as well as to binocular disparity cues as mentioned above (Tsutsui et al. 1998). Our study clearly shows bilateral activation of an area in the posterior part of the IPS in humans that is related to the discrimination of surface orientation in depth by texture gradients. This result is consistent with data by Taira and colleagues, who found that discrimination of surface curvature from shading activated various intraparietal areas in a traditional blocked fMRI group study (Taira et al. 2000a). We suggest that this region in the posterior part of the human IPS corresponds to monkey CIP.

Furthermore we found another activation in a more anterior and lateral location. This area is within the anterior part of IPS and most likely corresponds to area AIP in the monkey in which neuronal activity is related to visually guided hand manipulations (Murata et al. 2000; Sakata et al. 1995). In a clinical study, a lesion of this area led to a deficit in correctly shaping the hand required to grasp an object (Binkofski et al. 1998). Some AIP neurons are highly selective for 3D geometrical objects such as a cube or plate during the fixation of the object in the absence of movements (Murata et al. 1996, 2000). Moreover, some of these neurons show selectivity for the orientation of the long axis or the surface of objects of different shapes. Our results are in accord with the hypothesis that hand-manipulation-related neurons in AIP are involved in coding object shape and/or orientation in three-dimensional space to match hand movements with 3D objects (Murata et al. 2000; Sakata et al. 1999).

Texture and color information are processed in the ventral ("what") visual pathway (Ungerleider and Mishkin 1982). Texture discrimination tasks in human fMRI studies have shown to activate areas in the ventral pathway (Beason-Held et al. 1998; Kastner et al. 2000). The lack of activation of the ventral system in our data could be related to the fact that the areas in question were outside the field of view.

In the hierarchy of visuo-spatial information processing within the dorsal stream (Ungerleider and Mishkin 1982), our results would suggest that CIP neurons represent surface orientation in depth. This information is then integrated into the 3D properties of objects coded in AIP, which projects to premotor cortex. This scenario is in accord with recent data showing that the dorsal stream is involved in processing information for hand movement and could be characterized as a "how" system (Goodale and Milner 1992; Goodale et al. 1991). In this context, it is interesting to note that Sakata and colleagues demonstrated that in the dorsal stream 3D features of objects are processed separately from their position (Sakata et al. 1997). The hypothesis that orientation discrimination per se is mainly a property of the posterior area (CIP) is further supported by a stronger positive modulation of the signal in this area by performance compared with AIP. This correlation between behavior and BOLD signal changes suggests a major involvement of this area in the task.

Our data demonstrate that surface-orientation discrimination from monocular stimuli involves discrete areas within the posterior and anterior intraparietal sulcus in humans. A stronger modulation of the posterior intraparietal area (CIP) by performance suggests that this area is primarily related to orientation discrimination whereas the more anterior area (AIP) lies en route to the premotor cortex and is involved in the integration of orientation information into a representation of 3D shape of objects.

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