Neural Correlates of Spontaneous Direction Reversals in Ambiguous Apparent Visual Motion

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Looking at bistable visual stimuli, the observer experiences striking transitions between two competing percepts while the physical stimulus remains the same. Using functional imaging techniques, it is therefore possible to isolate neural correlates of perceptual changes that are independent of the low-level aspects of the stimulus. Previous experiments have demonstrated distributed activations in human extrastriate visual cortex related to switches between competing percepts. Here we asked where extrastriate responses still occur with a bistable stimulus that minimizes the cognitive difference between the two percepts. We used the “spinning wheel illusion,” a bistable apparent motion stimulus of which both possible percepts correspond to the same object, share the same center, and are perceived as identically patterned stimuli moving at the same speed and changing only in direction. Using functional magnetic resonance imaging, we analyzed the spatial distribution of event-related activations occurring during spontaneous reversals of perceived direction of motion. In accordance with earlier neuroimaging findings for bistable percepts, we observed event-related activations in several frontal and parietal areas, including the superior parietal cortex bilaterally, the right inferior parietal cortex, and the premotor and inferior frontal cortex of both hemispheres. Furthermore, we found bilateral activations in the occipitotemporal junction (hMT+/V5) and in the lateral occipital sulcus (“KO”) posterior to hMT+/V5, but not in areas of the “ventral stream” of cortical visual processing. Our data suggest that, while a frontoparietal network subserves more general aspects in bistable visual perception, the activations in functionally specialized extrastriate visual cortex are highly category- or attribute-specific.

Key Words: functional magnetic resonance imaging; human visual cortex; perceptual rivalry; bistable percepts; apparent motion.

INTRODUCTION

To identify neural activity related to changes in perceptual awareness, one needs to show that these correlations are not simply the consequence of concomitant physical changes in stimulation (Frith et al., 1999; Rees, 2001). An experimental approach to isolate neural activity related to conscious perception from that related to physical stimulus properties is the use of stimuli evoking bistable perception, a situation in which perceptual awareness changes while sensory stimulation remains constant. When bistable visual stimuli are viewed continuously, perception alternates between two possible interpretations of the visual input. Paradigms using bistable visual stimuli have been applied in studies with awake reporting nonhuman primates (Leopold and Logothetis, 1996) and more recently in functional neuroimaging studies of the human brain (Kleinschmidt et al., 1998; Lumer et al., 1998; Tong et al., 1998). While the study by Tong et al. used binocular rivalry to identify differential activity in predefined areas during one or the other stable dominant percept (house/face), Lumer et al. and Kleinschmidt et al. focused on the neural activity associated with transitions between alternative percepts using binocular rivalry and classical ambiguous figures, respectively. In these latter two studies, the two competing percepts pertained to two different categories (e.g., moving grating/face, vase/face) or to different exemplars within a given category (e.g., young/old woman). This means that each switch was perceptually multidimensional, involving categorical changes along with spatial attention shifts. Hence, the interpretation of the related distributed brain activations in visual association cortex remained difficult as these could signal either nonspecifically that a change occurred or specifically what types of change occurred.

For the experiment reported here, we therefore chose a perceptually unidimensional ambiguity, the spinning wheel illusion in visual-motion perception (see www.illusionworks.com, “The spinner”). As opposed to binocular rivalry, this paradigm uses a single visual stim-
ulus allowing two different perceptual interpretations rather than a dichoptic discrepancy with two dissimilar images competing for perceptual dominance. The spinning wheel illusion is generated by presenting in alternation two frames showing wheels that are offset to each other by half the interspoke angular distance, resulting in a bistable apparent motion stimulus (see Fig. 1A) (Wertheimer, 1912). Both possible percepts correspond to the same object and share the same spatial extent and center. They are perceived as identically patterned stimuli moving at the same speed and changing only in direction. The spinning wheel illusion may be closely related to the “wagon wheel effect,” an illusion of reverse rotation when viewing real motion of a spoke wheel that is stroboscopically flashed (Finlay et al., 1984; Finlay and Dodwell, 1987). Recent evidence suggests that real motion is coded in discrete time quanta (Purves et al., 1996; Ramirez et al., 2000), making a common mechanism underlying the two phenomena likely.

As opposed to other ambiguities, the cognitive difference between the two percepts is minimized in the case of the spinning wheel. We could hence study whether the activations in extrastriate cortices during perceptual switches of a single attribute occur selectively in those visual areas that are sensitive to this attribute within a sensory stimulus. According to the perceptual content (motion direction) of switches with the spinning wheel, we hypothesized that activations would be localized in the area commonly referred to as the human motion complex (hMT+/V5). This brain region has been shown to be activated by continuous motion perception and direction changes of visual motion stimuli (Ahlfors et al., 1999; Cornette et al., 1998; Morrone et al., 2000) as well as during apparent motion perception and motion imagery (Goebel et al., 1998). This would be different from the fusiform activations observed in previous studies on bistable perception, the latter then presumably being related to categorical changes. At the same time, we hypothesized that even with a perceptually sparse ambiguity such as the spinning wheel we would still observe switch-related responses in a similar frontoparietal network as in the aforementioned studies (Kleinschmidt et al., 1998; Lumer et al., 1998).

**METHODS**

**Subjects**

Ten right-handed subjects (three females and seven males) with normal or corrected-to-normal vision participated in the functional imaging experiment. None had any history of significant medical, neurologic, or psychiatric disease. Their mean age was 29.3 ± 5.1 years. Subjects were initially selected on the basis of performance in a behavioral experiment (see below) prior to imaging. All subjects gave written informed consent before the experiment.

**MR Imaging Procedure**

We performed functional magnetic resonance imaging (fMRI) using a 1.5-T scanner with gradient booster and standard head coil (Siemens Vision, Erlangen, Germany), obtaining a structural (T1-weighted) scan.
and then a series of blood-oxygenation-sensitive (T2*-weighted) echo-planar image volumes every 4.1 s (echo time 40 ms; 18 contiguous transverse slices, voxel size $1.7 \times 1.7 \times 6.25 \text{mm}^3$). To minimize head motion, subjects were restrained with bitemporal pressure pads. During the functional imaging procedure, subjects looked at the ambiguous apparent motion stimulus which was projected onto a screen located 3 m from their eyes outside the scanner and viewed via a mirror attached above the head coil.

The stimulus consisted of a modified version of the spinning wheel as it had been described by Wertheimer (1912), an annulus of a white radial grating on a black background including a central fixation point (Fig. 1A). The radial grating was sinusoidally modulated (12 cycles/360°) between 61 and 9 cd/m$^2$ (= background luminance) and the outer and inner radius of the annulus were 60 and 57 min, respectively, of visual angle (see Fig. 1). Two frames with identical annuli that were offset to each other by half a cycle of sinusoidal modulation were presented for 90 ms each. Between these two frames a uniformly gray annulus (19 cd/m$^2$) was shown for 45 ms. This sequence yielded the perception of a spinning wheel moving with the same speed either clockwise or counterclockwise, both respective directions of circular motion being mutually exclusive.

Subjects were instructed to maintain fixation on the central point and to indicate direction changes by right index key presses. Since preceding offline eye movement recordings (see below) revealed that good fixation could be maintained only for approximately 2 min during this effortful task, the MR scanning sessions were divided into eight short subsessions of 123 s (30 image volumes) duration with short breaks in between, but without removing subjects from the scanner. Stimuli were displayed and key presses registered online using ERTS (Experimental Run Time System, Version 3.18, 1996; J. Beringer, Germany) on a Pentium-based personal computer. Since we were interested not only in activations in posterior parts of the brain, but also in frontal, and especially in prefrontal, regions, online eye movement recordings were precluded due to image artifacts that our current system would have induced. We therefore obtained eye movement recordings in offline sessions using an infrared eye tracker with a sampling rate of 100 Hz (Ober 2 digital eye movement registration system; Permobil Meditech, Timra, Sweden) under identical conditions while subjects reported their percepts during rivalry. Significant eye movements (>0.5° of visual angle) occurred with a frequency of less than 0.1 Hz and were not systematically related to perceptual switches. Comparing the frequency of eye movements during periswitch time spans of both ±1 s and ±200 ms with their frequency during periods of stable perception, we found no significant increase in eye movements around perceptual switches (t test, $P < 0.05$). In addition, subjects were chosen for imaging only if they could clearly distinguish between the two percepts without experiencing further percepts (e.g., flickering) and if at least some percept epochs lasted for more than 10 s. Even though perceptual transitions occurred at a higher frequency most of the time, this criterion was applied in order to achieve a high enough variability of interreversal time spans (see $\gamma$ distribution in Fig. 1B) to allow for an event-related analysis similar to randomized experimental designs with rapid presentation rates (Burock et al., 1998; Josephs and Henson, 1999).

### MR Imaging Data Analysis

The fMRI data were analyzed using the statistical parametric mapping (SPM99) software (Welcome Department of Cognitive Neurology, London, UK; www.fil.ion.ucl.ac.uk/spm) running under the MATLAB environment (Mathworks, Inc., Sherborn, MA). After removal of the first five scans, all functional images were realigned to the first of the remaining volumes. Subsequently, they were spatially normalized into standardized neuroanatomical space (Talairach and Tournoux, 1988) and smoothed using an 8-mm full width at half-maximum Gaussian kernel. Using the analytical technique of event-related fMRI (Josephs and Henson, 1999; Josephs et al., 1997), the evoked hemodynamic responses to all perceptual switches as indicated by key-presses were modeled as delta functions convolved with a synthetic hemodynamic response function, in the context of the general linear model used by SPM99. We removed low-frequency fluctuations by a high-pass filter with a cut-off at 90 s. Since the focus of this experiment was neither to examine the neural activity during alternating periods of stable motion perception (i.e., clockwise or counterclockwise rotation) nor to differentiate between the two possible directions of switches, all perceptual switches were modeled in a single condition independent of their respective direction. This procedure resulted in statistical parametric maps of the t statistic for every voxel showing activations or deactivations during switches relative to the interswitch baseline. A fixed-effects model was applied and statistical inferences were corrected for multiple nonindependent comparisons by using Gaussian random field theory (Friston et al., 1995). Responses were considered significant at $P < 0.05$, corrected, and alternatively at $P < 0.001$, uncorrected, if predicted by previous findings or our current hypothesis or in case of a response in the homologous contralateral area at $P < 0.05$, corrected.

### RESULTS

#### Behavioral Results

All subjects confirmed after scanning that they had experienced perceptual alternations between both pos-
sible directions of motion and that they had been able to clearly determine and report these transitions. Interreversal time spans between perceptual switches, i.e., the durations of the two percepts, followed gamma distributions (Fig. 1B) as has been previously described for bistable percepts (Borsellino et al., 1972, 1982; Kelso et al., 1995; Scotto et al., 1990). The mean duration of stable unidirectional circular motion perception across subjects was $4.70 \pm 2.69$ s (standard deviation). The variance of mean percept durations between subjects was small ($4.88 \pm 0.98$ s).

**Imaging Data**

The rationale of our experimental design is based on the fact that the two possible perceptual interpretations of apparent motion produced by the spinning wheel illusion differ only in direction of motion (clockwise or counterclockwise) and not in any other quality such as speed of motion, spatial distribution, or object category or exemplar. The only experimental parameter of interest in our study was therefore the neural activity related to spontaneously occurring switches irrespective of their direction. In separate analyses, we found no differential response to the two alternating percepts. Table 1 lists stereotactic coordinates (Talairach and Tournoux, 1988) of the voxels with the highest significance levels within regional clusters of activation during perceptual switches.

In accordance with our hypothesis, we found responses in extrastriate visual cortex, most prominently in the occipitotemporal junction, corresponding to hMT+/V5 bilaterally (Figs. 2A, 2B, and 3) (Tootell et al., 1995b; Watson et al., 1993). Another site of activation, about 15 mm posterior to, and obviously distinct from, area hMT+/V5 (Fig. 2A), was found in the lateral occipital sulcus of both hemispheres, putatively corresponding to a region that has been previously described as the “kinetic occipital” (KO) area (Dupont et al., 1997; Van Oostende et al., 1997). At a threshold of $P < 0.001$, uncorrected, no significant activations were detected at locations corresponding to early visual areas (V1, V2, V3) or to V3A, an area that has been found to respond to visual motion stimuli (Tootell et al., 1997) and seems to play an important role in directing attention to visual motion (Büchel et al., 1998; Chawlala et al., 1999).

Note. ACL, anterior cerebellar lobe; FEF, frontal eye field; FO, frontal operculum; hMT+/V5, human motion complex; IPL, inferior parietal lobe; IPLL, inferior parietal lobule; IPS, intraparietal sulcus; KO, kinetic occipital area; LOS, lateral occipital sulcus; OTJ, occipitotemporal junction; PCG, precen tract gyrus; PCS, precentral sulcus; SPL, superior parietal lobe; TPJ, temporoparietal junction; VLPFC, ventrolateral prefrontal cortex.

* $P < 0.001$, uncorrected.

In accordance with previous imaging studies using bistable percepts, we observed event-related activations in several frontal and parietal areas (Table 1). Parietal activations were found in the anterior intraparietal sulcus (IPS) close to its junction with the postcentral sulcus bilaterally (Figs. 2A and 2C), but with a higher level of significance in the left hemisphere, and in the superior parietal lobule (SPL, Fig. 2B) bilaterally. In addition, we observed event-related activations in the inferior parietal lobe (IPL), specifically in the right inferior parietal lobule (IPLL), and at the temporoparietal junction (TPJ) near the posterior end of the superior temporal sulcus of both hemispheres (Fig. 2A). Frontal activations were observed in the region of the frontal opercula bilaterally with a higher level of significance in the right hemisphere and in the right ventrolateral prefrontal cortex (VLPFC, Figs. 2A and 2D). Perceptual switches were also associated with bilateral activations in the precen tract sulcus, corresponding to the human frontal eye fields (FEF) (Paus,

**TABLE 1**

Activations during Perceptual Switches at $P < 0.05$, Corrected

<table>
<thead>
<tr>
<th>Coordinates</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Z score</th>
</tr>
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<tbody>
<tr>
<td>Frontal</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FO</td>
<td>54</td>
<td>14</td>
<td>−2</td>
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<tr>
<td></td>
<td>−58</td>
<td>6</td>
<td>2</td>
<td>5.08</td>
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<tr>
<td>Right VLPFC</td>
<td>42</td>
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<td>4</td>
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</tr>
<tr>
<td>Left PCG</td>
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<td>−8</td>
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<td>9.36</td>
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<tr>
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<td>0</td>
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<td>7.53</td>
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<tr>
<td>PCS (FEF)</td>
<td>38</td>
<td>0</td>
<td>60</td>
<td>5.31</td>
</tr>
<tr>
<td></td>
<td>−32</td>
<td>4</td>
<td>66</td>
<td>7.57</td>
</tr>
<tr>
<td>Parietal</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>IPS</td>
<td>44</td>
<td>−42</td>
<td>60</td>
<td>5.34</td>
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<td></td>
<td>−38</td>
<td>−42</td>
<td>66</td>
<td>7.33</td>
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<tr>
<td>IPL</td>
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<tr>
<td>Right IPLL</td>
<td>58</td>
<td>−34</td>
<td>48</td>
<td>4.44*</td>
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<tr>
<td>TPJ</td>
<td>60</td>
<td>−30</td>
<td>20</td>
<td>4.88</td>
</tr>
<tr>
<td></td>
<td>−54</td>
<td>−22</td>
<td>18</td>
<td>4.39*</td>
</tr>
<tr>
<td>SPL</td>
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<td>−62</td>
<td>64</td>
<td>5.25</td>
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<tr>
<td></td>
<td>12</td>
<td>−66</td>
<td>56</td>
<td>4.71*</td>
</tr>
<tr>
<td>Occipital</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>OTJ (hMT+/V5)</td>
<td>54</td>
<td>−66</td>
<td>−4</td>
<td>5.71</td>
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<tr>
<td></td>
<td>−46</td>
<td>−66</td>
<td>4</td>
<td>5.55</td>
</tr>
<tr>
<td>LOS (KO)</td>
<td>42</td>
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<td>0</td>
<td>5.57</td>
</tr>
<tr>
<td></td>
<td>−44</td>
<td>−80</td>
<td>2</td>
<td>5.55</td>
</tr>
<tr>
<td>Cerebellum</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ACL</td>
<td>32</td>
<td>−56</td>
<td>−24</td>
<td>5.88</td>
</tr>
<tr>
<td></td>
<td>−28</td>
<td>−66</td>
<td>−24</td>
<td>5.18</td>
</tr>
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</table>
1996), which raises the concern that these activations could be due to reversal-related eye movements (Fig. 2A). Offline oculography, however, showed no evidence for an association of eye movements and perceptual switches. In addition, we found no deactivations in striate visual cortex (VI), where neuronal activity (Duffy and Burchfield, 1975) as well as regional cerebral blood flow and blood oxygenation level (Paus et al., 1995; Wenzel et al., 2000) have been shown to decrease during saccadic eye movements.

Additional transient activations were found in a pattern consistent with the preparation and execution of motor reports by the right hand as reported by others (Lumer et al., 1998). Activated areas include anterior cingulate cortex, left primary motor cortex in the region of the “hand knob” (Yousry et al., 1997), the corresponding region in the left primary sensorimotor cortex, and the hand area of the cerebellum bilaterally (Cui et al., 2000; Luft et al., 1998; Nitschke et al., 1996) with a higher level of significance in the ipsilateral cerebellar hemisphere.

DISCUSSION

In previous neuroimaging studies on brain activity related to visual ambiguity, the two percepts evoked in alternation differed in both spatial configuration and categorical and/or exemplar identity. One study using binocular rivalry found that perceptual dominance correlated with activity levels in areas with categorical preference for either faces or places (Tong et al., 1998). Another study employed two percepts for which a functional segregation might also be expected, e.g., human motion complex (hMT+/V5) activation during the perception of a moving grating and fusiform activation during face perception (Lumer et al., 1998). Yet, short percept durations and category-dependent differences between these durations did not allow the clear separation of switch- and percept-related activations. Employing an event-related analysis, these authors reported fusiform but not occipitotemporal activations occurring with every switch irrespective of its direction. Finally, Kleinschmidt et al. (1998) also specifically addressed switch-related activations. To that purpose, they deliberately reduced categorical differences between the two percepts that might evoke sustained differential processing and thus used classical ambiguities involving faces, bodies, and objects. They also found switch-related activations in the fusiform gyrus, along with frontoparietal activations in line with Lumer et al. (1998). Even in this experimental setting, however, what is perceived by the subject undergoes a profound change of content or meaning with each perceptual switch. Our current findings suggest that this change of perceptual content accounts for the fusiform activations observed in those earlier studies.

Here, we used a bistable visual motion stimulus in which the only difference between the two percepts is the perceived direction of motion of an otherwise identical spinning wheel. This bistability was achieved by using a stimulus generating apparent circular motion of ambiguous direction. Hence, two possible percepts rival and perceptual dominance undergoes spontaneous changes. The activation of frontoparietal cortices we observed during such switches is in line with previous work (Kleinschmidt et al., 1998; Lumer et al., 1998). Activations in extrastriate visual cortex, however, were found in motion-sensitive areas, namely in hMT+/V5 and KO, but not in areas of the “ventral stream.” Fusiform activations in previous studies may therefore be accounted for by changes between or within categories of object percepts preferentially processed in the ventral stream. In the present study, however, the perceived object remained the same and perceptual switches were characterized by a change in just one specific object attribute (direction of motion). This indicates that activity in visual associative areas during perceptual reversals is highly attribute-specific.

Changes in the direction of visual motion are a salient feature in visual information. However, data on neuronal activity related to direction changes in human visual motion are still relatively sparse. A positron emission tomography study by Cornette et al. did not find significant responses specifically to changes in the direction of motion (Cornette et al., 1998). In a combined magnetoencephalography and fMRI study, responses were found in hMT+/V5, in the superior temporal sulcus, in the FEF, and, to a lesser extent, in V3A and V1/2 during sudden changes in motion direction (Ahlfors et al., 1999). A recent fMRI study demonstrated a selective response in a subregion of hMT+/V5 to flow stimuli gradually changing direction as opposed to constant flow (Morrone et al., 2000). To our knowledge, however, the present study is the

**FIG. 2.** Event-related activations during perceptual reversals. (A) Lateral view of the right hemisphere of a T1-weighted anatomical template image with superimposed areas of activation determined in a group analysis. (P = 0.05, corrected). Coronal sections show activations in SPL, OTJ (hMT+/V5), and cerebellum bilaterally (B), in IPS (C), and in the anterior cingulate and FO (D) bilaterally (P = 0.001, uncorrected). The significance levels (Z scores) are color-coded as indicated in the color bars. FO, frontal operculum; IPS, intraparietal sulcus; LOS, lateral occipital sulcus; OTJ, occipitotemporal junction; PCS, precentral sulcus; TPJ, temporoparietal junction; VLPFC, ventrolateral prefrontal cortex.

**FIG. 3.** Peristimulus time histogram of the response (% signal change) at x = 54, y = −66, z = −4 (right hMT+/V5) averaged across all subjects (± standard error). Data are shown over twice the mean percept duration.
first to demonstrate transient activations in the human motion complex in response to perceived sudden changes in motion direction using event-related fMRI. As a possible explanation for neuronal activity in hMT+V5 during direction changes—no matter whether they are "real" or apparent, as in the present study—one might suspect an adaptation of motion-sensitive neurons during continuous visual motion stimulation that is followed by an increase in activity when motion direction changes. There is electrophysiological evidence from single-cell studies in nonhuman primates that both motion onset and abrupt changes in flow trajectory are followed by peaks in the response of MSTd neurons (Duffy and Wurtz, 1997; Paolini et al., 2000). Accordingly, a recent fMRI study in monkeys demonstrated an adaptation of the of BOLD response in motion-sensitive areas during unidirectional rotation of a visual motion stimulus, whereas sudden direction changes were followed by a peak in the BOLD response (Tolias et al., 2001). This rebound response was particularly strong in the middle temporal area (MT). We assume that, in analogy to the direction selectivity of neurons in the MT of the monkey (Maunsell and van Essen, 1983; Zeki, 1974), separate neuronal populations encode the different motion directions and that at switches, one of these displays a transient rise in activity. This assumption is supported by the observation that fMRI measurements of neural activity in hMT+V5 correlate with spiking activity in MT in monkeys (Heeger et al., 1999; Rees et al., 2000). In a more general context, the good correspondence between activity in hMT+V5 and the observed perceptual experience of motion is in accordance with earlier reports on apparent motion and motion imagery (Goebel et al., 1998), motion opponency (Heeger et al., 1999), and illusory motion (Tootell et al., 1995a; Zeki et al., 1993). Together, these studies suggest a correlation of neural activity in this region with more global aspects of motion perception in the visual scene, going beyond the detailed information contained in the physiological composition of visual stimuli.

In addition to the "classical" motion area hMT+V5 at the occipitotemporal junction, we found activations in a posteriorly adjacent region that by virtue of localization should correspond to what has been called the KO. This region has been shown to process both shape and motion information, the conjunction of which is typically present in kinetic contours (Dupont et al., 1997; Van Oostende et al., 1997). The fact that we observed activity in this area might be related to the nature of our stimulus which, in contrast to commonly used motion stimuli such as random dot fields or gratings, evokes the impression of a moving object contour in front of a stationary background.

Apart from attribute-specific activations that point to a high degree of functional specialization in extra-striate visual areas, we observed activations in distributed higher order areas that are in broad agreement with earlier findings. We found superior parietal activations in the SPL and the IPS bilaterally that, together with the activations in the FEF, are very similar to what is commonly referred to as the frontoparietal network for visuospatial attention (Corbetta, 1998; Posner and Petersen, 1990). Tonic attention as well as shifting attention activates a similar network including precentral frontal areas and parietal regions, namely along the postcentral and intraparietal sulci (Corbetta et al., 1993; Nobre et al., 1997; Vandenberghe et al., 1996, 1997). A recent fMRI study investigating the neural correlates of the detection of changes in the sensory environment showed activations in the superior parietal lobe associated specifically with visual changes (Downar et al., 2000). Whether the bilateral frontoparietal activations observed in the present study reflect spontaneous attentional fluctuations that might slightly precede or even elicit perceptual reversals or whether this is a repercussion of the salience associated with the reversals cannot be resolved by hemodynamic signals.

In addition to the bilateral frontoparietal network described, we identified a more ventral and predominantly right-sided frontoparietal activation pattern including the IPL and the frontal opercula. Within the IPL, we identified two subfoci of activation, one in the IPLL of the right hemisphere and a more ventral one at the TPJ bilaterally, which reached a higher level of significance in the right hemisphere. Furthermore, reversal-related activations were prominent in the frontal opercula, again with a higher level of significance and larger extent in the right hemisphere. Taken together, the right-lateralized inferior parietal and frontal opercular activations are largely congruent with those suggested to be related to the process of attentional selection (Lumer et al., 1998).

Further frontal activations associated with perceptual reversals occurred in the anterior cingulate and the right VLPFC. Like those in the left precentral gyrus and the right more than the left anterior cingulate lobe, anterior cingulate activations in our study can readily be ascribed to the preparation and execution of motor responses. However, they could also—at least in part—be due to the perception of changes. Responses in this region have been observed not only in the above-mentioned study by Downar et al. (2000) in which motor responses were not part of the task, but also in a study on binocular rivalry by Lumer et al., even after activity related to motor responses was subtracted using a "replay" control condition (Lumer et al., 1998). In addition, anterior cingulate cortex seems to be engaged in making and monitoring decisions (Liddle et al., 2001). It is therefore conceivable that, compared to periods of stable perception, a short-lasting uncertainty regarding motion direction during switches contributed the anterior cingulate activation. The same
explanation could hold for activation in the VLPFC, which has been shown to be recruited by a variety of cognitive demands, including working memory, but also executive tasks (Duncan and Owen, 2000). For instance, tasks involving decision-making, such as guessing, response conflict, or perceptual difficulty, have been shown to activate regions in the VLPFC similar to the one observed in our study (Barch et al., 1997; Elliott et al., 1999; Grady et al., 1996).

In conclusion, we have identified neural correlates of unpredictable endogenous, as opposed to externally induced, changes in visual-motion perception. The distribution of activations we observed during perceptual reversals suggests an intimate linkage of higher order and specialized sensory processes in bistable perception. In parallel with previous work on bistable visual perception, we found a frontoparietal network that presumably subserves more general aspects in visual perception such as attentional selection and processing of perceived salience. In contrast, no event-related activations in specialized motion-sensitive areas. This latter finding indicates that perceived changes of the visual input are represented in activity patterns of functionally specialized extrastriate visual cortex in a highly attribute-specific fashion. It also points to the fact that in these areas the neural processes underlying or recruited by perceptual changes overlap with those that occur in response to actual physical changes in the environment.

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REFERENCES


