

Human brain activity during spontaneously reversing perception of ambiguous figures

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Looking at ambiguous figures results in rivalry with spontaneous alternation between two percepts. Using event-related functional magnetic resonance imaging, we localized transient human brain activity changes during perceptual reversals. Activation occurred in ventral occipital and intraparietal higher-order visual areas, deactivation in primary visual cortex and the pulvinar. Thus, without any physical stimulus changes, salient perceptual flips briefly engage widely separated specialized cortical areas, but are also associated with intermittent activity breakdown in structures putatively maintaining perceptual stability. Together, the dynamics of integrative perceptual experience are reflected in rapid spatially differentiated activity modulation within a cooperative set of neural structures.

Keywords: visual system; human brain; perceptual rivalry; bistable percepts; visual awareness; functional magnetic resonance imaging

1. INTRODUCTION

It has been difficult to study the human cerebral correlates of object perception because neuronal processing is sensitive to changes in stimulus properties. To dissociate perceptual from stimulus-driven mechanisms, cognitive neuroscientists have used stimuli that generate bistable percepts such as ambiguous figures or dichoptic stimulation with different monocular views. When performed continuously such stimulation results in perceptual rivalry between equally legal but mutually exclusive interpretations of the visual input (Gregory 1998; Sheinberg & Logothetis 1997). An observer can only be aware of one of the two incompatible percepts at any given moment, but over time experiences striking spontaneous reversals ('flips') between the two percepts.

In the present study, we defined the neural correlates of flips in visual perception by asking human observers to look at ambiguous figures (figure 1) during functional magnetic resonance imaging (fMRI). Correlated activity can be identified because, with bistable percepts but a constant physical stimulus, it is isolated from stimulus-driven activity in the afferent pathways. The subjects were instructed to repetitively report their conscious experience of the visual scene by key-presses, defining the occurrence of perceptual reversals and the presence of stable percepts. This experimental design allowed us to generate a comparison of interest that was matched for the behavioural report within the real-time sequence of perceptual fluctuations and thus to tag brain processes related to visual perception.

We hypothesized that during these perceptual transitions we would observe bilateral activations reflecting the bihemispheric cooperation for full-field stimuli, and that these would occur in ventral occipital (Farah 1990;

Logothetis & Sheinberg 1996; Wallis & Rolls 1997; Malach *et al.* 1995; Dolan *et al.* 1997), and also in parietal areas implicated in higher-order visual processing, object perception, and visual awareness (Milner 1995; Treisman & Kanwisher 1998). We further hypothesized that with such stimuli the activity changes would be transient, and thus parallel the salience experienced during perceptual reversals but differ from percept-related steady-state activity. To dissociate reversal-related responses from those reflecting preference for the dominant percept we chose ambiguous figures with little categorical difference between the two possible percepts. Finally, the bidirectional perceptual significance of transitions between two percepts, which include a 'pop-out' and also a 'drop-out' phenomenon, led us to explore the data for the occurrence of deactivations during reversals relative to perceptual stability.

2. METHODS

Data were acquired from six healthy subjects (with written, informed consent; two females, four males, age range 23–33 years), by using a 2T magnetic resonance imager (Siemens Vision, Erlangen, head coil), obtaining a structural (T_1 -weighted) scan, and then a series of blood-oxygenation-sensitive (T_2^* -weighted) echoplanar image volumes every 2.3 s (175 image volumes, 6.7 min duration, image repetition time/echo time = 80.7/40 ms; 24 parallel oblique transverse slices, voxel size = 3 mm × 3 mm × 5 mm). Prior to each scanning series, subjects started looking at one ambiguous figure (from a set of four halftone black-and-white pictures), covering approximately 8° × 8° of the visual field and including a central fixation cross. Inter-reversal time-spans for these bistable percepts, whilst individually variable, follow gamma distributions (figure 1) with parameters that depend on stimulus type, visual field coverage and fixation (Borsellino *et al.* 1982; Scotto *et al.* 1990). In our experiment, appropriate visual field coverage and fixation of a

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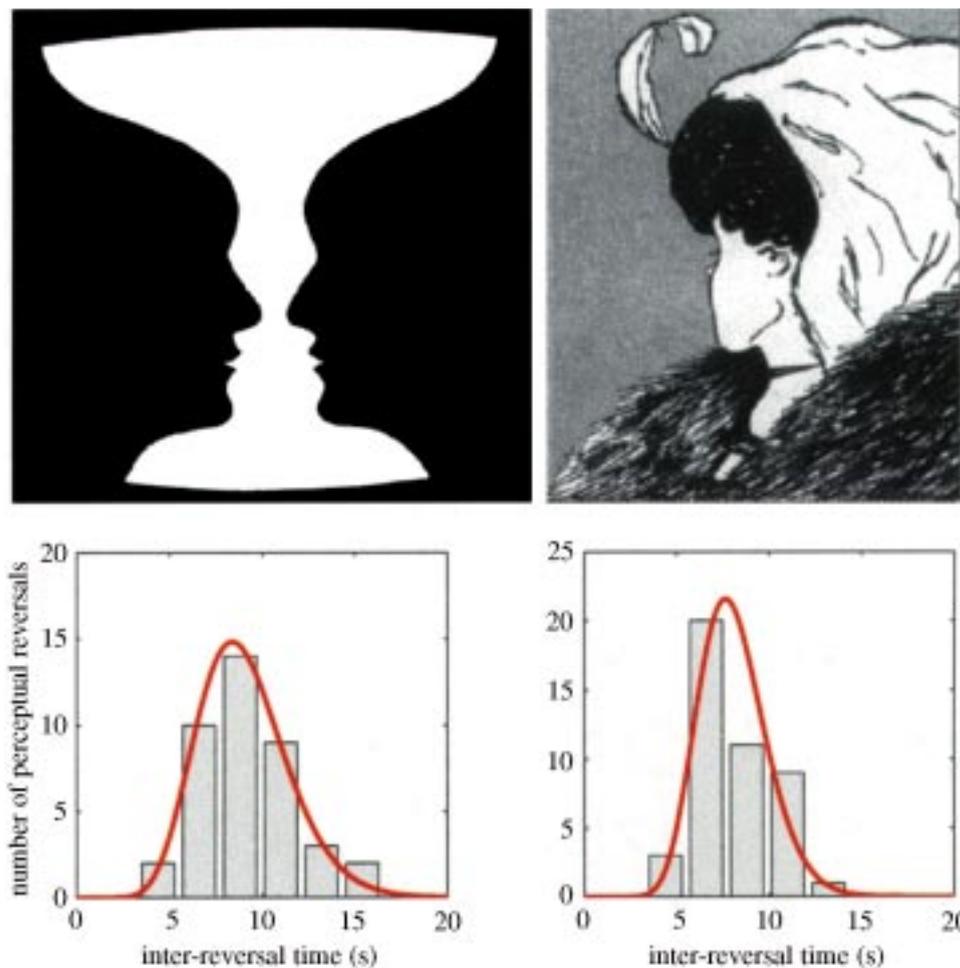


Figure 1. Ambiguous figures and their bistable perception. The vase–profile illusion (top left) was introduced to psychology by E. Rubin in 1915, the ‘my wife and mother-in-law’ illusion (top right) by R. W. Leeper and E. G. Boring in 1930. Both have their origins in older popular art, the Rubin figure in the 18th century, the Boring figure in the 19th century. Below, the distributions of inter-reversal times (left: 9.0 ± 2.6 s, right: 8.1 ± 1.9 s, bin width 2.3 s, i.e. equivalent to image volume sampling rate) are shown from one of the participating subjects. These are approximated by gamma functions (red, parameters left 13.7/0.7, and right 19.4/0.4).

central cross resulted in low enough reversal rates (figure 1) to discriminate separate events, despite the temporal low-pass filter characteristic of the haemodynamic responses monitored by imaging (Friston *et al.* 1995; Josephs *et al.* 1997). A convention linked right- and left-hand key-presses to indicate one or other of the two possible directions of perceptual transitions. After reporting a transition, subjects performed a second key-press with the identical hand while the ensuing percept was stable. They were instructed to maintain fixation on a central cross throughout scanning. From the reports we derived four classes of time-point, i.e. event, two indicating reversals in one or other of the directions and two locked to one or other stable percept.

The data set acquired for this study comprised 100 800 functional images. For analysis, all image volumes were realigned to the first volume, corrected for motion artefact, coregistered with the subjects’ corresponding anatomical (T_1 -weighted) images, normalized into standard stereotactic space (template provided courtesy of the Montreal Neurological Institute), and smoothed using a 12 mm full-width-at-half-maximum Gaussian, kernel. The analytical technique of event-related fMRI, as performed in this laboratory (Josephs *et al.* 1997), models the evoked haemodynamic responses for events (key-presses) as delta functions convolved with a synthetic haemodynamic response function, in the context of the general linear model

used by statistical parametric mapping SPM97. We removed low-frequency fluctuations by a high-pass filter with a cut-off at 60 s. We tested statistically for differential brain responses between separate event classes. The comparisons of interest were performed by contrasting the events indicating a perceptual reversal with those reporting a stable percept, thus removing any motor executive component common to both event types. This procedure resulted in two statistical parametric maps of the t -statistic for every voxel showing activations and deactivations during flips relative to stable percepts, respectively. Statistical inferences were corrected for multiple non-independent comparisons by using Gaussian random-field theory (Friston *et al.* 1995).

3. RESULTS

Contrasting perceptual reversals with perceptual stability, our first analysis determined regions that transiently increase activity during flips. We found responses in prestriate visual cortical areas, most prominently in bilateral ventral occipital cortex (middle fusiform gyrus) and posterior intraparietal cortex (figure 2), as well as in other occipital and some frontal areas (table 1), but not in sensorimotor cortices. The occurrence of bilateral

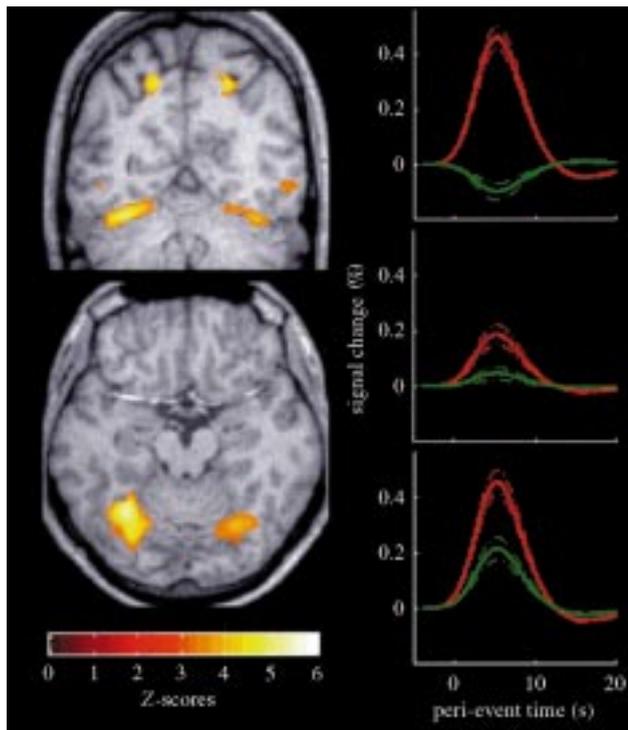


Figure 2. Activations during perceptual reversals. Statistical parametric maps (left) showing areas with transient activity increases in the group analysis (six subjects, 100 800 images). Activations were thresholded at $p < 0.001$, colour-coded, and superimposed onto a coronal section (top) and a transverse section (bottom) of one structural data set (intersectioned at the fusiform response maximum). Reader's left is subjects' left. The findings reflect the relative difference between event-related responses to the two event classes (reversal versus stable percept). The response functions in the right fusiform gyrus modelled for events indicating perceptual reversal (red) and stable percept (green) are shown from three subjects (right-side panel). In the context of their sequential natural occurrence, only their differential behaviour is meaningful, and not the estimates of their absolute time-courses.

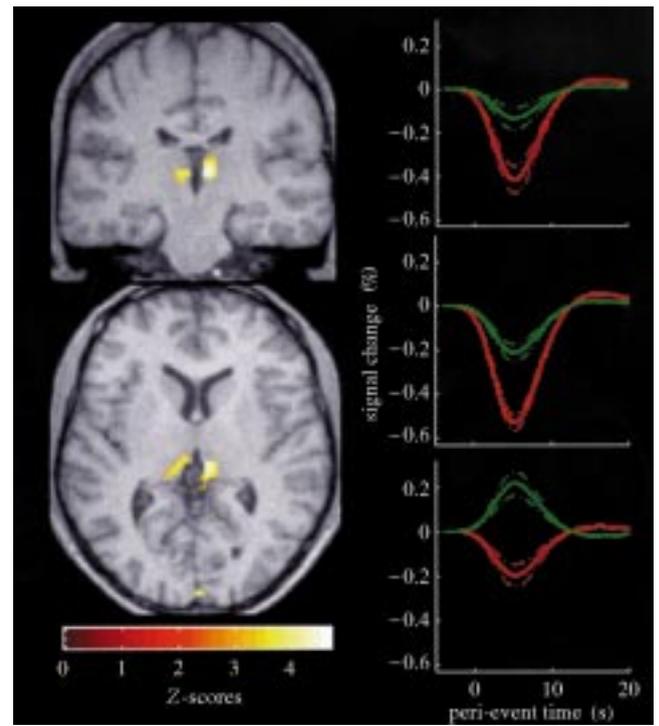


Figure 3. Deactivations during perceptual reversals. Statistical parametric maps (left) showing areas with transient activity decreases in the group analysis. Deactivations were thresholded at $p < 0.001$, colour-coded, and superimposed onto a coronal section (top) and a transverse section (bottom) of one structural data set (intersectioned at the thalamic response maximum). The findings reflect the opposite comparison as in figure 2, i.e. the location of greater event-related responses during a stable percept than during reversals. This is reflected in a contrary differential behaviour in the time-courses in these foci that were modelled for perceptual reversals (red) and stable percepts (green) and are shown from the right pulvinar for the same three subjects as in figure 2 (right-side panel).

Table 1. Stereotactic coordinates of areas that show differential behaviour when comparing events indicating perceptual reversals and stable percepts

| location | coordinates | | | Z-score |
|---|-------------|---------|---------|--------------|
| | x | y | z | |
| <i>(a) perceptual reversal > stable percept (activation)</i> | | | | |
| occipital | -33 | -54 | -21 | 6.1** |
| | 36,42 | -42,-51 | -27,-27 | 4.9**, 4.8** |
| parietal | -18 | -57 | 45 | 4.9** |
| | 21 | -60 | 48 | 4.9** |
| frontal | -57 | 12 | 9 | 5.0** |
| | 48 | 24 | 9 | 4.4* |
| | -30 | 0 | 42 | 4.9** |
| | 36 | 0 | 45 | 4.1* |
| <i>(b) perceptual reversal < stable percept (deactivation)</i> | | | | |
| occipital | 3 | -99 | 6 | 4.6** |
| thalamus | 9 | -24 | 9 | 4.7** |
| | -9 | -30 | 3 | 4.0* |
| cingulate | -3 | -42 | 27 | 4.7** |

* $p < 0.001$, uncorrected.
 ** $p < 0.05$, corrected.

ventral occipital and parietal responses is in line with our first hypothesis. These responses were localized to visual areas that have previously been functionally dissociated by different stimuli or tasks to show specialized processing of separate object characteristics (Haxby *et al.* 1991).

Frontal activations were located in ventral prefrontal areas and the frontal eye fields bilaterally (table 1). Under natural (unrestrained) viewing conditions, observers will usually perform orientating saccades during perceptual reversals according to the shifts in centres of interest, or will experience flips triggered by eye movements performed for scanning the image. One concern relative to frontal eye-field activation might therefore be that, despite instructions to fixate a central cross, these activations could reflect reversal-related eye movements. Since on-line electro-oculographic recordings were precluded by imaging-related artefacts, we addressed this confounding factor by off-line eye movement recordings in the scanner, i.e. under identical conditions of stimulus presentation. These recordings showed no reversal-related saccades. Additionally, the activity recorded in occipital areas post hoc does not suggest contamination by systematic gaze shifts (Burr *et al.* 1994). Thus, the

functional significance of these frontal responses must be interpreted as a correlate of covert shifts of spatial attention. From other functional neuroimaging studies (Nobre *et al.* 1997; Law *et al.* 1997), such a mechanism—that may include considerable efforts to suppress saccades—has been found to account for potent haemodynamic responses in frontal areas similar to those found during overt attentional shifts that are accompanied by saccades. In our experiment, although attentional shifts were inevitably associated with salient perceptual reversals, pretraining of subjects to fix continuously was effective in suppressing the reversal-related gaze shifts found in uninstructed observers.

Probing our final hypothesis, we found transient deactivations associated with perceptual reversals compared to stable percepts in several structures (table 1), most notably in calcarine cortex and the posterior thalamus (pulvinar complex) bilaterally (figure 3). Given the sequence of stable visual percepts alternating with spontaneous reversals, we interpret deactivations to indicate that activity during a stable percept, i.e. during maintained 'binding', is transiently disrupted during the 'de-' and 're-binding' associated with perceptual reversals. Hence, these findings suggest a crucial functional contribution of primary visual cortex to perceptual stability. This behaviour of 'early' visual cortex is sign-inverted to that in the 'late' stages of the two specialized visual pathways that displayed activity increases during perceptual reversals.

Similar to primary visual cortex, the pulvinar is, by virtue of massive interconnection, a key node in the visual system and displays complex response properties that combine sensitivity to different stimulus attributes (Benevento & Port 1995). However, it differs from primary visual cortex because beyond visual excitability its activity is more readily modulated by attentional mechanisms (Robinson & Petersen 1992; LaBerge 1995). These properties suggest a candidate role for the pulvinar in the integration of specialized visual processing subserving perception. From this perspective, the activity breakdown during a transition, i.e. when a meaningful percept is lost and a different one established, could reflect the temporary absence of a clear-cut winner in the rivalry between two percepts. Conversely, and in line with our finding, regained coherence of perceptual interpretation after such a transition could be associated with elevated activity levels.

4. DISCUSSION

Previous studies have emphasized functional segregation between separate visual pathways, rather than their integrative cooperation in the context of natural visual perception. Our findings, using ambiguous figures, provide an experimental demonstration of how these areas dynamically activate together when processing meaningful and relatively natural stimuli instead of experimentally isolated visual features. Functionally, this conjoint activation in ventral occipital and parietal areas can be understood to show that the reversal-related reinterpretation of an ambiguous figure—like the novel perception of any object in a visual scene—inevitably induces a perceived change in both categorical and spatial aspects.

Even if due to sensitivity limitations these activations represent only the 'tip of the iceberg' of transient activity

changes in the visual system during perceptual reversals, it is noteworthy that these activations occur across areas with considerably differing responsiveness to visual stimulus properties. When construing a hierarchical functional specialization in the primate visual system (Zeki 1978; Ungerleider & Mishkin 1982; Felleman & Van Essen 1991), these areas are not only very distinct from each other but they also represent quite advanced processing levels in the two separate pathways that preferentially process either categorical or spatial stimulus attributes. We conclude from this that the perceptual transitions, i.e. changes of meaning assigned to a (constant) stimulus, engage cortical activity most prominently in visual areas remote from multidimensional and elemental early processing but dedicated to specialized higher-order attributes of the scene viewed (Ungerleider & Mishkin 1982; Felleman & Van Essen 1991; Milner 1995; Treisman & Kanwisher 1998).

Conversely, since the actual visual input remained constant in our experiment, we expected no pronounced signal increase in early visual processing stages where activity is more rigidly locked to the afferent input. Mirroring the position of the ventral and parietal areas in a hierarchical view of the visual system, primary visual cortex is by far the most prominent target of retinogeniculate afferents and, as the dominant 'early' visual area, forms the shared cortical origin for processing multiple visual stimulus features and relaying them into divergent, functionally more specialized visual areas (Felleman & Van Essen 1991). We thus expected to find no activity increases in primary visual cortex during perceptual reversals but were surprised to find that activity there actually displayed transient decreases during flips.

The contribution of primary visual cortex to visual perception remains ill-defined. In primary visual cortex of strabismic cats exposed to discrepant monocular stimuli (binocular rivalry), it has been established that discharge synchronization levels, within non-overlapping neuronal populations, for the left or right eye change as a function of which percept dominates (Fries *et al.* 1997). It is a current matter of debate to which extent such changes of synchronization are reflected in overall mean synaptic activity rates as assessed by haemodynamic signals. In our study, we deliberately minimized the possibility of resolving the activity patterns related to either percept (avoiding the afferent inter-retinal conflict used in binocular rivalry and applying ambiguities with little categorical discrepancy) so as to maximize our sensitivity to the transitions between these. However, if there is a repercussion of percept-locked synchronization within neuronal subpopulations onto haemodynamic responses, it can be understood how activity breakdown could occur during transitions between percepts.

Other electrophysiological studies on binocular rivalry in non-human primates have mainly reported prefrontal percept-related signal changes (Sheinberg & Logothetis 1997). Recently, magnetoencephalographic recordings in humans exposed to binocular rivalry have revealed widespread changes of macroscopic electromagnetic surface activity as a function of perceptual dominance (Tononi *et al.* 1998). Furthermore, and again using binocular rivalry, a recent neuroimaging study in humans that focused on ventral areas with high-level

categorical response preferences, e.g. for faces or places, showed that activity levels in these ventral areas reflect which percept dominates (Tong *et al.* 1998). Together, all these studies used the very specific experimental paradigm of interocular conflict to generate perceptual rivalry out of dichoptic retinal image discrepancy instead of the ambiguities of actual scenes, as here. They thus established that neuronal response preferences cannot only be detected as a function of altered stimulus characteristics but also reproduced by alternating percepts when the stimulus is constant but discrepant for the two eyes.

Extending beyond this view of functional specialization, our study sought to address the dynamics of neural activity within distributed areas when processing perceptual ambiguity, rather than sustained response preferences among different areas that have already been successfully charted in previous studies. We therefore, in contrast to the aforementioned studies, not only chose stimuli with little categorical change between the two percepts (one face–object reversal, two face–body reversals, one face–face reversal), but also obtained two reports (appearance and presence) for each percept. We then performed a differential comparison between these two, thus matching for percept-related brain activity and isolating dynamic components. Finally, we made our result robust against category-related activity shifts by contrasting perceptual reversals in both directions with time-points locked to both percepts. This result cannot therefore be explained by differences in activity associated with differential categorical (or spatial) features of the two percepts. We found no differential activity comparing one direction of perceptual reversal with the other, or by comparing the two stable percepts. Hence, the dominant source of variance in our data is the fact that a perceptual change occurred and not which percept was available to awareness. In other words, our findings reflect the spontaneous appearance (and disappearance) rather than the specific presence of a percept. Confirming our hypotheses, we found this cognitive event to engage transiently multiple segregated visual areas that process different attributes of visual stimuli.

A recent study from this laboratory also found that in binocular rivalry haemodynamic responses during perceptual alternation are widely distributed and include occipital, parietal, and frontal areas (Lumer *et al.* 1998). More specifically, however, these activations were compared to those from a non-rivalrous alternation of the two different monocular views that mimicked the previously experienced sequence of fluctuating dominance of the two alternative percepts. Greater activity in the rivalry condition was observed in a right-sided frontoparietal network. These findings can be related to neural processes subserving attentional selection (provided the subjects experience no attentional set shift between the two conditions). Conversely, they remain limited in relating brain activity to changes in perception for two reasons: (i) in either of the two single conditions, the brain activity changes recorded pool the perceptual shift and the congruent behavioural report, as confirmed by prominent activations in several motor areas; (ii) when attempting to control for the motor response component by comparing rivalrous and non-rivalrous conditions, one inevitably also compares the identical perceptual sequences generated in the two conditions. Thus, the comparison of interest in that

study eliminated those signal changes related to perceptual alternation and focused on those related to the difference between the rivalrous and non-rivalrous conditions, i.e. to the processes of attentional selection.

In this study, we therefore did not compare identical reports of one cognitive situation (perceptual alternation) when using two different stimulation types (rivalrous and non-rivalrous). Instead, we used one stimulus (ambiguous picture) and obtained one type of behavioural report defined to tag two different cognitive situations (perceptual flip and stable percept). Our experimental design thus went beyond the aforementioned studies and disambiguated event (transition)- from state (percept)-related brain activity changes. Our findings allow for this discrimination because the reversals were temporally well-spaced and interleaved with periods of perceptual stability that were of comparable duration and induced percepts of similar categorical value, e.g. old woman and young woman. These experimental and behavioural characteristics were necessary because haemodynamic responses are sluggish and an imbalance between the mean duration of the two percepts could confound event-related responses to transitions with state-related responses during the briefer percept. This confound could be an important bias in the case when one percept was more powerful than the other, e.g. an object or face compared to a mere texture.

The distributed and transient bilateral activations we found to accompany these perceptual reversals occur in specific brain areas of ventral occipital and parietal cortex. In each of these areas, modulation of activity can be induced separately by directing attention to selective visual attributes (Corbetta *et al.* 1991; Haxby *et al.* 1994; Maunsell 1995). Attention in our paradigm, however, was not continuously directed to any type of attribute but modulated by fluctuation between two percepts, each of which comprises a set of attributes. In other words, the perceptual ambiguity of our stimuli meant that we were able to study endogenously emergent, as opposed to externally instructed and isolated, attentional modulation of brain activity. Saliency from percept appearance (and disappearance) is inevitably transient and bridges perceptual and attentional domains. With ambiguous figures, it is exclusively related to the subjects' visual awareness, in which stable figure–ground distinctions are only briefly disrupted during change from one percept to another. These reversals generate repetitive 'pop-out' (and 'drop-out') equivalents even though the stimulus remains unchanged. We therefore propose that the transient, event-like activity changes that we observed during perceptual flips parallel and may indeed form a substrate of perceived saliency.

The activation in the frontal eye fields is also compatible with this interpretation. The link between attention and gaze orientation, although dissociated by many experimental paradigms, including ours, is manifest in behaviour (Bowman *et al.* 1993; Sheliga *et al.* 1995) and implemented by a colocalized or even shared functional anatomy (Nobre *et al.* 1997; Corbetta 1998). The frontal eye fields play a key role in this system by virtue of their anatomical connections (Jouve *et al.* 1998) and integrate visual and attentional with oculomotor processes. Indeed, visual and attentional components have been shown to

activate this area in the absence of eye movements (Mohler *et al.* 1973; Burman & Segraves 1994; Bichot *et al.* 1996; Kodaka *et al.* 1997; Nobre *et al.* 1997; Law *et al.* 1997).

From this perspective, the distribution of activations during perceptual reversals confirms an intimate linkage of perceptual and attentional processes in the dynamic of metastable visual awareness. The activations observed cannot be attributed to stimulus-related influences determining perception or to task-related instruction directing attention. Specifically, we compared events that shared a motor response (key-press), and required continuous attention to the perceptual state (reversing or stable). Causality, or at least fine-scale temporal order, between these activations cannot be clarified in this setting. However, the interpretation that they could correspond to attentional processes inducing (instead of accompanying) perceptual reversals is unlikely or at least insufficient in the light of the strongly different response topography recently described by isolating attentional selection in perceptual rivalry (Lumer *et al.* 1998).

The responses in bilateral ventral occipital and parietal cortex may therefore be understood as an emergent activation, yet this could still be considered a rather non-specific activity gain occurring across all attentionally modulated structures that participate in visual information processing. However, the occurrence of a pulvinar (and posterior cingulate) deactivation, i.e. outside of specific visual cortices, reveals a more differentiated picture in which the activity modulation during perceptual flips differs regionally in sign and therefore, presumably, in functional significance.

In conclusion, we applied event-related functional neuroimaging to study unpredictable endogenous, as opposed to externally induced, changes of brain activity. Hence, we describe neural correlates of a type of visual awareness that manifests as brain-generated and consciously experienced perceptual changes that occur without change in sensory input. The transient activity fluctuations we find suggest that perceptual metastability elicited by ambiguous stimuli is associated with rapid redistributions of neural activity between separate specialized cortical and subcortical structures. The findings provide experimental evidence for cognitive models of visual perception that propose widespread cooperation between functionally distinct and spatially segregated cortical areas (Damasio 1989). These cortical processes display a dynamic interaction with activity in integrative subcortical structures (Olshausen *et al.* 1993) and together with these conjointly, but differentially, parallel perceptual experience.

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