84 Neural Correlates of Visual Consciousness in Humans

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ABSTRACT The immediacy and directness of conscious experience belies the complexity of the underlying neural mechanisms, which remain incompletely understood. This chapter focuses on the neural correlates of visual consciousness in humans. Activity in functionally specialized areas of ventral visual cortex is necessary for visual awareness, but recent evidence suggests that such activity may not be sufficient to support conscious vision without a contribution from parietal and prefrontal areas, reflecting processes such as selective attention and working memory. Reciprocal interactions between parietal and ventral visual cortex can serve to selectively integrate internal representations of visual events in the broader behavioral context in which they occur. Such network interactions may account for the richness of our conscious experience and may provide a fundamental neural substrate for visual consciousness.

We all have first-hand knowledge of what it is to be conscious, as opposed to not being conscious (for example, in deep dreamless sleep). When we are conscious, our experiences have specific phenomenal content, and when consciousness is absent, phenomenal content is also absent. During waking, the phenomenal content of our experience is constantly changing. Yet at the same time, our sense of self, of the person having the experience, remains constant. These phenomenal differences highlight a useful distinction between factors that influence the overall *level* of consciousness, those that determine its *content*, and those associated with *self-awareness*. The contents of consciousness can vary independently of the level of consciousness. Specific brain lesions can alter the contents of consciousness without having any effect on the level of consciousness. For example, lesions of the fusiform and lingual gyri can result in loss of awareness of color (achromatopsia) while the awareness of other aspects of the world remains normal (Verrey, 1888; Pearlman, Birch, and Meadows, 1979; Damasio, 1980). This chapter describes what is known about the neural correlates of the contents of consciousness in humans.

Questions about the neural correlates of the contents of consciousness are invariably questions about the relationship between mental representations and neural representations (Frith, Perry, and Lumer, 1999). It is generally accepted (though see O'Regan and Noe, 2001, for a contrasting view) that a neural representation of a particular feature or object is necessary for that feature or object to be present in consciousness. Some property of a neural population (for example, instantaneous spike rate or coherence) may encode a specific dimension of conscious visual experience. The search for neural correlates of consciousness is therefore a search for those neural populations and neural properties that encode a corresponding dimension of the contents of consciousness. It is assumed that a change in a mental representation of some phenomenal property entails a corresponding change in its neural representation, but the converse is not true: changes in neural representations may occur in the absence of changes in mental representations (Frith, Perry, and Lumer, 1999). Such an account necessarily eschews many philosophical debates (see Noe and Thompson, 2002) in favor of a pragmatic, empirical approach (Crick and Koch, 2003).

The neural correlates of the contents of consciousness have been studied most extensively in the visual system (Rees, Wojciulik, et al., 2002) and will be focused on here. The primate visual system is organized in a distributed and hierarchical fashion; in the monkey, different aspects of the visual scene are analyzed in different cortical areas (Zeki, 1978; Felleman and Van Essen, 1991). An organization into dorsal and ventral streams leading away from primary visual cortex is apparent (Ungerleider and Mishkin, 1982). In humans, the organization of visual cortex appears broadly similar to that in monkeys, including retinotopically mapped striate and extrastriate visual areas (Engel et al., 1994; Sereno et al., 1995; Brewer et al., 2002) with specific functional specializations (e.g., Zeki et al., 1991). However, there also appear to be differences in both overall organization and specific functional roles between human and macaque monkey visual cortex (Culham and Kanwisher, 2001), including substantial differences in the organization and relative size of parietal and prefrontal cortex. These differences should be borne in mind when comparing both the study of visual perception (Povinelli and Vonk, 2003) and physiological data (Tootell, Tsao, and Vanduffel, 2003) in human and nonhuman primates. This chapter will focus almost entirely on data from humans.

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Human primary visual cortex

Human primary visual cortex (V1) is located in the calcarine sulcus in occipital cortex (Henschen, 1893). Damage to this area leads to a circumscribed retinotopic visual field defect (scotoma) in which conscious perception of all visual attributes, including form, brightness, and contrast, is typically absent. There is a topographic mapping between field defects and the physical location of cortical damage (Inouye, 1909; Holmes and Lister, 1916), consistent with the retinotopic representation observed in monkeys (Hubel and Wiesel, 1968, 1974) that was subsequently revealed in humans by functional imaging (Engel et al., 1994; Sereno et al., 1995) and the distribution of phosphenes (perceived flashes of light) produced by direct electrical stimulation (Brindley and Lewin, 1968; Dobelle et al., 1979)

Within a scotoma, conscious perception of all visual properties, including brightness, contrast, and form, is lost, and cannot be induced in patients with striate lesions by transcranial magnetic stimulation (TMS) over ipsilesional extrastriate cortex (Cowey and Walsh, 2000). By comparison, phenomenal experience in the remainder of the visual field appears to be well preserved, although there may be subtle abnormalities detectable psychophysically (Rizzo and Robin, 1996). Some patients with primary visual cortex damage can show a surprising range of preserved abilities to detect and discriminate stimuli within a phenomenally blind scotoma. This ability, in the absence of awareness, has become known as blindsight (Weiskrantz, 1986). An apparently similar phenomenon, dissociating awareness and discrimination performance, can be seen with dichoptic displays in normal observers (Kolb and Braun, 1995), though this has not always been replicated (Morgan, Mason, and Solomon, 1997; Robichaud and Stelmach, 2003). These data suggest that intact primary visual cortex may be necessary for conscious awareness of brightness, contrast, and at least some aspects of form. However, whether altered awareness following damage to primary visual cortex reflects disruption of neural representations just in V1 itself, impaired onward passage of signals to extrastriate cortex, or altered feedback from extrastriate areas is unclear.

The relationship between neural representations in intact primary visual cortex and the contents of consciousness has been studied directly using functional imaging techniques (Rees, Kreiman, and Koch, 2002; Tong, 2003). Binocular rivalry provides a powerful experimental paradigm with which to study the neural correlates of visual awareness (e.g., Levelt, 1965; Leopold and Logothetis, 1999). When dissimilar images are presented to the two eyes, they compete for perceptual dominance. Each image may be visible in turn for a few seconds while the other is suppressed. Because perceptual transitions between each monocular view occur spontaneously without any change in the physical stimulus, neural correlates of consciousness may be distinguished from neural correlates attributable to stimulus characteristics. In nonhuman primates, most visually responsive neurons early in visual cortex show patterns of firing that mirror the stimulus, rather than the contents of consciousness. In contrast, human functional magnetic resonance imaging (fMRI) studies have shown quantitatively much stronger modulations of primary visual cortex. Over the whole of V1, fluctuations in activity during rivalry have been measured for monocular stimuli differing in contrast, and can be about half as large as those evoked by real stimulus alternation (Polonsky et al., 2000; Lee and Blake, 2002). In a region of primary visual cortex corresponding to the blind spot (a monocular representation corresponding to just the other eye), fluctuations during rivalry and physical stimulus alternations are approximately equal (Tong and Engel, 2001) (figure 84.1). Such an association between V1 activity (as measured with fMRI in humans) and visual experience is not restricted to bistable perception. In a contrast detection task, false alarms (i.e., incorrect reports of seeing a stimulus in its absence) evoke more activity in primary visual cortex than misses, despite the stimuli being physically identical (Ress and Heeger, 2003). Neuromagnetic responses localized to V1 correspond more closely to the perceived than the physical contrast of a briefly flashed stimulus (Haynes et al., 2003). Taken together, these data suggest that hemodynamic activity in human primary visual cortex (as measured with fMRI) can more closely reflect the contents of consciousness than the physical properties of the stimulus, at least for certain stimulus features (e.g., perceived brightness or contrast). However, the discrepancy between some monkey electrophysiological results, which show minimal perceptual modulation among V1 or V2 cells during binocular rivalry (Leopold and Logothetis, 1996), and the corresponding human fMRI results, with strong perceptual modulation in V1, remains to be resolved. Such an understanding will depend on the exact relationship between spiking activity in cortical neurons and the corresponding fMRI blood-oxygen-level-dependent (BOLD) activity (see Logothetis, this volume).

Necessity and sufficiency of striate cortex activity

The data discussed in the previous section could be taken to suggest that when certain visual features are represented in consciousness, activity is present in primary visual cortex. However, awareness of other stimulus features appears possible even when V1 is damaged. Some patients with blindsight seem to have residual impressions of salient moving stimuli (Riddoch, 1917; Barbur et al., 1993; Stoerig and Barth, 2001), and one such patient has awareness of visual afterimages despite his inability to perceive the original adapting stimulus (Weiskrantz, Cowey, and Hodinott-Hill,

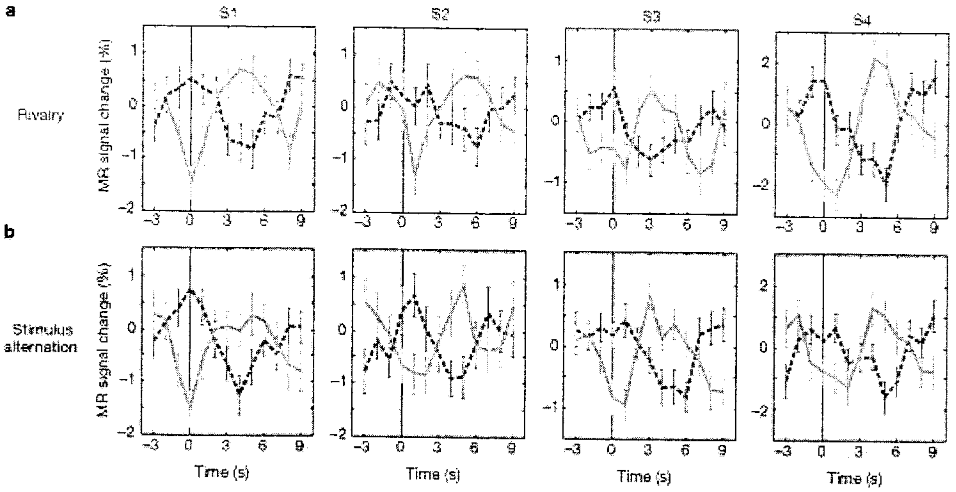


FIGURE 84.1 Rivalry in the V1 blind-spot representation. Average fMRI activity in the V1 blind-spot representation is shown for four subjects during perceptual switches to a grating presented ipsilaterally (solid line) or blind-spot grating (dotted line) for both rivalry (a) and physical stimulus alternation (*b*). Vertical lines at time zero indicate the time of the subject's response. Activity during binocular rivalry and physical stimulus alternation is very similar. (*a*) During rivalry, fMRI activity increases sharply soon after the ipsilateral grating becomes dominant in awareness and decreases when the blind-spot grating becomes dominant. (*b*) Very similar fMRI responses occur during stimulus alternations between the two monocular gratings. (fMRI responses typically peak 2–6 s after stimulus onset because of haemodynamic lag.) (Reprinted with permission from F. Tong and S. A. Engel, Interocular rivalry revealed in the human cortical blind-spot representation. *Nature* 411:195–199. © 2001 by the Nature Publishing Group.)

2002). Thus, phenomenal vision within scotomas in blindsight is severely degraded but not always completely absent. Consequently, V1 damage may impair only the contents of consciousness whose neural representation is contingent on V1 activity, specifically brightness, contrast, and some aspects of form.

It is also apparent that not all features that are neurally represented in V1 are also represented in consciousness. For example, signals from the two eyes remain segregated as they arrive at the input layers of V1 (Hubel and Weisel, 1968, 1974). However, although this information is available unconsciously (for example, in the computation of perceived depth; von Helmholtz, 1867), psychophysical studies suggest that reliable eye-of-origin discriminations are not possible (Ono and Barbeito, 1985). Thus, eye-of-origin information is strongly represented in some layers of V1 but not ordinarily in the contents of consciousness. Similar conclusions have been reached from the study of orientation-specific adaptation. Such adaptation is presumed to reflect changes in the activity in V1, the first location in the visual pathway where neurons respond to oriented stimuli (Hubel and Wiesel, 1974). The orientation of a grating can be rendered invisible and impossible to discriminate when it is presented in the periphery, with four similar gratings positioned above and below it, due to crowding. However, adaptation to such a grating can result in an orientation-dependent aftereffect (where the earlier adaptation influences the perceived orientation of a subsequently presented stimulus) that is indistinguishable from that produced when it is presented alone with its orientation clearly (and consciously) perceived (He, Cavanagh, and Intriligator, 1996). Similarly, very high-frequency gratings that are perceptually indistinguishable from a uniform field can nevertheless produce robust orientation-dependent aftereffects (He and MacLeod, 2001). The presence of aftereffects from stimuli that are not consciously perceived (Blake and Fox, 1974) indicates that stimulus properties must be represented outside awareness. Thus, the mere presence of a feature representation in V1 is not a useful guide to whether V1 activity correlates well with the contents of consciousness for that feature.

Moreover, physiological observations of human V1 indicate that activity in V1 is not always well correlated with the contents of consciousness. A lesion of the extrastriate visual cortex that isolates primary visual cortex can result in blindness, yet evoked potentials from V1 can still be recorded (Bodis-Wollner et al., 1977). In normal observers, some V1 activity can be evoked even when a stimulus is judged to be phenomenally absent (Ress, Backus, and Heeger, 2000), and activity in primary visual cortex may also be evoked during a period of expectation when visual stimulation (and phenomenal experience) is absent (Kastner et al., 1999). Following damage to parietal cortex causing visual extinction (deficient awareness for contralesional visual stimuli, particularly when a competing stimulus is also present ipsilesionally), visual stimulation can evoke activity in primary visual cortex in the absence of awareness (Rees, Wojciulik, et al., 2000; Vuilleumier et al., 2002). Finally, high-frequency flickering stimuli evoke responses from human V1 despite being above the flicker fusion frequency and hence consciously perceived as of constant brightness (Maier et al., 1987; Krolak-Salmon et al., 2003). Thus, some changes in activity in primary visual cortex can be seen in the absence of changes in the contents of consciousness.

Taken together, these data suggest that activity in V1 may be necessary but not sufficient for awareness of some stimulus features such as brightness, contrast, and some aspects of form (Crick and Koch, 1995). For awareness of other stimulus features, such as some aspects of motion, V1 activity may not be necessary at all (Riddoch, 1917; Zeki and ffytche, 1998).

Human extrastriate and ventral visual cortex

Extrastriate visual cortex in humans consists of multiple functionally specialized areas, many of which are retinotopically organized (Wandell, 1999), as in monkey (Felleman and Van Essen, 1991). A prominent clinical finding is that damage to cortical areas containing neurons that represent particular features of the visual environment leads to remarkably specific deficits in the corresponding contents of visual consciousness. For example, damage to V5/MT leads to akinetopsia (the inability to see fast movement; Zihl, von Cramon, and Mai, 1983), but has no effect on color perception (Vaina, 1994). Indeed, the clinical syndrome of akinetopsia following V5/MT damage may be specific for particular types of motion perception. Patients with bilateral V5/MT lesions may have some preservation of conscious perception of motion at low velocities (Hess, Baker, and Zihl, 1989; McLeod et al., 1989; Zihl, von Cramon, and Mai, 1983; Zihl et al., 1991; Rizzo, Nawrot, and Zihl, 1995) and spared perception of biological motion (McLeod et al., 1989; Vaina et al., 1990). Nevertheless, the general principle appears to be that damage to an area specific for the analysis of visual motion leads to a specific deficit in the conscious representation of visual motion. Similarly, damage to different areas of the fusiform or lingual gyri may cause prosopagnosia (the inability to recognize faces) or achromatopsia (the inability to see color; Verrey, 1888; Pearlman, Birch, and Meadows, 1979; Damasio, Tranel, and Rizzo, 2000), which may be restricted to particular quadrants of the visual field (Gallant, Shoup, and Mazer, 2000). In each case, although a specific aspect of phenomenal awareness is impaired, contents of consciousness reflecting undamaged feature representations remain intact. This suggests that appropriate activity in a functionally specialized cortical visual area is required to evoke consciousness of the attribute analyzed in that area (Zeki, 2003).

Neuroimaging data appear consistent with this general notion. Phenomenal contingent aftereffects based on color or motion activate either V4 (Sakai et al., 1995; Hadjikhani et al., 1998; Barnes et al., 1999) or V5/MT (Tootell et al., 1995; He, Cohen, and Hu, 1998; Culham et al., 1999; though see Huk, Ress, and Heeger, 2001), respectively, and the time course of such activation reflects phenomenal experience (Tootell et al., 1995; He, Cohen, and Hu, 1998; but see Huk, Ress, and Heeger, 2001). Perception of illusory or implied motion in a static visual stimulus results in activation of V5/MT (Zeki, Watson, and Frackowiak, 1993; Kourtzi and Kanwisher, 2000). Disruption of activity in V5/MT using TMS disrupts motion perception (Beckers and Zeki, 1995) and perception and storage of the motion aftereffect (Theoret et al., 2002). Both transcranial and direct electrical stimulation of V5/MT in the absence of visual stimulation can induce motion hallucinations (Penfield and Rasmussen, 1950; Lee et al., 2000; Pascual-Leone and Walsh, 2001). Perception of subjective figures activates extrastriate cortex (Hirsch et al., 1995; ffytche and Zeki, 1996; Stanley and Rubin, 2003). Finally, differential activity in word-processing areas is present when subjects are consciously aware of visually presented words versus consonant letter strings, and absent when they are not due to inattention (Rees et al., 1999) (figure 84.2). Common to all these experimental paradigms are changes in subjects' phenomenal experience without corresponding physical stimulus changes. Altered brain activity is observed in areas of the brain known (or suspected) to contain neurons whose stimulus specificities encompass the attribute represented in consciousness.

Activity corresponding to phenomenal experience can also be seen in the absence of visual stimulation. Patients with schizophrenia who experience visual and auditory hallucinations show activity in modality-specific cortex during hallucinatory episodes (Silbersweig et al., 1995; Dierks et al., 1999). Similarly, patients with damage to the peripheral visual system who experience hallucinations with specific phenomenal content show activity in functionally specialized areas of visual cortex corresponding to the content of their hallucinations (ffytche et al., 1998). In normal subjects, visual imagery activates category-specific areas of visual cortex (D'Esposito et al., 1997; Goebel et al., 2001; Howard et al., 1998; O'Craven and Kanwisher, 2000; Ishai, Ungerleider, and Haxby, 2000).

Investigations of bistable perception are consistent with the general picture outlined above. Responses in fusiform face area (FFA) or parahippocampal place area (PPA) as a function of awareness for faces or houses during binocular rivalry are larger than those in VI, and equal in magnitude to responses evoked by real alternation of stimuli (Tong et al., 1998). This suggests that neural competition during rivalry has been resolved by these later stages of visual processing, and that activity in FFA (or PPA) therefore reflects the contents of consciousness rather than the retinal stimulus. In addition, fluctuations in activity in human V5/MT are seen during reversals in the motion of a bistable stimu-

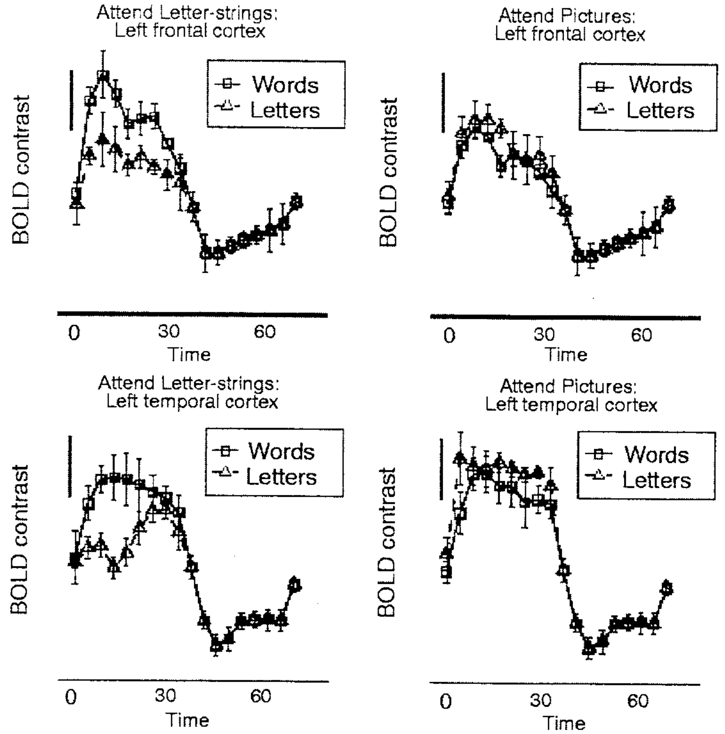


FIGURE 84.2 Attention is necessary for conscious word perception. Time course of activity in left frontal (upper) and left posterior basal temporal cortex (the visual word form area; lower). All four panels use the same plotting conventions. Average BOLD contrast evoked at each locus is plotted as a function of time, collapsing across epochs and participants. The areas whose time courses are shown were identified as those areas showing a maximal simple main effect of words under attention to letters. Unshaded areas represent scans acquired in the experimental conditions and shaded areas represent those acquired during the passive fixation baseline. Error bars indicate interparticipant standard error and dark scale bar represents 0.5% BOLD signal change. Activity evoked when the letter stream contained meaningful words is plotted with black squares and a solid line, and activity when the same stream included only meaningless letter strings is plotted with triangles and a dotted line. (Reprinted with permission from G. Rees et al., Inattentional blindness versus inattentional amnesia for fixated but ignored words. *Science* 286:2504–2507. © 1999 by the American Association for the Advancement of Science.)

lus (Muckli et al., 2002; Sterzer et al., 2002). Qualitatively, these observations are compatible with findings in monkeys demonstrating that the majority of neurons in inferior temporal cortex show responses that reflect the monkey's percept rather than the retinal stimulus (Logothetis and Schall, 1989; Leopold and Logothetis, 1996).

The activity of single neurons can be recorded in even more anterior regions of the medial temporal lobe in epileptic patients in whom electrodes have been implanted for presurgical mapping. Category-specific neural responses are seen both during visual stimulation (Kreiman, Koch, and Fried, 2000a) and during visual imagery (Kreiman, Koch, and Fried, 2000b), and such neurons fire selectively when their preferred stimulus is perceived, but not when it is perceptually suppressed (and so invisible), during binocular rivalry or flash suppression (Kreiman, Fried, and Koch, 2002). These single-cell findings complement neuroimaging studies that show activation of common brain areas during both visual processing and recall during imagery of specific types of stimulus (O'Craven and Kanwisher, 2000; Kosslyn, Ganis, and Thompson, 2001).

Necessity and sufficiency of extrastriate neural activity

The data discussed in the previous section suggest that for visual features such as color, motion, or facial category to be represented in consciousness, appropriate activity must be present in the relevant functionally specialized area of extrastriate ventral visual cortex. However, activation of extrastriate ventral visual cortex may be necessary but not sufficient for awareness of a corresponding specific property. When volunteers incorrectly report the absence of a visual stimulus, some stimulus-specific activity can nevertheless still be seen in extrastriate visual cortex (Ress, Backus, and Heeger, 2000). In FFA, changes in the identity of a face stimulus can evoke some activity even when the subject is blind to the change (Beck et al., 2001). Masked words of which a subject is unaware can nevertheless still evoke some activity in the ventral visual pathway (Dehaene et al., 2001). Objects presented dichoptically in complementary colors, so that they are not consciously perceived during binocular vision, nevertheless evoke activity in appropriate specialized areas of ventral extrastriate cortex (Moutoussis and Zeki, 2002).

Event-related potential (ERP) components that are thought to have generators in ventral visual cortex can also be seen in some form for stimuli that are not consciously perceived. For example, the P300 response to "oddball" stimuli that are not consciously perceived is reduced, but not totally absent (Bernat, Shevrin, and Snodgrass, 2001). Semantically anomalous words that are not perceived when presented during the attentional blink nevertheless evoke an N400 response (Luck, Vogel, and Shapiro, 1996), as do masked words that are not consciously perceived (Kiefer and Spitzer, 2000; Stenberg et al., 2000). Consistent with this observation, words that are masked or unseen due to the attentional blink can produce semantic priming effects (Maki, Frigen, and Paulson, 1997; Dehaene et al., 1998). Finally, prior to conscious detection of change, ERPs indicate a cortical signature of unconscious change detection (Niedeggen, Wichmann, and Stoerig, 2001).

These findings complement recent work addressing the neural correlates of visual extinction, a common component of the neglect syndrome following right parietal damage (see Driver and Mattingley, 1998; Driver et al., this volume). Patients with visual extinction show deficient awareness for contralesional visual stimuli, particularly when a competing stimulus is also present ipsilesionally. Extinction illustrates that visual awareness can be lost even when V1 and extrastriate cortex are structurally intact. Two neuroimaging studies show that areas of both primary and extrastriate visual cortex that are activated by a seen left visual field stimulus can also be activated to some extent by an unseen and extinguished left visual field stimulus (Rees, Wojciulik, et al., 2000; Vuilleumier et al., 2001, 2002) (figure 84.3). Indeed, the unconscious processing of an extinguished face stimulus extends even to the FFA (Rees, Wojciulik, et al., 2002) (figure 84.4), and, for emotional faces, to the amygdala and orbitofrontal cortex (Vuilleumier et al., 2002). Thus, the presence of some activity in these areas is not sufficient to evoke awareness following right parietal damage.

Conscious and unconscious representations in visual cortex

The data just reviewed give strong support to a direct link between neural representations in both primary and extrastriate ventral visual cortex and the contents of visual consciousness. The link is stronger for some features, such as motion, than for others. However, it is also apparent that the mere presence of feature-specific activity in primary or extrastriate cortex is not always sufficient for awareness. Conscious and unconscious representations may differ in several respects, including the overall level of activity that is evoked (as measured with fMRI) in a given visual area. For example, conscious recognition of objects shows a strong correlation with fMRI signal strength in object-responsive regions of visual cortex (Grill-Spector et al., 2000). Dichoptically presented objects that are not perceived evoke lower levels of activity than objects that are consciously identified (Moutossis and Zeki, 2002). The P300 potential evoked by

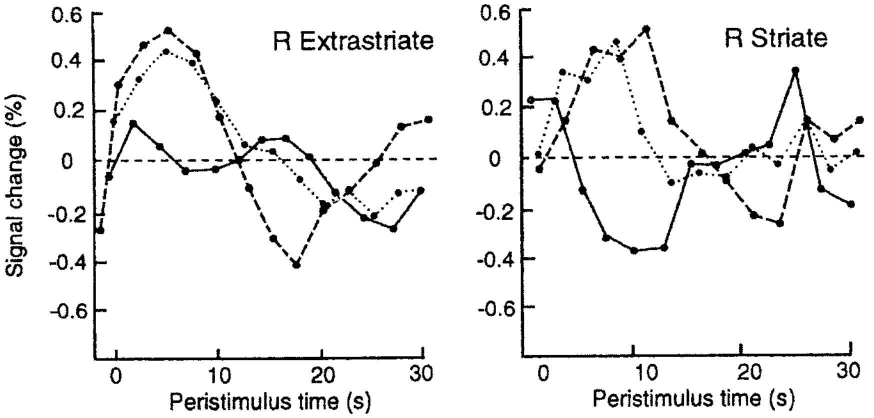


FIGURE 84.3 Visual cortex responses to unseen visual stimuli in parietal extinction. The left graph plots the change in fMRI signal, as a function of peristimulus time, for activation in right hemisphere extrastriate cortex. Lines plot activity for one type of extinction trial (dashed line: left house plus right face) versus the corresponding unilateral trials, on which just a left unilateral house (dotted line) or a right unilateral face (solid line) was presented. This right hemisphere area shows activity time-locked to the visual stimulus that is similar for trials where extinction of a left house occurred versus trials where just a unilateral left house was presented. There is little differential activity when a right-sided face is presented. The right graph shows a similar peristimulus time plot of mean cortical activity for right striate cortex. Lines plot activity for one type of extinction trial (dashed line: now a left face plus a right house) versus the corresponding unilateral trials, on which just a left unilateral face (dotted line) or a right unilateral house (solid line) was presented. Note again that this area also increases its activity following a left visual field stimulus, whether unilateral or extinguished, with no such increase for a right visual stimulus (if anything, some tendency for a decrease is apparent). (Reprinted with permission from G. Rees et al., Unconscious activation of visual cortex in the damaged right hemisphere of a parietal patient with extinction. *Brain* 123:1624–1633. © 2000 by Oxford University Press.)

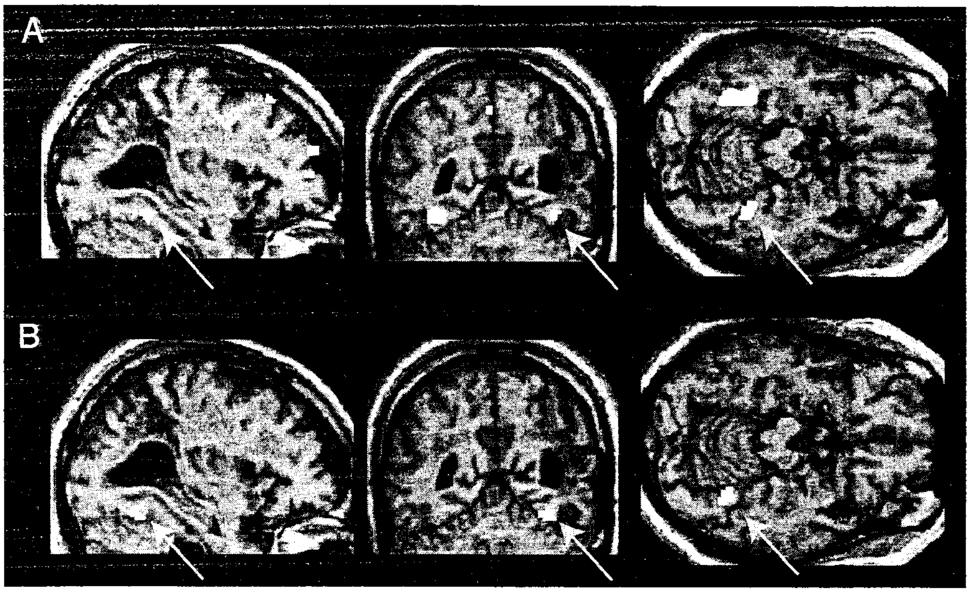


FIGURE 84.4 Category-specific unconscious activation in ventral visual cortex. (*A*) Loci activated by foveally presented and consciously perceived faces (versus houses) are superimposed in white on three sections (sagittal, coronal, and axial) of an anatomical image of the brain of a patient with parietal extinction. Bilateral activation of areas in the fusiform gyrus consistent with the locus of the fusiform face area (FFA) is seen, with the gray arrows indicating the right FFA. (*B*) Three equivalent anatomical sections on which are superimposed loci that showed greater activity for an extinguished left visual field face stimulus compared to an extinguished left visual field house stimulus. The gray arrows indicate activation in a location consistent with the right FFA shown in *A*. These data demonstrate unconscious category-specific activation of the FFA in parietal extinction. (Reprinted with permission from G. Rees et al., Neural correlates of conscious and unconscious vision in parietal extinction. *Neurocare* 8:387–393. © 2002 by Swets and Zeitlinger.)

oddball stimuli that are not consciously perceived is smaller than the P300 for consciously perceived oddball stimuli (Bernat, Shevrin, and Snodgrass, 2001). Activity evoked by masked and unseen words in ventral visual cortex is significantly lower than activity evoked by unmasked and consciously perceived words (Dehaene et al., 2001). These data suggest that one difference between conscious and unconscious representations in visual cortex may be quantitative, differing in the amount of activity (or its time course, or the specific neurons involved) that is evoked, rather than qualitatively in the topographic distribution of activity. In this sense, cortical areas that process visual stimuli appear also to be involved in their conscious perception (Zeki and Bartels, 1998).

Although it is clear that brain activity can differ in a quantitative fashion in human visual cortex when comparing conscious and unconscious representations, the interpretation of this activity in neural terms is not yet clear. Methodological caution in interpretation is appropriate for many of the techniques used in humans. For example, direct electrical stimulation and TMS may have remote effects distant from the site of stimulation (Paus et al., 1997). The mapping between electrical measurements on the scalp and their underlying neural generators in cortex and subcortical structures is indeterminate (Phillips, Rugg, and Friston, 2002). And the physiological link between functional MRI signals and underlying neuronal activity is only just starting to be elucidated (Rees, Kreiman, and Koch, 2002; Smith et al., 2002; Logothetis, 2003; see also Logothetis, this volume). In addition, the spatial resolution of fMRI (on the order of millimeters) may be insufficient to distinguish activity in interdigitating populations of neurons. Thus a quantitative difference in fMRI activity may reflect activation of a separate population of neurons, rather than more activity in the same population of neurons.

It is therefore not clear exactly what aspect of underlying neural activity differs when comparing conscious and unconscious representations that reveal a quantitative difference in fMRI signal (or, for that matter, ERP signals). In addition to overall differences in level of spiking, there are several other possibilities. For example, a minimum duration of neural activity might be required for conscious experience (Libet et al., 1964). In potential agreement with this possibility, patients experiencing visual hallucinations show a rise in fMRI signal in visual cortex some time before they report the presence of the hallucination (ffytche et al., 1998). The precise timing of neural activity might also be important. For example, in humans, the perception of moving phosphenes caused by stimulation of area V5/MT with TMS can be reduced by stimulation of V1, but only if stimulation of V1 is applied after the TMS pulse to V5/MT (Pascual-Leone and Walsh, 2001). Finally, a specific form of neural activity such as recurrent processing or synchrony might be required (von der Malsburg, 1981; Engel et al., 1991; Lamme and Roelfsema, 2000). For example, it has been suggested that synchronized electroencephalographic (EEG) oscillations in the high-frequency range (40–150 Hz) might underlie feature integration (thus representing a candidate solution to the binding problem; Singer and Gray, 1995) and form one potential substrate for visual awareness (Crick and Koch, 1990; Engel and Singer, 2001), although this idea remains controversial (Shadlen and Movshon, 1999). In support of this theory, cognitive processes that are thought to be closely associated with awareness, such as attention (Rock et al., 1992; Rees and Lavie, 2001), can modulate neural synchrony in monkey (Steinmetz et al., 2000; Fries et al., 2001). In humans, neuromagnetic responses show a correlation between perception of a visual stimulus during binocular rivalry and both interhemispheric and intrahemispheric coherence (Tononi et al., 1998). Viewing ambiguous visual stimuli that can be perceived as either faces or meaningless shapes leads to a long-distance pattern of synchronization in the scalp EEG that is specific for face perception and corresponds to the moment of conscious perception itself (Rodriguez et al., 1999). These findings suggest a possible role for synchronous processes in human conscious vision, but a clear synthesis has not yet emerged.

Parietal and prefrontal correlates of visual awareness

Conscious vision does not depend solely on the integrity of posterior and ventral visual cortex (Driver and Mattingley, 1998; Le et al., 2002). The longstanding clinical observation that disturbances of visual awareness may follow parietal damage provides strong evidence for a contribution of cortical areas distant from striate and extrastriate cortex to conscious vision (Driver and Mattingley, 1998). Although it has been argued that dorsal frontoparietal cortex activity might be related only to unconscious processing associated with visually guided action (Milner and Goodale, 1995), there is now compelling evidence to support a direct role for frontal and parietal cortex in visual awareness. In monkeys, chronic blindness follows a massive cortical ablation of parietal and frontal areas that spares most of the modality-specific visual cortex (Nakamura and Mishkin, 1986). Similarly, removal of frontoparietal cortex in cats produces as much or more decrement in visual discrimination than does removal of temporal cortex (Sperry, Myers, and Schrier, 1960). Furthermore, anatomical and electrophysiological studies show that parietal and prefrontal cortex are reciprocally connected and act together with visual cortex (Friedman and Goldman-Rakic, 1994). Direct evidence in normal humans for parietal and prefrontal correlates of visual awareness has come from recent studies of bistable perception. Brain activity during spontaneous fluctuations in awareness has been examined both for binocular rivalry and for a variety of bistable figures (Kleinschmidt et al., 1998; Lumer, Friston, and Rees, 1998; Lumer and Rees, 1999) (figure 84.5). Unlike the rivalry studies discussed previously (Tong et al., 1998; Polonsky et al., 2000), these studies focused on activity that was time-locked to the transitions between different perceptual states rather than to the contents of one or other perceptual state. Cortical regions whose activity reflects perceptual transitions include not only ventral extrastriate cortex, but also parietal and frontal regions previously implicated in the control of attention (Lumer, Friston, and Rees, 1998). However, whereas extrastriate areas are also engaged by nonrivalrous perceptual changes, activity in frontal and parietal cortex is specifically associated with the perceptual alternations during rivalry. Similar parietal and frontal regions are active during perceptual transitions that occur while subjects view a range of bistable figures such as the Necker cube and Rubins face/vase (Kleinschmidt et al., 1998), and during fluctuations in the direction of motion of a bistable motion stimulus (Sterzer et al., 2002). Clinically, it has been observed that patients with prefrontal cortex lesions typically exhibit abnormal bistable perception (Wilkins, Shallice, and McCarthy, 1987; Ricci and Blundo, 1990; Meenan and Miller, 1994) and that patients with parietal neglect exhibit abnormal patterns of transitions in binocular rivalry (Bonneh, Pavlovskaya, and Soroker, 2002). These data suggest that activity in frontal and parietal cortex might be causally associated with the generation of transitions between different percepts.

A number of other paradigms reveal a similar association between frontoparietal activity and awareness. The pop-out in depth of stereographic images activates areas of superior parietal and prefrontal cortex, compared with regions active during continued stable viewing of the same figures (Portas et al., 2000). In addition, similar areas of frontal and parietal cortex are activated when subjects become consciously aware of the presence of a change in a visual scene, compared with when they are blind to that change (Beck et al., 2001) (figure 84.6). During visual imagery, fMRI reveals content-independent activity in frontal and parietal cortex (Ishai, Ungerleider, and Haxby, 2000). Unmasked and consciously perceived visual words, compared with masked and unseen words, also evoke activity in frontal and parietal cortex (Dehaene et al., 2001) (figure 84.7). Finally, the attentional blink may be associated with right intraparietal sulcus and prefrontal cortical activations (Marois, Chun, and Gore, 2000).

These data are complemented by experiments on patients with visual extinction resulting from right parietal damage. As mentioned earlier, fMRI evidence suggests that extinguished stimuli are processed and activate contralesional ventral visual cortex in the absence of awareness (Rees,

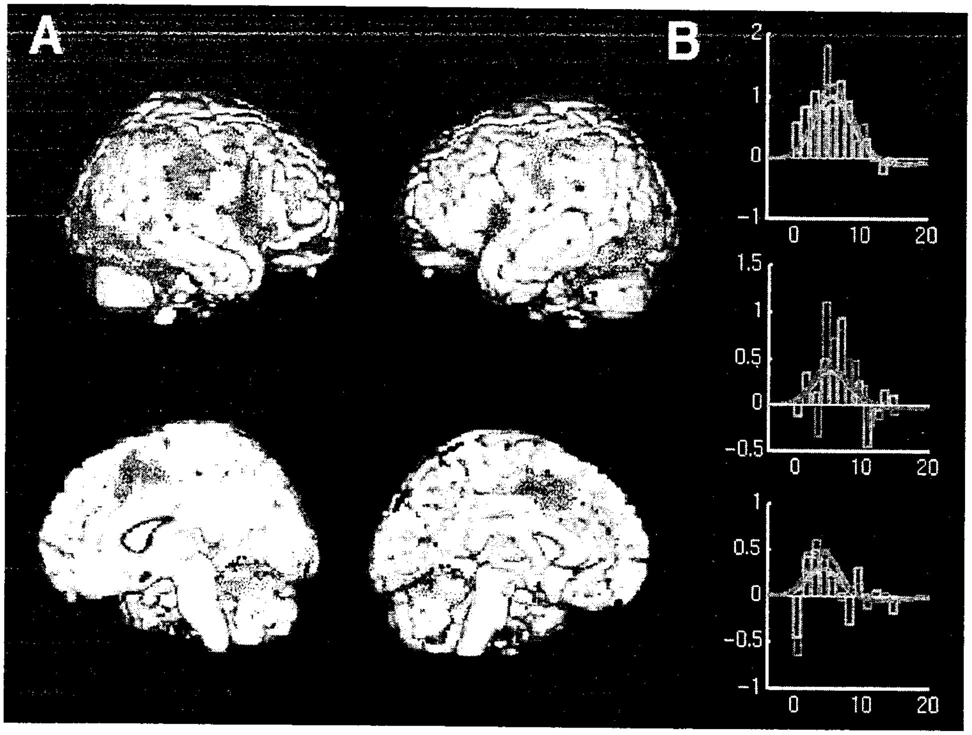


FIGURE 84.5 Event-related activity associated with binocular rivalry perceptual switches. (*A*) Four views of the medial and lateral surfaces of a rendering of an anatomical template image in Talairach space, on which are superimposed areas where evoked activity was specifically related to perceptual transitions in either binocular rivalry (red) or physical stimulus alternation (green). Areas modulated by perception during both rivalrous and physical stimulus alternation, and the bilateral symmetry of the evoked activity are apparent. (*B*) Illustrative postevent histograms of the modulation of activity produced by transition events in rivalry (red) and physical stimulus alternation (green) conditions from three different subjects. The evoked activity (percent change in BOLD contrast) is shown as a function of postevent time (in seconds) for each subject, with the fitted models of hemodynamic response function superimposed in solid lines. The modulation of activity shown here is taken from a voxel in right anterior fusiform gyrus. (Reprinted with permission from E. D. Lumer et al., Neural correlates of perceptual rivalry in the human brain. *Science* 280:1930–1934. © 1998 by the American Association for the Advancement of Science.) (See color plate 75.)

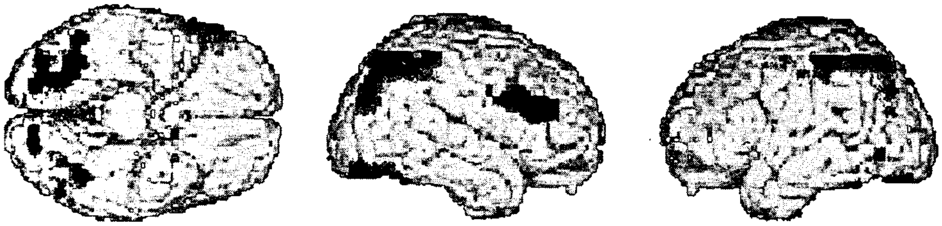
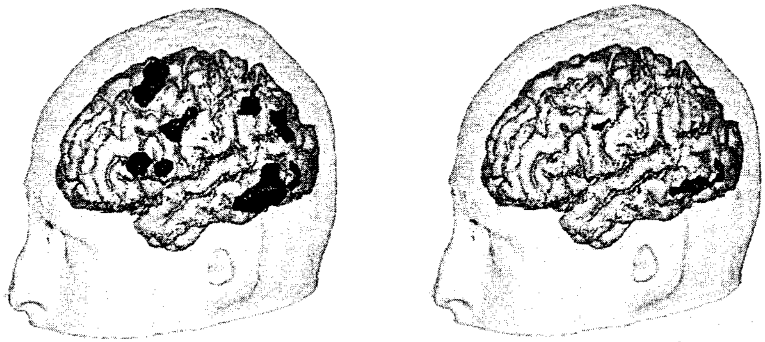


FIGURE 84.6 Conscious awareness of change. Three views of an anatomical template brain on which are superimposed loci (in black) where evoked activity was greater when subjects consciously detected a change in two sequentially presented visual images, compared to when the same physical change remained undetected. Conscious change detection activates not only the ventral visual cortex but also areas of right dorsolateral prefrontal and bilateral parietal cortex. (Reprinted with permission from D. M. Beck et al., Neural correlates of change detection and change blindness. *Nat. Neurosci.* 4:645–650. © 2001 by the Nature Publishing Group.)



Visible words **Masked words**

FIGURE 84.7 fMRI activations to visible and masked words. Activations produced by single words that are either masked and not consciously perceived (right) or visible and consciously perceived (left). Only the left hemisphere is shown, as seen through a translucent three-dimensional reconstruction of the skull and brain of one of the participants. In these transparent views, the deep activations in fusiform, parietal, and mesial frontal cortex appear through the overlying lateral cortices. Masked words that are not consciously perceived activate a large area of the left fusiform gyrus, while visible words produce greater activation in this area combined with widespread activity in left parietal and prefrontal cortex. (Reprinted with permission from S. Dehaene et al., Cerebral mechanisms of word masking and unconscious repetition priming. *Nat. Neurosci.* 4:752–758. © 2001 by the Nature Publishing Group.)

Wojciulik, et al., 2000, 2002; Vuilleumier et al., 2001). However, because extinction does not arise on all bilateral trials, this also affords an opportunity to compare trials in which the patient reports awareness with physically identical trials when awareness of one of the stimuli is absent. In trials in which one patient (correctly) reports seeing bilateral stimulation, awareness is specifically associated with covariation of activity in a distributed network involving primary visual cortex, inferior temporal cortex, and areas of prefrontal and left parietal cortex (Driver et al., 2001; Vuilleumier et al., 2001; Rees, Wojciulik, et al., 2002). Conscious perception of emotional faces leads to enhanced activity in fusiform, parietal, and prefrontal areas of the left hemisphere, independent of emotional expression (Vuilleumier et al., 2002).

Loss of awareness for objects in the contralesional visual field in parietal extinction is typically complete, affecting all stimulus features (even those such as color and motion thought to be represented in extrastriate visual cortex). In this respect, the effects of parietal damage on phenomenal experience are distinct from the effects of extrastriate damage, where awareness of only an isolated visual feature may be lost. This profound loss of the ability to consciously represent different objects in different egocentric spatial locations may depend on the putative function of parietal cortex in remapping retinotopic space represented in ventral visual cortex into more complex head-and-body-centered representations (Cohen and Andersen, 2002). Bilateral parietal lesions can give rise to even more pronounced visual deficits, with unpredictable perception and recognition of only parts of the visual field (simultanagnosia), together with impairments of visually guided reaching and visual scanning (Balint, 1909; Husain and Stein, 1988). Patients with simultanagnosia may show nonspatial extinction, failing to perceive the second of two objects presented simultaneously in overlapping locations (Humphreys et al., 1994). Of course, patients with parietal extinction (and even patients with bilateral parietal damage) remain conscious of *some* kinds of phenomenal experience, such as in the ipsilesional visual field. But the lesions encountered in patients are typically too small to stand comparison with the large ablations of the dorsal stream that render monkeys blind (Nakamura and Mishkin, 1986). The effect on phenomenal awareness in humans of bilateral damage to the entire frontal and parietal cortex therefore remains an open question.

Despite varied paradigms and types of visual stimulation, the anatomical location of the areas in parietal and prefrontal cortex activated by changes in the contents of visual consciousness is relatively consistent. Meta-analysis suggests two prominent foci in the superior parietal lobule and dorsolateral prefrontal cortex (Rees, 2001; Rees, Kreiman, and Koch, 2002) (figure 84.8). These observations suggest the existence of a general mechanism in these areas that is specifically related to visual consciousness, active during transitions between different types of perceptual experience, and associated with content-independent spatial representation rather than content-specific visual features (e.g., Driver and Mattingley, 1998; Driver and Vuilleumieur, 2001; Kanwisher, 2001). Although frontal and parietal areas play a prominent role in the organization of behavior, their involvement in rivalry is independent of motor report (Lumer and Rees, 1999). During transitions in binocular rivalry, activity is coordinated between ventral visual areas, parietal areas, and prefrontal areas in a way that is not linked to external motor or sensory events but instead varies in strength with the frequency of perceptual events. In parietal extinction, awareness of bilateral visual stimulation is specifically associated with covariation of activity in a distributed

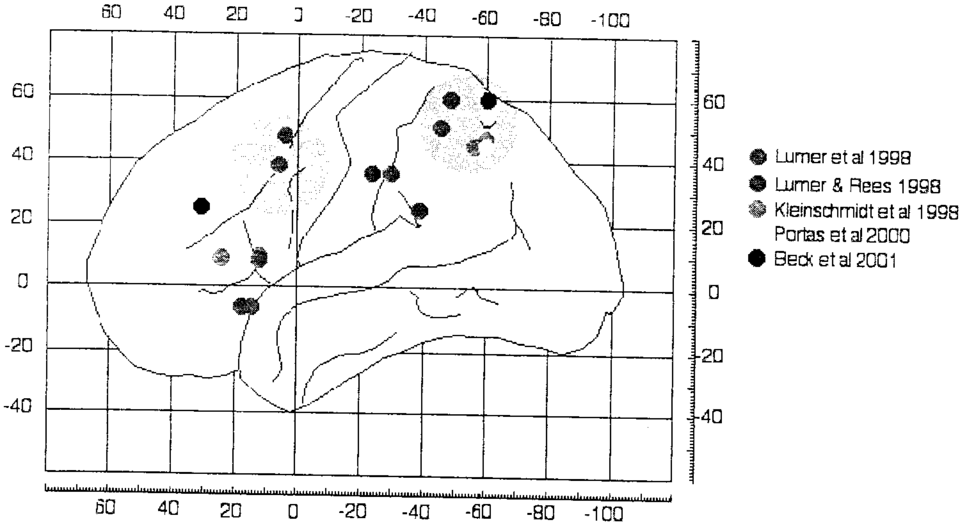


FIGURE 84.8 Neural correlates of conscious vision in parietal and prefrontal cortex. Areas of parietal and prefrontal cortex that show activation correlated with changes in visual awareness in a number of selected studies (Lumer et al., 1998; Lumer and Rees, 1999; Kleinschmidt et al., 1998; Portas et al., 2000; Beck et al., 2001) are plotted on a standardized brain in Talairach space (Talairach and Tournoux, 1988). Each circle is placed at the center of a cluster of activation, with different shades representing different studies; overlapping loci from the same study are omitted for clarity. There is prominent clustering of activations in superior parietal and dorsolateral prefrontal cortex, highlighted by large, light circles. (See color plate 76.)

network involving primary visual cortex, inferior temporal cortex, and areas of prefrontal and left parietal cortex (Driver et al., 2001; Vuilleumier et al., 2001). These observations represent direct evidence that awareness may be specifically associated with covariation between visual cortex and nonvisual areas of cortex, complementing earlier studies showing similar distributed interactions associated with consciousness in normal subjects (Dolan et al., 1997; Lumer and Rees, 1999; McIntosh, Rajah, and Lobaugh, 1999). This suggests that functional interactions between visual and frontoparietal cortex may make an important contribution to the contents of consciousness. Such an interaction has been proposed on theoretical (Crick and Koch, 1995) and empirical (Driver and Mattingley, 1998) grounds; one possibility is that this represents activity in a global neuronal workspace (Baars, 1988; Dehaene and Naccache, 2001; Baars and Franklin, 2003; Dehaene, Sergent, and Changeux, 2003).

Synthesis

The evidence reviewed in this chapter suggests that although activity in visual cortex may be necessary, it does not appear sufficient for conscious vision without some contribution from parietal and/or prefrontal cortex. What is the nature of that contribution? It is striking that the studies reviewed here all focused on transitions between experiences with different types of phenomenal content. James (1890) made a phenomenal distinction between the experience of rapid changes in perceptual awareness (transitive states) and stable contemplation (substantive states). Both are part of our everyday experience of the visual environment. Perhaps the neural correlates of conscious experience in parietal cortex are thus more specifically correlates of transitive states? The anatomical loci associated with these correlates substantially overlap areas previously associated with covert spatial attention (Corbetta et al., 1995). Indeed, the deployment of spatial attention and the phenomenal experience of binocular rivalry both entail the suppression of visual information from conscious perception. Monocular stimuli become periodically invisible during rivalry; sensory events associated with unattended (or neglected) stimuli have a diminished impact on awareness. Both phenomena may call on common neural machinery in frontoparietal cortex that is involved in the selection of neuronal activity leading to visual awareness (Rees, 2001; Rees and Lavie, 2001).

This phenomenological distinction raises the possibility that the maintenance of a conscious perceptual state may involve different cortical mechanisms from those involved in generating transitions (Portas et al., 2000). Sustained perceptual experience is an obvious feature of consciousness but is inconsistent with the observation that the brain is designed to represent only the unexpected (Friston, 2002). For a percept to be sustained requires either the filling in of missing information or prevention of adaptation when stimulation remains constant. Such mechanisms might depend on top-down signals from higher-level brain regions. Future work in this area may prove rewarding, as there are tantalizing indications that such mechanisms do exist. For example, when a stereo image becomes visible, transient activity is seen in frontal and parietal cortex (Portas et al., 2000). However, in a subsequent period where perception of the same image is sustained, activity is seen in different regions of prefrontal cortex and in the hippocampus. Thus, sustaining a visual percept recruits different anatomical loci from those associated with immediate conscious recognition. Similarly, regions of brain activation in frontal and parietal cortex associated with transient selection of an item from spatial working memory differ from those associated with sustained maintenance of items in working memory (Rowe et al., 2000). Finally, as previously reviewed, brain areas activated during epochs of sustained face perception in binocular rivalry include the FFA (Lumer, Friston, and Rees, 1998; Tong et al., 1998; Lumer, 2000). However, several prefrontal areas also show greater activity during sustained face perception (Lumer, 2000). These areas show strong overlap with those previously implicated in maintaining working memory for faces in a delayed match-to-sample task (Courtney et al., 1997). The phenomenological distinction between transitive and substantive states of mind may perhaps reflect the involvement of distinct regions of dorsal and ventral frontoparietal cortex associated with attention and working memory.

Concluding remarks

The evidence reviewed here suggests that ventral visual cortex is undeniably (and unremarkably) crucial for conscious vision in humans; both primary visual cortex and ventral extrastriate cortex contain neuronal populations whose activity closely correlates with the contents of consciousness. Different areas emphasize different features in consciousness; primary visual cortex appears to be more important for brightness and contrast, while V5/MT and areas of the fusiform gyrus are more important for motion and color, respectively. Within these areas, level of activation is one factor that may distinguish conscious and unconscious representations. However, even strong activation in visual cortex can be insufficient for awareness without a contribution from parietal and/or prefrontal cortex. The minimal sufficient conditions (in humans) for a visual scene to be represented in consciousness may therefore be the combination of an activated representation of its constituent features in striate and extrastriate visual cortex, coupled with activity in specific regions of parietal and prefrontal cortex.

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