

Functional Magnetic Resonance Imaging and Evoked Potential Correlates of Conscious and Unconscious Vision in Parietal Extinction Patients

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We describe recent functional magnetic resonance imaging (fMRI) and event-related potential (ERP) studies of visual extinction in patients with right parietal damage who can detect isolated visual stimuli on either side, yet often miss contralesional (left) stimuli during bilateral stimulation. We consider the neural fate of such extinguished visual stimuli and how neural responses differ for consciously detected versus extinguished stimuli. fMRI findings indicate that extinguished stimuli evoke activity in striate and ventral extrastriate visual cortex, despite escaping awareness. Activations for extinguished stimuli can be found even in category-specific (face-responsive) areas of the fusiform gyrus. On the other hand, activations in visual cortex are stronger for consciously detected versus extinguished stimuli, with parietal and frontal areas of the intact left hemisphere also implicated in this comparison. Recent ERP data likewise suggest differential neural responses for consciously detected versus extinguished stimuli. We discuss these findings in relation to current speculations about the neural basis of conscious and unconscious perception.

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Visual extinction is a relatively common neurological sign after unilateral brain injury, particularly when right posterior-parietal cortex is damaged (Bisiach and Vallar, 1988; Driver *et al.*, 1997; Driver and Vuilleumier, 2001). It frequently manifests as one component of the spatial neglect syndrome (Bisiach and Vallar, 1988), though in some cases it may dissociate from other aspects of neglect (Cocchini *et al.*, 1999). In visual extinction, patients can detect isolated visual stimuli

on either side (i.e., visual fields are intact, consistent with sparing of posterior occipital cortex); yet they often miss contralesional (typically, left) stimuli during bilateral stimulation. This has commonly been attributed to a pathological bias in spatial attention following the lesion (Posner *et al.*, 1984; Desimone and Duncan, 1995; Driver *et al.*, 1997), that disadvantages contralesional stimuli in situations where multiple stimuli compete to attract attention, as on bilateral but not unilateral trials.

Some evidence already exists, from purely behavioral experiments, to suggest that extinguished visual stimuli may undergo residual unconscious processing. Reaction times to detect or locate stimuli on the ipsilesional side can be affected by the presence versus absence of concurrent undetected stimuli on the contralesional side (Marzi *et al.* 1996; Vuilleumier and Rafal, 2000). More complex properties of an extinguished stimuli, such as its color, shape, or even its identity and semantics, can also influence performance in an implicit manner (for reviews, see Driver, 1996; Driver and Vuilleumier, 2001). Finally, the rate of extinction for bilateral trials can be modulated by the relationship between concurrent contralesional and ipsilesional stimuli. Typically extinction is reduced if these stimuli group visually to form a single Gestalt (Mattingley *et al.*, 1997), but is increased if two ungrouped stimuli are identical in the visual property to be reported (Baylis *et al.*, 1993; Vuilleumier and Rafal, 2000).

On the basis of such behavioral findings in parietal extinction patients, Driver (1996; Driver *et al.*, 1997; Driver and Mattingley, 1998) and others (e.g., Heilman *et al.*, 1997; Robertson *et al.*, 1997) have suggested that unconscious residual processing of extinguished stimuli might arise in posterior visual cortex and/or more anterior areas along the ventral visual stream. These areas are often structurally intact in neglect and extinction patients with parietal damage. However, the function of such areas could in principle be compro-

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mised by damage to interconnected areas in the extensive neural network for vision and attention (e.g., areas in parietal cortex). Recently, event-related functional magnetic resonance imaging (fMRI) has been used to assess directly the neural fate of extinguished visual stimuli in parietal patients (for a related visual PET study in normals, see Fink *et al.*, 2000; see also Beversdorf *et al.*, 1999; Remy *et al.*, 1999; and Staines *et al.*, 2000, for imaging studies of tactile rather than visual extinction).

fMRI EVIDENCE FOR UNCONSCIOUS PROCESSING OF EXTINGUISHED VISUAL OBJECTS

Rees and colleagues (Rees *et al.*, 2000) used event-related fMRI to study a patient (GK) with left extinction and neglect after a focal right inferior-parietal lesion. Photographs of faces or houses were briefly presented in either the right, left, or both hemifields. Comparing bilateral trials on which the left stimulus was extinguished, with unilateral right trials (for which the patient's conscious report was identical) revealed activation of primary visual cortex and extrastriate visual areas in the damaged right hemisphere by extinguished contralesional (left) stimuli. This confirmed that occipitotemporal visual areas can be activated by extinguished stimuli that escape the patient's awareness.

The comparison of extinguished faces with extinguished houses in this study also revealed activation in a region of right fusiform cortex, whose anatomical coordinates overlapped (see Fig. 1) with activation for blocked faces versus houses at fixation in the same patient (as conventionally used to localize the "fusiform face area" or FFA in normal subjects; Kanwisher *et al.*, 1997). This category-specific activation for extinguished faces was relatively weak in the initial study, but still survived correction for multiple comparisons within the predefined FFA. The finding has since been replicated in a subsequent study with the same patient (Rees *et al.*, submitted) but using a rapid trial rate to increase power (3 s SOA, rather than 9 s as in the original study). In this second study, category-specific activation within the right FFA, when comparing extinguished face versus extinguished houses, reached a conventional global level of significance ($P < 0.001$ uncorrected), in addition to surviving correction for multiple comparisons within the predefined FFA small volume.

A similar event-related fMRI study was independently carried out by Vuilleumier and colleagues (2001) on another right-parietal patient (CW), again using face and nonface stimuli (now represented with line drawings). The patient was asked to detect the presence of a face in particular, rather than merely to

report whether there was any stimulation on the left and/or right as in Rees *et al.* (2000). Like Rees *et al.*, the fMRI findings revealed some preserved activations for extinguished left stimuli in right striate and inferior temporal cortex, albeit at low threshold ($P < 0.005$ uncorrected). Differential activation for an extinguished face was found just lateral to the fusiform area activated by seen faces. Note that the activation specific to extinguished faces in Rees *et al.*'s study also peaked slightly lateral to the FFA, although extending into it (see Figs. 1C and 1D).

Taken together, these new fMRI results show that early visual cortex and also category-specific ventral cortex can be activated in the damaged hemisphere of right-parietal patients, by an extinguished stimulus that escapes their awareness. This provides a plausible neural basis for the unconscious residual processing that has been demonstrated for extinguished stimuli in purely behavioral studies (Audet *et al.*, 1991; Berti and Rizzolatti, 1992; Baylis *et al.*, 1993; McGlinchey-Berroth *et al.*, 1993; Cohen *et al.*, 1995). However, the observed activations in visual areas for extinguished stimuli raise the question of what is lacking in the cerebral response to these stimuli that precludes them from reaching awareness.

INITIAL fMRI EVIDENCE FOR DIFFERENTIAL ACTIVATIONS TO SEEN VERSUS EXTINGUISHED STIMULI

Extinction can arise on just a proportion of bilateral trials, and stimulus properties can be titrated to achieve this in a given patient (Driver *et al.*, 1997). Neural activity can then be compared for those trials where both stimuli are consciously detected, versus trials where the contralesional stimulus is extinguished from awareness (see also Marzi *et al.*, 2000). Patient CW in Vuilleumier *et al.*'s (2001) fMRI study extinguished left faces on 68% of bilateral trials. Activations were greater in right striate cortex and cuneus, bilateral fusiform gyrus and left parietal cortex for bilateral trials on which the left face was consciously detected, rather than extinguished (Fig. 2B). Moreover, an analysis of effective connectivity (Buchel and Friston, 1997) revealed that coupling between right striate cortex and left inferior frontal cortex was stronger on bilateral trials with the left face seen rather than extinguished. Similarly, activity in the fusiform gyrus was more strongly coupled with left inferior frontal cortex and left parietal cortex when the left face stimulus was seen (Fig. 2C).

In their recent follow-up study of patient GK, Rees *et al.* (submitted) were also able to compare activations for bilateral trials where both stimuli were consciously detected, versus trials with left extinction. Their pa-

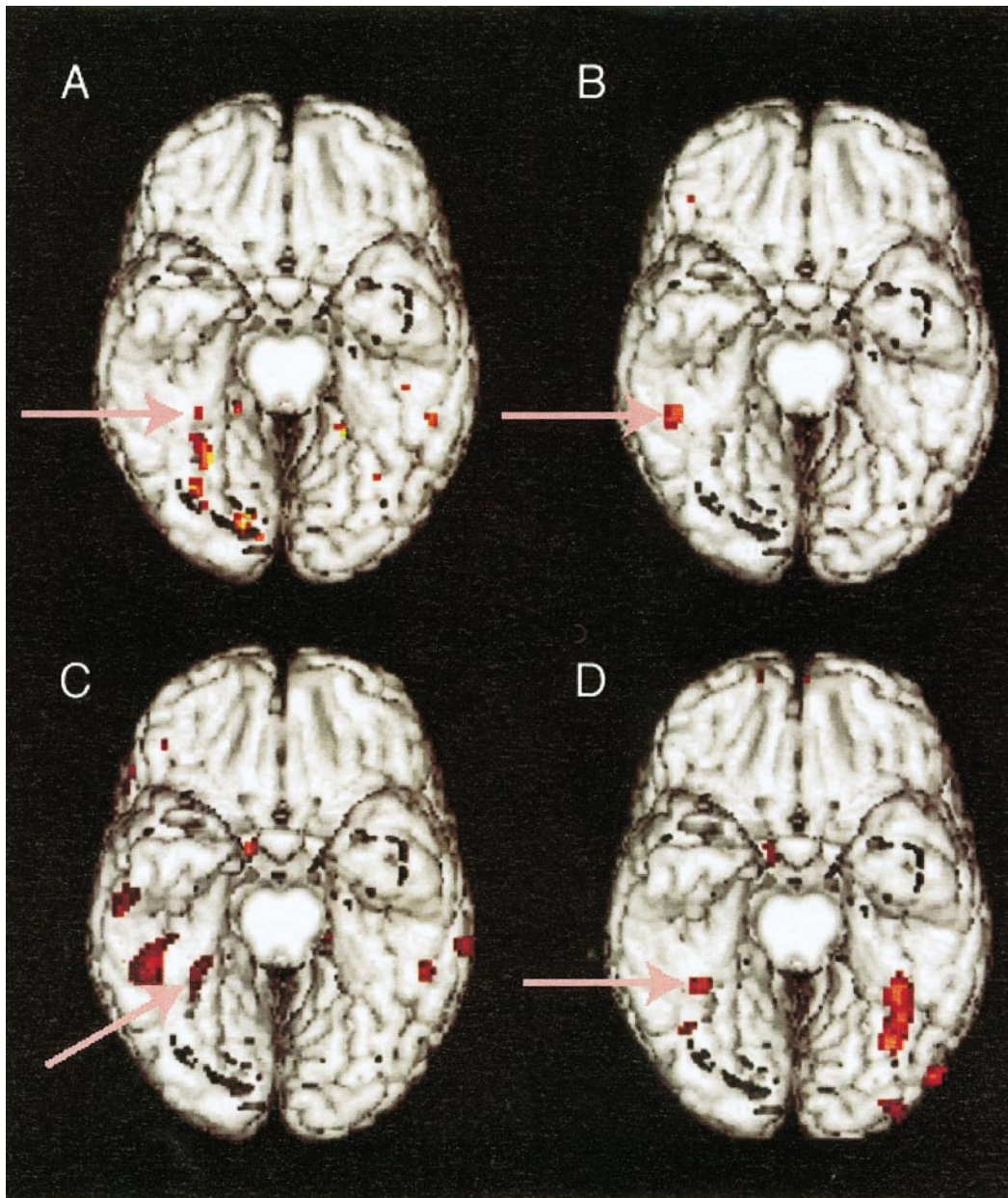


FIG. 1. Activation produced by extinguished faces in a patient with visual extinction and right parietal damage, in the data from Rees *et al.* (2000). (A) Ventral view of the rendered surface of a template brain in Talairach space, on which are superimposed activations ($P < 0.001$, uncorrected) produced by an extinguished face presented in the left visual field for patient GK ($P < 0.001$, uncorrected). Note activation in several locations of the ventral visual cortex, including a location consistent with the right fusiform face area or FFA [pink arrow, coordinates (34 -42 -26), $t = 3.42$, $P < 0.05$ corrected for the small volume examined in the predefined fusiform face area]. (B) Loci where activation produced by an extinguished face stimulus in the left visual field was greater than that produced by an extinguished left house ($P < 0.001$, uncorrected). Activation is seen in a location (pink arrow) slightly lateral to the right FFA [coordinates (05 -40 -24), $t = 3.95$]. (C) Examination of the same data presented in C but at a lower global threshold ($P < 0.01$, uncorrected). Differential activation to extinguished faces (compared to extinguished houses) now extends into the right FFA [coordinates (34 -46 -24), $t = 2.66$, $P < 0.05$ corrected for the small volume examined in the predefined FFA]. (D) Activations produced by blocked foveal faces compared to blocked houses (FFA localizer) in the same patient. Note the presence of bilateral activation in locations consistent with previous FFA results in normal subjects (e.g., Kanwisher *et al.*, 1997). The pink arrow indicates an activation peak in the right fusiform gyrus [coordinates (38 -46 -22), $t = 4.04$ and (40 -60 -20), $t = 3.50$].

tient had now recovered to the point where instead of extinguishing all left stimuli on bilateral trials as in the initial study, he now did so on only 28% of such

trials. In general accord with Vuilleumier *et al.* (2001), right ventral cortex was more strongly activated for bilateral trials where the left visual stimulus was con-

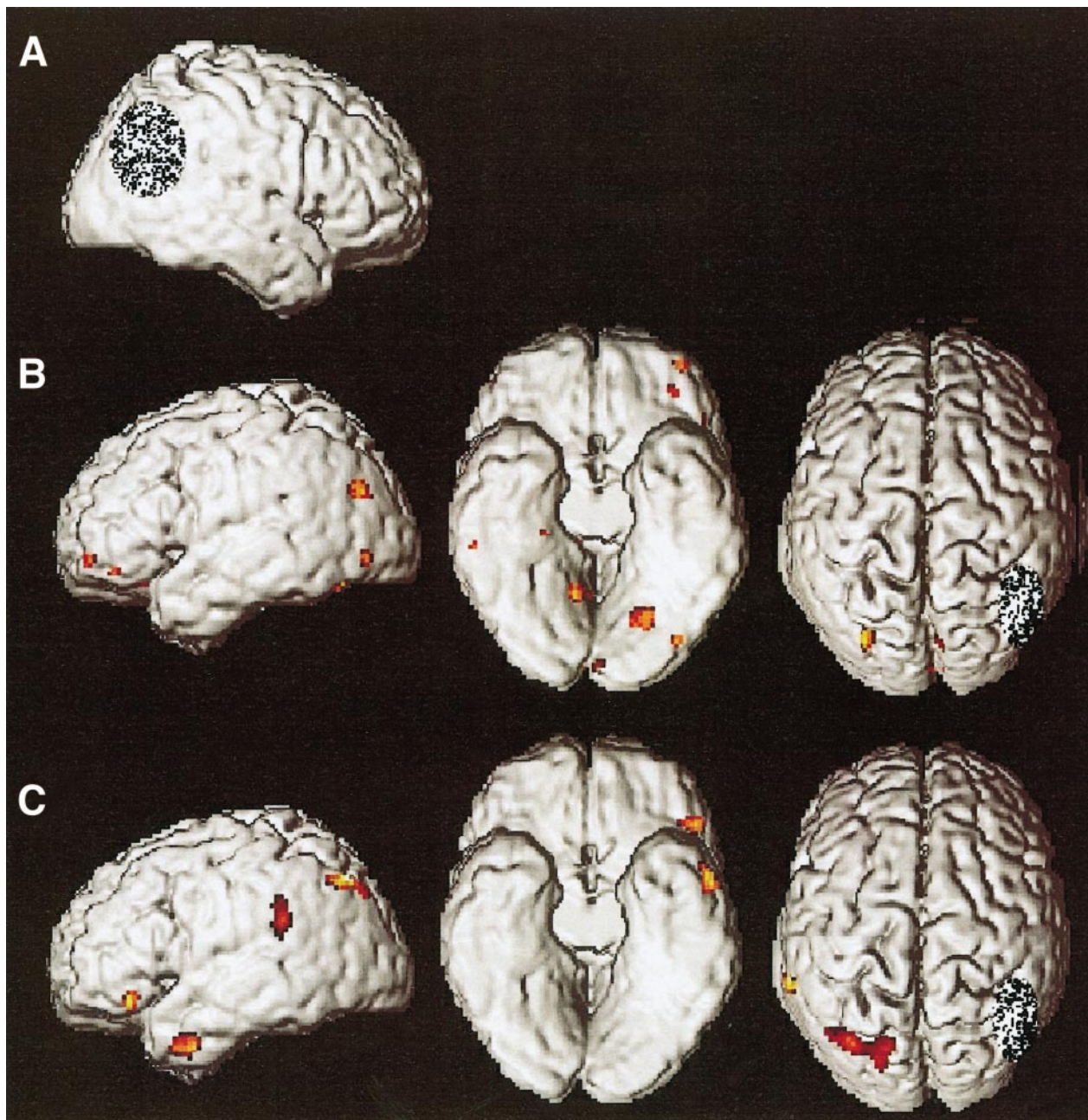


FIG. 2. Activation associated with consciously perceived versus extinguished faces in patient CW, data from Vuilleumier *et al.* (2001). Lateral, ventral, and dorsal views of a rendered template brain in Talairach space are shown. (A) Location of right hemisphere parietal damage in this patient is schematically illustrated by the speckled area. (B) Activation evoked ($P < 0.001$ uncorrected) by left faces on bilateral trials, when consciously perceived versus extinguished. Note increased responses in primary visual cortex of the damaged right hemisphere (peak coordinates $8 -94 0$, $t = 3.60$), bilaterally in ventral temporal areas (including left fusiform, $-22 -68 -20$, $t = 4.69$; right fusiform, $32 -66 -22$, $t = 3.57$; and right parahippocampal gyrus, $14 -56 -6$, $t = 3.95$), as well as in left parietal ($-28 -76 30$, $t = 4.25$) and frontal ($-38 54 -4$, $t = 3.84$; $-34 42 -10$, $t = 3.53$) cortex. (C) Changes in effective connectivity on bilateral trials when left faces were seen versus extinguished, showing areas in which activity covaried with that in the left fusiform gyrus more for bilateral trials where a left face was seen rather than extinguished. Note increased covariation in several areas of the intact left hemisphere, including superior parietal ($-34 -72 46$, $t = 4.04$) and inferior parietal ($-66 -42 28$, $t = 4.18$) cortex; inferior frontal cortex ($-46 32 -10$, $t = 4.15$); and anterior temporal cortex ($-54 6 -32$, $t = 4.43$). These data suggest a specific coupling of fusiform activity with parietal and frontal areas during trials associated with face awareness.

sciously detected rather than extinguished. Areas in left parietal and left frontal cortex also showed this pattern.

These recent findings provide initial evidence that neural activations for consciously seen versus extinguished stimuli may differ systematically on bilateral

trials, with posterior areas of visual cortex (in the damaged hemisphere contralateral to the critical stimulus) being implicated, and also more anterior areas of parietal and frontal cortex (in the intact hemisphere). These results require further corroboration in additional patients, but they raise the possibility that some interplay between posterior visual areas and parietal-frontal circuits may be critical for a visual stimulus to reach awareness (see also Driver and Vuilleumier, 2001; Lumer and Rees, 1999; Rees, in press). Such a notion is consistent with the clinical fact that damage to parietal-frontal circuits, as in neglect and extinction patients, can disrupt awareness for visual stimuli despite structural preservation of posterior visual areas (Driver and Vuilleumier, 2001).

ERP EVIDENCE FOR CONSCIOUS AND UNCONSCIOUS PROCESSING IN EXTINCTION

ERP methods can be used to address similar issues concerning extinction to those considered for fMRI above. Several pioneering studies have examined ERPs for visual stimuli in neglect and extinction patients (e.g., Lhermitte *et al.*, 1985; Vallar *et al.*, 1991; Spinelli *et al.*, 1994; Verleger *et al.*, 1996). However, this method has only recently been applied to study brain responses for concurrent bilateral visual stimulation, on trials where extinction does or does not arise (Eimer *et al.*, unpublished data; Marzi *et al.*, 2000; Vuilleumier *et al.*, 2001).

Marzi and colleagues (Marzi *et al.*, 2000) studied a single case with a large lesion centered on right inferior parietal cortex, who showed left visual extinction on a proportion (39%) of bilateral trials with the stimuli used. They found that P1 and N1 components (which are relatively early components, traditionally considered to be "sensory") were reduced over the damaged hemisphere on bilateral trials with extinction, compared to those without extinction. This appears consistent with the fMRI findings of Vuilleumier *et al.* (2001) and Rees *et al.* (submitted) described in the previous section, which showed greater activation of visual cortex in the damaged hemisphere for bilateral trials without extinction, compared to those trials where the contralesional stimulus was undetected. However, the visual stimuli used in Marzi *et al.*'s study were small peripheral LEDs, quite unlike the face and object stimuli used in the fMRI work, so no direct comparison can be made.

Eimer and colleagues (Eimer, Wojciulik, Husain, and Driver, unpublished data) recently used ERP measures to study extinction with face and house stimuli. Moreover, they tested the same patient (KG) that had been studied with fMRI by Rees *et al.* (2000, and submitted), using exactly the same stimuli and task. Similar results were observed to those reported by Marzi *et al.*

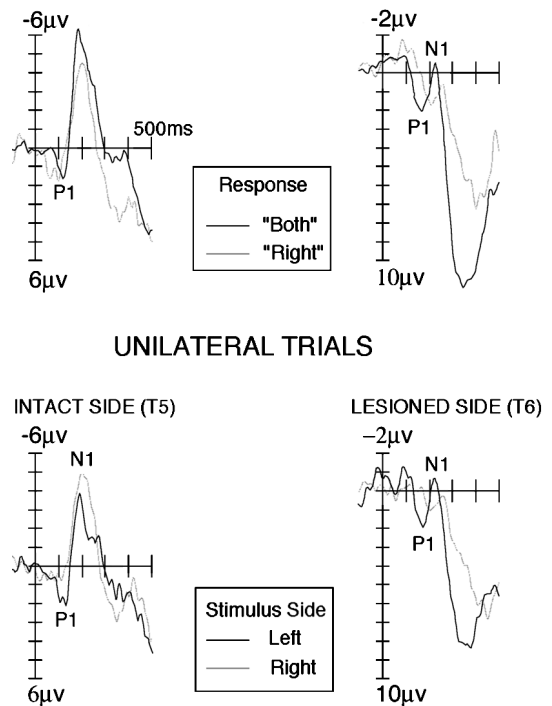


FIG. 3. ERPs recorded at lateral posterior electrodes over the intact left hemisphere (T5) or lesioned hemisphere (T6) of patient GK, who was studied with fMRI by Rees *et al.* (2000, and submitted) using the same face and house stimuli. Data from an unpublished study by Eimer, Wojciulik, Husain, and Driver. The upper two graphs show ERPs for bilateral trials, with (dotted lines; 25% of trials) versus without (solid lines) extinction. The lower two graphs are for unilateral trials, with a stimulus presented in just the left (solid lines) or right (dotted lines) visual field. Results are similar to those reported by Marzi *et al.* (2000), using very different stimuli. P1 and N1 components are delayed and/or attenuated over the lesioned hemisphere. N1 is attenuated over both hemispheres for bilateral trials where the left stimulus is extinguished rather than detected. P1 and N1 are absent or attenuated over the damaged hemisphere for unilateral stimuli in the ipsilateral (right) visual field.

al. (2000), despite the very different stimuli. ERPs recorded at lateral posterior electrodes over the intact and damaged hemisphere are shown in Fig. 3. Over the intact hemisphere, P1 and N1 components were apparent on bilateral trials with and without extinction, although the N1 was attenuated when extinction arose. P1 and N1 components were also present over the damaged hemisphere (albeit reduced relative to the intact hemisphere) on those bilateral trials where both stimuli were correctly reported; but appear absent on the 25% of bilateral trials where extinction arose. Unlike the fMRI findings from the very same patient (Rees *et al.*, 2000, and submitted), no ERP evidence was found for unconscious face-specific responses such as an N170 to an extinguished left face (Allison *et al.*, 1994; Bentin *et al.*, 1996). However, in this patient the N170 was absent over the right hemisphere even for single faces that were consciously seen.

Vuilleumier *et al.* (2001) also conducted ERP recordings with their patient CW, using the same face/object stimuli and face-detection paradigm as in their fMRI study. They compared bilateral trials where a left face was detected against bilateral trials with extinction. A right occipital P1 was found when the left face was detected, but not when it was extinguished, consistent with the above findings. Moreover, comparing trials with an extinguished left face (plus a right object) against those with only a right object was reported to show some N170 response to the extinguished face, demonstrating residual unconscious processing of extinguished stimuli, as also suggested by the fMRI activations to extinguished faces described above.

Although the pathology of extinction patients is most apparent behaviorally during bilateral rather than unilateral stimulation, the neural responses to unilateral stimuli may also show lateralized abnormalities in at least some cases (e.g., Spinelli *et al.*, 1994; but see Verleger *et al.*, 1996). The ERPs for unilateral trials in Rees *et al.*'s (2000) patient KG, recorded by Eimer and colleagues, demonstrate this (see Figs. 3c and 3d). Both P1 and N1 components were considerably delayed at occipital sites over the damaged right hemisphere (and the N1 was also attenuated) relative to those found over the intact hemisphere. Moreover, no detectable P1 and N1 components were elicited over the damaged right hemisphere by stimuli in the ipsilateral (right) visual field, as if callosal transmission to the damaged hemisphere might be disrupted (Marzi *et al.*, 1997; see also Marzi *et al.*, 2000; Vuilleumier *et al.*, 2001, for similar results from further patients). Thus, sensory ERP responses over the damaged hemisphere may be abnormal in some extinction patients, even to unilateral stimuli that are consciously detected. This may reflect an underlying deficit in unilateral processing that is exacerbated by competition on bilateral trials to produce the loss of awareness.

CONCLUSIONS AND ISSUES FOR FUTURE RESEARCH

Extinction after right-parietal injury involves a selective disturbance to perceptual awareness, which is most apparent during competing bilateral stimulation. In addition to its clinical importance, extinction offers an opportunity to study the neural correlates of conscious and unconscious perception, including the role of parietal cortex. The recent fMRI studies (Rees *et al.*, 2000; Vuilleumier *et al.*, 2001; Rees *et al.*, submitted) reveal that extinguished stimuli can activate occipitotemporal visual areas, including category-specific areas of ventral cortex. Such activation is apparently not sufficient to engender perceptual awareness when pa-

rietal cortex is damaged, despite past claims that ventral activity alone may provide the neural substrate of conscious vision (Milner and Goodale, 1995).

The initial fMRI findings for the comparison of seen versus extinguished visual stimuli, within particular patients, suggest increased activation of areas in visual cortex; plus, intriguingly, of more anterior structures in the intact left hemisphere, including parietal areas symmetric to those damaged in patients with extinction (see Fig. 2). Previous speculations about the neural correlates of visual awareness have typically emphasized either just the level of activity in posterior visual areas (e.g., Zeki and Bartels, 1999; Grill-Spector *et al.*, 2000), or instead a critical role for interactions between a diffuse network of brain areas (e.g., Baars, 1998; Dehaene *et al.*, 1998), including parietal and frontal cortex (e.g., Lumer and Rees, 1999; Driver and Vuilleumier, 2001; Rees, in press). These contrasting proposals may not be mutually exclusive, as suggested by our findings that conscious detection in extinction patients may be associated *both* with higher activity in posterior visual areas, and also with activity in parietal and frontal areas (see also Driver and Vuilleumier, 2001; Rees, in press).

The recent ERP studies of extinction (Marzi *et al.*, 2000; Vuilleumier *et al.*, 2001; Eimer *et al.*, unpublished) show that relatively early visual components (e.g., P1 and N1) may be attenuated for extinguished compared with consciously seen contralesional stimuli on bilateral trials. This might appear paradoxical, given the other evidence that extinguished stimuli can receive considerable residual unconscious processing (e.g., activation of the FFA and/or preserved N170). However, there is no logical inconsistency in processing of contralesional stimuli becoming abnormal quite early in visual processing, and yet still proceeding to higher levels. The parietal (and/or frontal) lesions typically associated with extinction and neglect may systematically disrupt early visual processing in more posterior areas (as some of the evidence already suggests even for unilateral stimulation). This may involve disruption of modulatory feedback from parietal and frontal areas to occipitotemporal areas. Such feedback is often invoked to explain the effects of attention on visual processing in neurologically healthy individuals (e.g., Lamme and Roelfsema, 2000). Further studies of lesioned patients may help to establish a causal role for such feedback in modulating early visual responses.

It will be important to combine fMRI and ERP (and possibly MEG) methods in future studies of extinction patients, given the complementary strengths and weaknesses of these techniques. Additional methodological improvements could include retinotopic mapping with fMRI, to define distinct visual areas functionally in each patient; precise eye-position monitoring, to ensure that

no saccades or small drifts in fixation can contaminate the comparison of seen and extinguished trials; and comparison of different patient groups. The existing studies already indicate the feasibility of such an approach.

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