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Awareness-related activity in prefrontal and parietal cortices in blindsight reflects more than superior visual performance

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ABSTRACT

Many imaging studies report activity in the prefrontal and parietal cortices when subjects are aware as opposed to unaware of visual stimuli. One possibility is that this activity simply reflects higher signal strength or the superior task performance that is associated with awareness. To find out, we studied the hemianope GY who has unilateral destruction of almost all primary visual cortices. He exhibits 'blindsight', that is, he claims to have no conscious visual phenomenology (i.e., no visual qualia), for stationary stimuli presented to his right visual field (the blind field), although he can press keys to distinguish between different stimuli presented there. We presented to him a visual discrimination task, and equated performance for stimuli presented to the left or right visual field by presenting low contrast stimuli to his normal (left) field and high contrast stimuli to his blind (right) field. Superior accuracy can be a serious confound, and our paradigm allows us to control for it and avoid this confound. Even when performance was matched, and the signal strength was lower, visual stimulation to the normal (conscious) field led to higher activity in the prefrontal and parietal cortices. These results indicate that the activity in the prefrontal and parietal areas that has been reported in previous studies of awareness is not just due to a (signal strength or performance) confounds. One possibility is that it reflects the superior 'metacognitive' capacity that is associated with awareness, because GY was better able to distinguish between his own correct and incorrect responses for stimuli presented to his normal field than to his blind field.

Introduction

Many brain imaging studies in healthy human participants have reported that visual awareness is associated with higher activity in the prefrontal and parietal cortices (Rees et al., 2002). Typically, when one compares a condition that involves consciously seen stimuli, against a condition where stimuli are not consciously seen, one finds heightened activity in these brain regions. It has been suggested that the activity reflects the global broadcast of the signal to a cortical network that is the critical mechanism for awareness (Dehaene et al., 2003).

However, there are alternative, and arguably more parsimonious, interpretations. Previous work shows that the prefrontal cortex is involved in metacognition (Fleming et al., 2010), and metacognition, though closely linked to awareness, is not identical to awareness (Lau and Maniscalco, 2010). Therefore, activations in the prefrontal cortex may simply reflect signal strength or superior task performance, as well as metacognition. Superior task performance has been shown for the dorsolateral prefrontal cortex (dlPFC) (Lau, 2008; Lau and Passingham, 2006; Nagel et al., 2009), though such activations are generally weaker and less widespread when subjects are unaware. In the 'aware' condition, participants typically perform visual judgments well above chance, whereas in the 'unaware' condition they typically perform at a near-chance level. So the activations in the prefrontal and parietal cortices could just reflect these confounds and not visual awareness.

It might be thought that task performance capacity is a hallmark of awareness, or perhaps that the two are even one and the same. However, the neurological condition of blindsight provides a clear counter-example (Stoerig and Cowey, 1997, 2007; Weiskrantz, 2009). Patients with blindsight typically have restricted lesions to the primary visual cortex, which lead them to claim a lack of visual awareness. For static stimuli that are presented to the 'blind' field

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there is no conscious visual phenomenology (Persaud and Lau, 2008). Nonetheless, these patients can perform well above chance when required to identify a stimulus in a forced-choice setting.

Many of these studies have been carried out with subject GY (Barbur et al., 1994; Bridge et al., 2008; Kentridge et al., 1997; Persaud and Lau, 2008; Silvanto et al., 2009; Weiskrantz et al., 1995). The damage to GY's primary visual cortex is restricted to the left hemisphere, which leads to his being subjectively 'blind' in his right visual field except for a few degrees of macular sparing. Both functional magnetic brain imaging (fMRI) and magneto-encephalography (MEG) have been used to compare brain activity when visual stimuli are presented to the blind and normal fields.

Sahraie et al. (1997) used fMRI and presented a single moving spot in GY's blind or normal visual field. They reported that he could discriminate between two directions of motion even when the stimulus was presented to the blind field, and that he could do this with slow motion even though he was perceptually unaware of it. When a moving stimulus was presented to the normal field, there was activity in the lateral prefrontal cortex, and the same was true when fast moving stimuli of which GY was aware were presented to the blind field. However, when slowly moving stimuli were presented to the blind field, GY was unaware, and there was no activity in the lateral prefrontal cortex.

Schurger et al. (2006, 2008) used MEG, and presented static stimuli. Among trials where stimuli were presented to the 'blind' field, for which GY has no conscious visual phenomenology, there were trials on which GY claimed to be "aware that something was presented". In blind side trials both with and without this "awareness", GY discriminated between the stimuli above chance levels, and the performance was similar between these trial types. It was found that this "awareness" was associated with heightened oscillatory activity in the gamma band in the occipito-parietal areas. Taken together, these studies suggest that activity in the prefrontal and parietal cortices can reflect awareness even when task performance does not differ.

However, it is important to distinguish this type of secondary awareness from the visual awareness that has been studied in fMRI studies performed on healthy volunteers (Rees et al., 2002). These have set out to address conscious visual phenomenology. Furthermore, in the studies of GY by Schurger et al. (2006, 2008), task performance typically differed depending on whether the stimuli were presented to the normal or blind visual field. For this reason, in the present experiment we took the opportunity to further study GY, and to carefully match for task performance between the fields. We did this by titrating the contrast of the stimuli for each field independently.

As previously documented (Barbur et al., 1994; Kentridge et al., 1997; Weiskrantz et al., 1995), GY can perform well above chance when stimuli are presented to his blind field. Since his performance depends on the strength of the stimulus (e.g., luminance contrast or speed) as suggested by Weiskrantz et al. (1995), this means that one can produce conditions in which performance is matched for stimuli that are presented to the 'blind' and 'normal' fields. This can be achieved by presenting a strong stimulus to the former and a weak stimulus to the latter, a method which has previously been used with GY to examine qualitatively different patterns of sensitivity between his normal and blind fields (Azzopardi and Cowey, 1997; Kentridge et al., 1999). This allowed us to ask whether, when performance was matched, there would still be higher activity in the prefrontal and parietal cortices when stimuli are presented to the normal as opposed to the blind field. To anticipate, the answer is: yes, there is. The implication is that the difference in activation does not reflect differences in performance, but something else, such as visual phenomenology or metacognitive activity, which may be closely linked to, but not identical to, visual awareness (Lau and Maniscalco, 2010).

Methods

Participant

The participant was GY, a 52-year-old man who incurred a unilateral traumatic destruction of almost his entire left striate cortex at the age of 8 years. This produced a right homonymous hemianopia with macular sparing extending 3.5° into the otherwise blind right field (Barbur et al., 1994). He has residual visual sensitivity within his scotoma that enables him to detect, localize, and discriminate certain transient stimuli all of which he denies seeing and for many of these he has no visual awareness. This is the defining characteristic of blindsight (Barbur et al., 1994; Weiskrantz, 2009; Weiskrantz et al., 1995). GY gave informed written consent.

Task

The task was to report the location (upper or lower quadrant) of a vertical square-wave grating while fixating a central cross (Fig. 1). Visual stimuli were back-projected by a liquid crystal display video projector onto a screen which the subject viewed through an angled mirror. On each trial two isoluminant 10° square gratings made up of ten bars each appeared for 500 ms in either the left (normal) field or the right (blind) field with the medial edge 5° from the vertical meridian. The bottom of the upper grating met the top of the lower grating at the horizontal meridian. The bars in one pseudo-randomly determined and equally-balanced grating were horizontal and the bars in the other were vertical. The locations of the low and high luminance bars within each grating were pseudo-randomly jittered between presentations to avoid retinal adaptation. Eye-movements were recorded using an ASL 5000 pupillometer (Applied Science Laboratories, MA). As expected based on previous experiments, GY was excellent in maintaining fixation, and therefore no rejection of trials was needed.

After the gratings disappeared, GY was prompted by the words 'Up/Down' to report the location of the vertical grating. He responded by pressing a button with either his right index or middle finger. He was then prompted to make one of two 'meta-responses' that were explained to him beforehand. In the first, referred to as 'Coin flip/Response', GY decided whether he wanted to be paid 50 p based either on the flip of a coin (i.e. he would have a 50% chance of winning 50 p and a 50% chance of losing 50 p) or on whether his 'Up/Down' response was correct (i.e., he would earn 50 p if his decision was correct or lose 50 p if his decision was incorrect). This was a variant of a postdecision wagering procedure (Persaud et al., 2007) called "no-loss wagering" (Dienes and Seth, 2010), which essentially tracked GY's confidence in his own response. In the second meta-response condition, referred to as 'Guess/Seen', GY had to report whether his 'Up/Down' decision was a mere guess or whether it was based on some awareness, and he always earned 50 p for correct visual discriminations, regardless of the meta-response. This 'Guess/Seen' reporting is a standard 'commentary key' procedure used in numerous previous studies on blindsight (Weiskrantz, 2009). Trials always ended 4 s after they began, regardless of when GY responded. The percentage of trials terminated due to lack of an answer was 2%; such trials were discarded from further analysis. Each prompt disappeared after GY made his response.

Blocks were composed of 36 trials, arranged in groups of 6 during which the stimulus appeared to the same hemifield. In each block, there were 4 blind hemifield groups and 2 normal hemifield groups. Contrast levels were independently titrated by hemifield in order to match 'Up/Down' discrimination accuracy between the two fields. Four different contrast levels were used (two for each hemifield), computed with standard 1-up–2-down and 1-up–3-down staircase procedures for each hemifield prior to the main experiment. The staircases compute contrasts that result in 71% and 79% accuracies

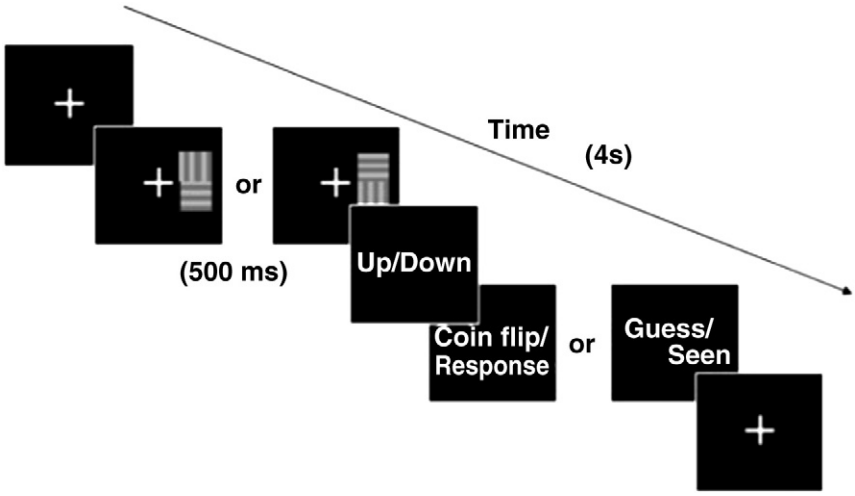

Fig. 1. Task design. After a fixation period, a pair of gratings appeared, one in the upper visual quadrant and one immediately to it in the lower visual quadrant, in the left or right hemifield for 500 ms. GY was then prompted to respond either 'Up' or 'Down' by pressing a button to indicate if the vertical grating was above or below the horizontal grating. In the 'wagering' blocks, immediately after this response was made he was prompted either to respond 'Coin flip' or 'Response'. 'Coin flip' means he would have equal random chance to gain or lose 50 British pence (~1 US dollar). 'Response' means that he would gain or lose depending on whether his visual judgment was correct. In other blocks, no monetary gains or losses were involved, and he simply indicated whether he saw the visual targets ('Seen') or not ('Guess'). If both responses were not made within 4 s, a 'Too late' message appeared on the screen.

(Levitt, 1971), respectively, for an average accuracy of 75% (assuming equal numbers of stimuli for each contrast). The resulting contrasts were 0.0012 and 0.002 in the normal field and 0.58 and 0.72 in the blind field.

In total, GY performed 20 blocks of 720 trials (480 blind, 240 normal) in the 'Coin flip/Response' performance-matched condition and 8 blocks of 288 trials (192 blind, 96 normal) in the 'Guess/Seen' condition. He first began with eight blocks of 'Coin flip/Response' responses, then four blocks making 'Guess/Seen' responses, eight blocks making 'Coin flip/Response' responses, four blocks making 'Guess/Seen' responses, and finally four more blocks making 'Coin flip/Response' responses. All blocks were run on the same day.

Data acquisition

Functional imaging was conducted with a Siemens (Erlangen, Germany) Allegra 3.0 T scanner to acquire gradient echo T2*-weighted echo-planar images (EPIs) with blood oxygenation level-dependent (BOLD) contrast as an index of local increases in synaptic activity. The image parameters were as follows: matrix size, 64×64; in-plane voxel size, 3×3 mm; echo time, 40 ms and repetition time, 2600 ms. A functional image volume comprised 40 contiguous slices of 2 mm thickness (with a 1 mm interslice gap), which ensured that the whole brain was within the field of view.

fMRI data analysis

All fMRI preprocessing and standard GLM analyses were done using SPM5. The initial 6 frames of data from each run were discarded to avoid equilibrium effects. Data were motion-corrected using rigid-body transformations. The first frame of each run was aligned to the first frame of the first run, and all other frames were aligned to the first frame of their run, using 2nd degree B-splines. Data were then spatially smoothed with an 8 mm FWHM Gaussian kernel.

Task-related hemodynamic responses were estimated with a finite impulse response (FIR) model with 6 bins of 2.6 s. Movement parameters from the motion-correction step were included as nuisance covariates. Constant terms were included to account for overall session effects. Serial correlations were estimated with an AR (1) autoregressive model. The model included a high-pass filter at 1/128 Hz. All contrasts were estimated using the sum of the appropriate FIR time bins, akin to estimating the area under the curve of the hemodynamic response function. The reason for choosing to use the FIR model was based on initial observation of the data, in which the canonical hemodynamic response function (HRF) showed a relatively poor fit to GY's data. The FIR model has the advantage of making no strong assumption regarding the shape of GY's hemodynamic responses. This procedure was used in one of our previous studies (Lau and Passingham, 2006). Initial height thresholds were set at $p<0.001$, uncorrected, and all the figures that show activations are displayed at this level.

Results

Behavioral results

Overall, GY performed at 76% correct for stimuli presented to the normal field and 79% correct for stimuli presented to the blind field. These values were within the expected range resulting from our procedure of contrast titration (see Methods). These values did not differ significantly (chi-square test, $p=0.34$, Fig. 2A). Interestingly, the reaction times were significantly shorter for trials for the blind field than for the normal field (796 vs. 937 ms, *t*-test, $p<0.0001$).

Although accuracy was matched between the hemifields, the level of visual awareness differed markedly. GY indicated that he consciously saw the targets in 43% of the trials in the normal field, and in only 3% of the trials in the blind field. These values differed significantly (chi-square test, $p<0.0000001$, Fig. 2B). Just as surprisingly, GY was equally willing to wager on trials for both hemifields. He chose to wager based on his visual judgment (rather than a coin flip) 66% of the time for the normal field, and 69% of the time for the blind field (chi-square test, $p=0.32$, Fig. 2C). Unlike his visibility judgments, this suggests that GY has fairly high confidence in his blindsight abilities, perhaps due to his long experience with blindsight and his knowledge that he can perform accurately.

Although objective performance overall is matched, the conditional distribution of % correct differed slightly. In the normal hemifield, trials reported "seen" were 95% correct, trials reported "guess" were 64% correct. In the blind hemifield, "seen" trials were 83% correct, "guess" trials were 74% correct. These values were not significantly different (chi-square test, $p=0.22$). Still, it's possible that the underlying processes are different (Lamy et al., 2009), so we

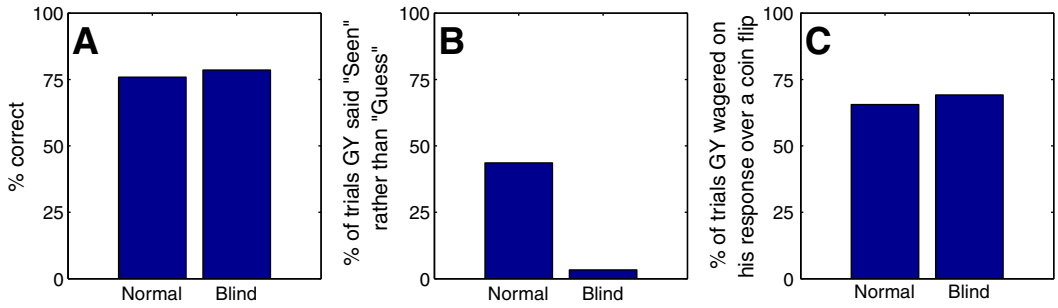

Fig. 2. Behavioral responses. A: Percentage correct is closely matched between hemifields. B: GY indicated that he consciously 'saw' the targets much more frequently in his normal field than in his blind field. C: After matching for performance, GY is equally willing to wager on his response in both conditions.

should compare the subjective reports between the two hemifields with caution. On the other hand, evidence suggests that the conscious experience between GY's hemifields does differ, and this could reflect this fundamental difference that is of critical interest to the present study.

fMRI differences between normal and blind fields

There was significantly higher cortical activity for stimuli presented to the normal field rather than to the blind field (Fig. 3). And this was true in spite of the fact that performance and confidence were matched as shown in the previous section.

Table 1 shows the coordinates for the peaks of activation. When contrasting stimulation of the normal as opposed to the blind field, the activations lay in the intra-parietal cortex and superior temporal sulcus posteriorly, and in the ventral prefrontal and polar cortices anteriorly. The peak at −58, −27, 52 lies on the borders between the tip of the intra-parietal sulcus and the postcentral sulcus, and is tentatively assigned to the former.

When contrasting stimulation of the blind as opposed to the normal field, there was an activation for the blind field that lay medially in the amygdala (Fig. 4).

In addition, we also looked at more specific comparisons such as "blind correct-unseen vs. normal correct-unseen" trials, but due to the restricted number of trials that involved Seen/Guess judgments, our power was heavily reduced, and we failed to find anything systematic. This is a limitation of single-subject studies, where only so much data can be collected.

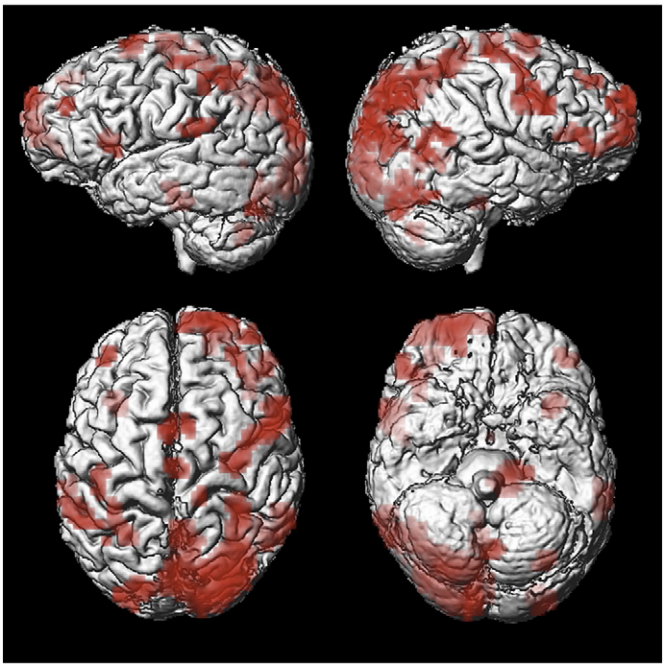

Fig. 3. Activations for all stimulations in the normal field over stimulations to the blind field, thresholded at $p<0.001$, uncorrected for display purposes. All clusters are significant at cluster-corrected p-values <0.05.

Differences between hemifields in the capacity for 'metacognition'

Although we succeeded in matching for accuracy between the hemifields, there are other cognitive processes besides awareness that may differ. Previous studies (Kornell et al., 2007) have measured the correlation between confidence ratings and accuracy, and used that as an index of metacognitive capacity. This is a measure of how well one can distinguish between one's own correct and incorrect trials, by placing confidence or wagering ratings appropriately (e.g., accurate answers should be associated more frequently with the 'Response' metacognitive rating) (Fig. 5).

In our study, we computed the correlation coefficient *r* between wagering choice and accuracy across all trials within a hemifield, and found it significantly higher in the normal field than in the blind field (0.52 vs. 0.30, test of differences using Fisher's r-to-z transform, $p<0.001$). Since we presented to each field two different levels of stimulus contrast, we attempted to match for metacognitive performance by comparing only the higher contrast trials in the blind field vs. the lower contrast trials in the normal field. However, even in that case, where objective performance was higher in the blind field than in the normal field, the metacognitive capacity (correlation coefficient *r*) was still higher in the normal field (0.45 vs. 0.25, test of differences using Fisher's r-to-z transform, $p<0.005$).

Table 1
Results of the contrasts between normal and blind hemifields, and within the blind hemifield, between correct and incorrect responses.

Contrast normal–blind		
Area	Coordinates (MNI)	p-value (cluster-corrected)
R caudal intra-parietal sulcus	24, −83, 34	<0.000001
L anterior intra-parietal	−58, −27, 52	0.01
R superior temporal sulcus	61, −47, 19	0.005
L parahippocampal cortex	−12, −23, −23	0.021
R pre-SMA	1, 17, 61	0.013
R ventral prefrontal cortex	58, 18, 22	<0.00001
R orbital prefrontal cortex	46, 37, −3	0.049
R frontal polar cortex	38, 61, 13	<0.000001
Contrast blind–normal		
Area	Coordinates (MNI)	p-value (uncorrected)
L amygdala	−12, −1, −18	0.029
Contrast blind correct–incorrect		
Area	Coordinates (MNI)	p-value (cluster-corrected)
L parahippocampal gyrus	−15, −17, −24	<0.0002

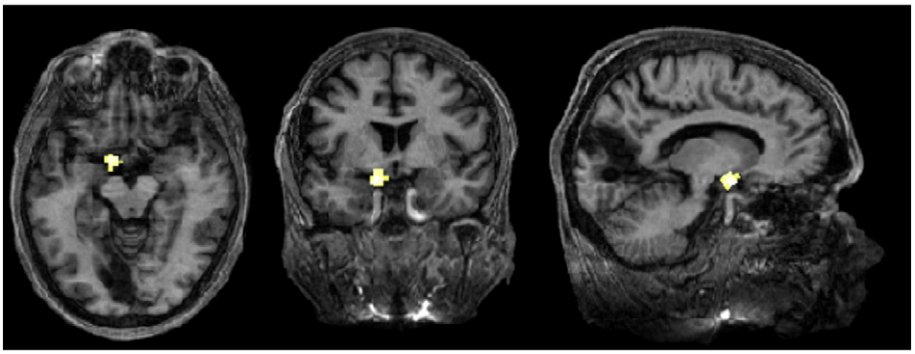

Fig. 4. Activations for all stimulations in the blind field over stimulations to the normal field, thresholded at $p<0.001$, uncorrected for display. The cluster at the subcortical location displayed did not survive correction for multiple comparisons ($p=0.289$). The coordinates were −12, −1, −18 in MNI space.

Discussion

Our question was whether activation in the prefrontal and parietal cortices genuinely reflects visual awareness per se, as suggested by previous studies. One alternative interpretation is that it reflects signal strength or the superior task performance that is typically associated with conditions in which the stimulus leads to conscious visual phenomenology. Our results rule out this alternative interpretation. We found activity in these areas even with weaker stimuli and controlling for task performance. We equated for performance by titrating the luminance contrast of the stimulus such that the accuracy between the normal and blind fields in GY was matched. The effect was that GY was equally confident of his responses in both fields, as shown by the fact that he was prepared to wager the same amount on being correct whether the stimuli were presented to his normal or blind field.

If anything, GY's reaction times were shorter for the blind field, which suggests that his overall performance capacity may even be somewhat higher in the blind field than in the normal field. Yet, there was more activity in the prefrontal and parietal cortices associated with stimulations of the normal visual field. The fact that his reaction times were significantly longer when the stimuli were presented to the normal field may explain the greater activation in the pre-SMA in this condition and that having a real visual percept actually makes one slower.

Awareness

When the stimuli were presented to the normal, as opposed to the blind field, there were also activations in the dorsal visual system and in the prefrontal cortex. The peaks in posterior cortex lay in the intra-parietal sulcus and in the superior temporal sulcus. The peaks in the prefrontal cortex lay in the ventrolateral and polar prefrontal cortices. The ventrolateral prefrontal cortex receives projections from both the intra-parietal (Borra et al., 2008) and superior temporal sulci (Seltzer and Pandya, 1989). There were also activations in these areas in a study by Lumer and Rees (1999) using binocular rivalry to identify regions that are active when the participants report transitions from awareness of one stimulus to awareness of the other. In that study the stimuli were a slow moving grating and a face.

In a previous fMRI study, we used metacontrast masking to create 'relative blindsight' in healthy participants. We arranged conditions in which performance was matched but there was a difference in the proportion of trials on which the subjects claimed that they had 'seen' the target. Activation in the anterior prefrontal cortex was associated with higher ratings of awareness. The peak at −46, 48, 14 in the study

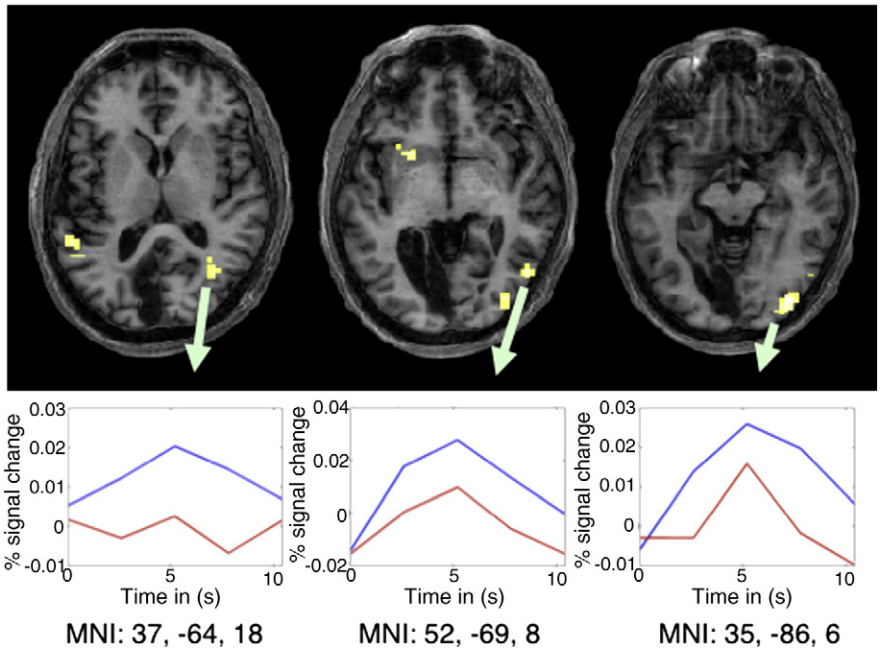

Fig. 5. Activity that distinguishes correct responses over incorrect responses for stimulations to the normal hemifield, thresholded at $p<0.001$, uncorrected for display purposes. Only the cluster indicated in the rightmost slide survived whole brain correction ($p<0.05$). All reported coordinates are in MNI space.

of relative blindsight lies near to, though posterior to, the peak at 38, 61, 13 for polar cortex in the present study of GY. However, the results of the study on healthy participants differ from those of the study on GY in that there were no significant activations in the parietal cortex.

Dehaene et al. (2003) have suggested that the parietal and prefrontal cortices act as a 'global workspace'. They suggest that perception is conscious when there is a 'global broadcast' through these areas. In a recent EEG study, those authors (Gaillard et al., 2009) reported that there is temporal synchrony in the beta band across long cortical distances when visual masking is used to compare conditions in which the participant is or is not aware. However, one would expect that a 'global broadcast' via the prefrontal and parietal cortices would have functional significance (Lau and Rosenthal, 2011). In other words, a stimulus that triggers such widespread activity should lead to higher task performance. But in the present study, task performance was matched, and yet we still found activations throughout the parietal and prefrontal cortices that were related to awareness. This does not mean that the global workspace theory is wrong, it just means that the activation in the PFC probably reflects more than solely global broadcast, which should affect task performance.

There are, however, alternate possibilities that also need to be considered. One is that widespread parietal–frontal activity reflects not awareness, but preparatory flexibility, or other processes that are only *associated* with awareness, but not awareness itself. Our data cannot rule this out. A second possibility relates to the strength of the stimuli themselves. In order to match for performance, we presented high-contrast stimuli to the blind hemifield, and low-contrast stimuli to the normal field. One possibility is that widespread activation is due to the brain working harder to amplify a weak signal. However, it's generally the case that brain activity increases monotonically with contrast (Boynton et al., 1999), so if anything, perhaps we should expect to see the opposite pattern based on stimulus contrast alone.

Another possibility is that these activations relate to metacognition instead of awareness per se. GY was better at monitoring his performance in the normal field than the blind field, i.e., the correlation between his willingness to wager his accuracy was higher when the stimuli were presented to his normal than to his blind field. In a previous study we used transcranial magnetic stimulation to temporarily inactivate the prefrontal cortex in healthy participants (Rounis et al., 2010). Theta burst stimulation was applied bilaterally before the visual stimuli were presented. The stimulation had no effect on task performance, but it did decrease the correlation between confidence ratings and accuracy. In other words, stimulation had the effect of lowering the metacognitive capacity. In addition, we found frontopolar activation in GY, which has been found to be associated with higher metacognitive ability (Fleming et al., 2010). So while there were substantial differences in awareness between GY's hemifields, the possibility that widespread activity reflects pure metacognitive capacity rather than awareness cannot be ruled out either.

Blindsight

Since GY exhibits blindsight, we were also able to assess whether, even when performance and wagering were matched, there were activations when the stimuli were presented to the blind as opposed to the normal field. We found one such activation, and this lay medially in the left amygdala (Table 1). Since wagering (and thus confidence) was matched, it is unlikely that the activation of the amygdala is due to GY being anxious about judgments that are made when the stimuli are presented to the blind field. Nor do the judgments concern fear-inducing items as in the experiments with GY on fearful vs. non-fearful facial expressions (Morris et al., 1999, 2001). The latter authors have claimed that there is a 'fast' pathway via which visual information from the eye to the superior colliculus reaches the amygdala. However, though it is true that the superior colliculus projects to the inferior pulvinar (Benevento and Rezak, 1976), it is the medial pulvinar that is connected with the amygdala (Jones and Burton, 1976). The alternative is to suppose that, when a stationary grating is presented to GY's blind field, there is activation in the infero-temporal cortex, since there are abundant connections between the infero-temporal cortex and the amygdala (Baizer et al., 1993). Activations of the infero-temporal cortex could be dependent on cortical input from the konio-cellular rich layers of the lateral geniculate, since it has been shown that inactivation of the region of the lateral geniculate nucleus corresponding to the field defect abolishes the extra-striate visual responses that survive a striate lesion (Schmid et al., 2010).

Even if this explanation were correct, the activation of the amygdala does not explain GY's ability to discriminate between stimuli that he does not see. There is no differential activation of this structure when his judgments for stimuli in the blind field are correct as opposed to incorrect. Instead the differential activation lies in the left parahippocampal gyrus (Table 1). The peak at −15, −17, −24 lies close to the peak at −12, −23, −23 for the comparison of normal–blind. Given that GY was more confident in his judgments that turned out to be correct than in his judgments that turned out to be wrong (as reflected by the fact that accuracy and tendency to wager on his response were correlated), it is possible that this activation related to some aspect of his subjective (non-visual) experience (Fig. 6).

Given that blindsight is generally accepted to be due to weaker, more proscribed subcortical pathways, one could argue that a lack of widespread activation for blind field stimulation is to be expected. However, several studies have demonstrated that unconscious stimuli can activate widespread cortical networks. In an unconscious cognitive control paradigm, Lau and Passingham (2007) found greater left dlPFC activity. Van Gaal et al. (2010) found bilateral inferior frontal cortex (IFC) and pre-supplementary motor area (pre-SMA) in an unconscious go/no-go task. Using frequency-tagged stimuli with a binocular rivalry paradigm, Tononi et al. (1998) found power at the frequency of the nondominant stimuli for multiple parietal and frontal sensors. Therefore, our present finding is not trivial.

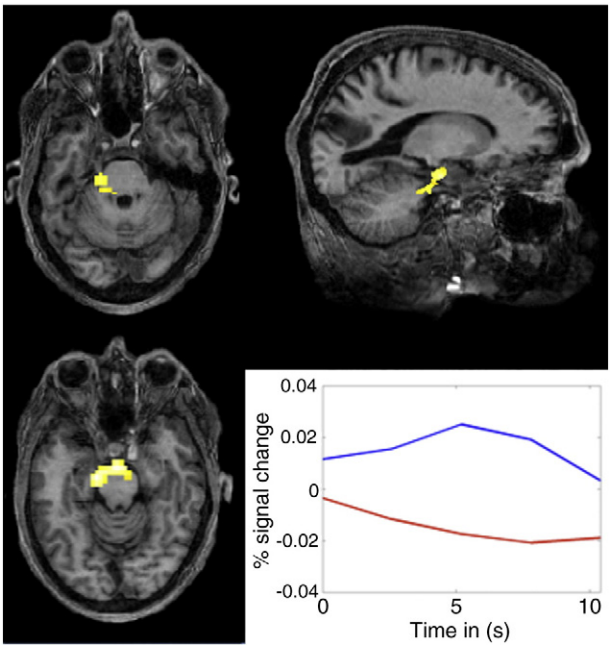

Fig. 6. Activity that distinguishes correct responses over incorrect responses for stimulations to the blind hemifield, thresholded at $p<0.001$, uncorrected for display purposes. Cluster-corrected p-value<0.001. All reported coordinates were in MNI space. ROI coordinates were normalized to MNI space: −15, −17, −24.

Finally, given that blindsight is a rare and unusual condition, it's not guaranteed that our findings generalize to the population at large. It could be that due to his lesion or his subsequent cortical reorganization that GY has a totally unique response. GY has an abnormal connection from the contralesional lateral geniculate nucleus (LGN) to his ipsilesional V5/MT+ and hypernormal connections between the two V5/MT+ areas. TMS stimulation to GY's ipsilesional V5/MT+ can influence the appearance of V1 phosphenes on his undamaged side (Silvanto et al., 2009), so it's possible that GY is recruiting cortex that normal subjects or other blindsight subjects would not. In such a case, these recruited areas would effectively disappear in Blind vs. Normal contrasts, due to being more closely matched in terms of activity levels between the two conditions. However, GY's results do accord with earlier findings from Lau and Passingham (2006), which used a metacontrast masking paradigm to match for performance, but not awareness, in normal subjects, and found a difference in activity in the left dlPFC.

Conclusion

Blindsight is a condition that is associated with destruction of the primary visual area. However, a lesion to one area may change activity in other distal brain regions. By presenting stimuli of different luminance contrast to the normal and blind fields of GY, we matched for his performance capacities between the two fields. We found that stimulation of the normal field was associated with significant activations in the prefrontal and parietal areas, as compared to stimulations of the blind field. These results are compatible with the suggestion that the mechanisms of conscious visual awareness may depend at least in part on activity in these regions.

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