

Induced gamma-band oscillations correlate with awareness in hemianopic patient GY

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Abstract

In normal vision gamma oscillations are involved in object perception, are modulated by attention, and have been linked to awareness by way of their putative role in perceptual integration, arguably as a mechanism for synchronizing activity in separate neural assemblies. We tested the hypothesis that the presence of gamma oscillations (~30–80 Hz) signal the entry of a neural representation into awareness (as indexed by direct report), while attempting to control for other measures of neural information processing such as discrimination accuracy and reaction time. Hemianopic patient GY sometimes reports an awareness “that something happened” in his blind visual hemifield, in response to stimuli of sufficiently high contrast, although he may deny “seeing” anything. At lower contrast levels GY denies any awareness, but may continue to exhibit greater-than-chance accuracy (blindsight). Using a near-threshold level of contrast offers a unique way to test hypotheses concerning correlates of perceptual awareness, since GY’s accuracy on certain tasks is independent of awareness. We tested GY on an orientation–discrimination task using stationary stimuli at a fixed near-threshold level of contrast, to which GY sometimes responded “aware” and sometimes “unaware”. We recorded brain activity using magnetoencephalography (MEG) in order to determine the relationship between local induced gamma-band oscillations and awareness. GY’s accuracy was significantly greater than expected by chance and no different whether or not he reported awareness of the stimulus. Oscillatory activity in the gamma band (44–66 Hz) over the left occipito-parietal region correlated significantly with awareness (but not accuracy), whereas activity in the alpha band (8–12 Hz) did not.

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1. Introduction

There is a strong and growing consensus that, in order for awareness to arise, different cortical areas must not only interact with one another, but must interact in a *reciprocal* manner (Bullier, 2001; Dehaene, Sergent et al., 2003; Hochstein & Ahissar, 2002; Lamme & Roelfsema, 2000; Pollen, 2003; Tononi, Edelman et al., 1998; Varela, Lachaux et al., 2001). Recent experiments involving trans-cranial magnetic stimulation (TMS) bear this out, suggesting, for example, that feedback from V5/MT to V1 is necessary for awareness of motion phosphenes (Cowey & Walsh, 2000; Pascual-Leone & Walsh,

2001). There is also a growing body of evidence linking induced (i.e. non-phase-locked, see Tallon-Baudry & Bertrand, 1999) oscillatory neural activity in the gamma frequency band (~30–80 Hz) with high-level cognitive and perceptual processing (for review see Herrmann, Munk et al., 2004; Kaiser & Lutzenberger, 2003; Tallon-Baudry & Bertrand, 1999). Such oscillations may figure prominently in the process of perceptual integration, arguably as a mechanism for maintaining coherent interactions among an ensemble of widely distributed neurons, columns, or functional areas (Engel, Roelfsema et al., 1997; Kaiser & Lutzenberger, 2003; Lee, Williams et al., 2003; Singer & Gray, 1995; Tallon-Baudry, 2003), which is thought to be necessary for awareness (Engel & Singer, 2001; Sauve, 1999; Treisman, 2003; Varela, Lachaux et al., 2001). This has led to a growing interest in gamma-band oscillations as a possible signature of the “entry” of an active neural representation into awareness.

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The term *awareness* is regrettably imprecise, meaning different things to different people in different contexts, so it is important for us to clarify what we mean by it. We start by contrasting it with *perception*, which is often taken to be synonymous with awareness. We take *perception* to refer to the representation or registration, of something, in the brain. If one can find neural activity somewhere in the brain whose pattern changes reliably in response to a stimulus, then we would say that the stimulus has been perceived. *Awareness*, on the other hand, refers to the representation or registration, of something, in the brain *such that* (at least some of) the relevant information is accessible to direct report (verbal or otherwise). So, according to this definition, awareness necessarily implies perception, but perception does not necessarily imply awareness. Perception can be more broadly defined as a form of information processing. We assume awareness to be an attribute of such information processing, not something independent from it (Kinsbourne, 1997).

Several recent studies have addressed the issue of a link between induced gamma-band activity and awareness more directly (i.e. providing evidence of perception without awareness, so that the effects related to awareness can be isolated from those related to perception in general). Summerfield, Jack et al. (2002) demonstrated a significant increase in local induced gamma-band oscillations in response to masked words when subjects reported awareness of the word, but not when they reported no awareness. Accuracy on a two-alternative forced-choice (2afc) discrimination remained above chance even for “unaware” trials. (Note, however, that although 2afc accuracy was significantly above chance at the level of awareness labeled “nothing”, it did decline monotonically with lower ratings of awareness.) In a study of memory, Burgess and Ali (2002) showed that gamma-band oscillations were significantly enhanced for correct recollection compared to correct familiarity, which differ only in the subject reporting that he/she consciously recalls having seen the correctly selected test stimulus before.

The aim of the present study is to examine the difference, in terms of neural dynamics, between perception *with* awareness and perception *without* awareness of the same type of stimulus, while attempting to control for other measures of information processing, such as discrimination accuracy and reaction time. Specifically, our objective is to test the hypothesis that induced oscillatory neural activity in the gamma frequency band (~30–80 Hz) distinguishes between perception with awareness and perception without awareness, perhaps signaling the “entry” of a neural representation into awareness.

Hemianopic patient GY offers a unique way to test hypothesis of this sort. Although clinically blind in the right half of visual space, GY sometimes reports an awareness “that something happened” in his blind visual hemifield, in response to stimuli of sufficiently high luminance contrast or speed. He insists that this awareness is not visual – he does not actually “see” the stimulus – and his awareness may not convey any information about the stimulus other than the fact that something occurred. Nevertheless, GY’s accuracy on forced-choice tasks may remain well above chance even when the contrast is lowered and he no longer reports awareness – i.e. “blindsight” (Covey, 2004; Stoerig &

Covey, 1997; Weiskrantz, Barbur et al., 1995). Sometimes (as was the case in the present study) GY’s accuracy without awareness is comparable to that obtained with awareness. This state of affairs allows us to experimentally dissociate awareness from accuracy to a much greater degree than is possible in normal subjects, “comparing, within the same subject [GY], the activity of the brain when the two stimulus conditions are matched at high levels of performance for the same type of discrimination, with and without conscious awareness” (Weiskrantz, Barbur et al., 1995).

2. Methods

2.1. Subject

GY, born in 1956 and 48 years old at the time of this experiment, suffered trauma to his left occipital cortex during an automobile accident at the age of 8 years, which left him with a right homonymous hemianopia, with approximately 2.5–3.0° of macular sparing. He also has slight damage to dorsal areas V2 and V3 and has an infarct in the parietal lobe of the opposite hemisphere. GY has been studied extensively and details concerning the extent of his lesion (Barbur, Watson et al., 1993; Baseler, Morland et al., 1999), perimetry (Barbur, Ruddock et al., 1980), residual visual sensitivity (Barbur, Ruddock et al., 1980; Barbur, Watson et al., 1993; Weiskrantz, Harlow et al., 1991), and sensitivity without awareness (Weiskrantz, Barbur et al., 1995) may be found elsewhere. GY gave informed consent to participate in the experiment.

Over the past 20 years GY has developed an increasing awareness of events in his blind hemifield, depending upon stimulus parameters. Stimuli of high-contrast, rapid onset/cutoff, rapid motion, or which flicker have become increasingly effective. In such instances, GY may deny actually “seeing” anything, but instead may report sensing “that something happened” in his blind visual hemifield, along with a non-visual “feeling” of its approximate location and/or whether it moved (for review see Covey, 2004). Especially with stationary (or slow moving), low-contrast stimuli, GY frequently reports no awareness of the stimuli, but may continue to exhibit greater-than-chance accuracy on a variety of discrimination tasks (Covey, 2004; Weiskrantz, Barbur et al., 1995).

2.2. Stimuli and apparatus

Stimuli were elongated, rectangular, random checkerboard patterns (see Fig. 1) presented in the lower quadrant of GY’s right (blind) visual hemifield. We used random patterns to avoid the possibility of local habituation in the region of GY’s blind visual field where the stimuli appeared, so that GY’s threshold for awareness, which we measured before the experiment (see below), would be less likely to change systematically over the course of the experiment. Stimuli could appear at one of two possible orientations: 45° (“top leaning right”) or 135° (“top leaning left”). The rectangles subtended 6° × 1.5° of visual angle (238 × 60 pixels at a display resolution of 1024 × 768 pixels) from a viewing

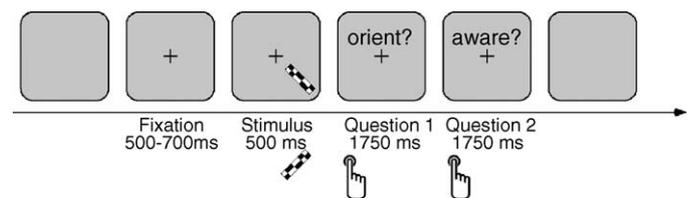


Fig. 1. Trial sequence. Each trial began with a fixation cross for a variable 500–700 ms interval, followed immediately by the appearance of the stimulus, always in the lower-right quadrant (GY’s blind hemifield), for 500 ms. Stimuli were oriented random checkerboard patterns presented at a near-threshold (for awareness) level of contrast. GY had to guess the orientation of the bar (“leaning right” or “leaning left”) and then indicate whether or not he had any awareness of something in his blind visual field (“yes” or “no”). The screen was blank (gray background) for 2.0–2.5 s between trials.

distance of 88 cm. They were positioned at 7.5° eccentricity (center of rectangle to fixation), with a radial displacement of -20° (with the origin at the center of the screen). With these parameters, the nearest edge of the stimulus to the fixation cross was outside of GY's region of macular sparing by at least 1.5°.

Stimuli were back-projected onto a translucent viewing screen from a computer data projector located outside of the shielded MEG testing room (the beam was directed to the screen by a set of mirrors). The background was a neutral gray (17 cd/m²) and the mean luminance of the stimuli was the same as the background. Areas of the MEG apparatus (which is an off-white color) facing the viewing screen were covered with sheets of low-reflectance black cardboard to eliminate detectable reflected light. The experiment was conducted under mesopic lighting conditions.

2.3. Contrast titration

Before beginning the main experiment we determined a near-threshold contrast level that yielded a similar proportion of aware and unaware judgements. A procedure was devised, similar to that described by Taylor and Creelman (1967), but developed independently, which begins with a binary search of contrast space in order to find an approximate threshold (12 trials), and then continues with a standard staircase algorithm with a small step size designed to delimit the threshold (40% aware¹ more precisely (88 trials). GY responded either “aware” or “unaware”, by pressing a button, after each presentation (marked in time by a dimming of the fixation cross). The mean of all reversals during the staircase sequence corresponded to a contrast of 0.25 (Michelson) and we used this contrast for the remainder of the experiment (light areas: 22.5 cd/m², dark areas: 13.4 cd/m², background: 17 cd/m²).

2.4. Trial sequence and task

The appearance of the fixation cross signaled the beginning of each trial (see Fig. 1). After a variable interval of 500–700 ms, the stimulus appeared in the lower quadrant of GY's right (blind) hemifield, oriented “left” or “right” at random. The onset of the stimulus was marked in time by a dimming of the fixation cross. The stimulus remained on the screen for 500 ms, followed immediately by a central prompt (the word “ORIENT?”) for GY to guess the orientation of the bar. GY responded by pressing a button with his left thumb to indicate “leaning left”, or his right thumb to indicate “leaning right”. After 1.75 s a second prompt appeared (the word “AWARE?”) at which time GY responded (by button press) whether or not he had been aware of the stimulus. The screen then went blank (gray background) signaling the end of the trial. The inter-trial interval was varied randomly between 2 and 2.5 s. We conducted eight blocks of 80 trials each, all on the same day, with short breaks between each block, and a longer break after the fourth block.

2.5. MEG recording and data analysis

The experiment was conducted at the Centre MEG of the Hôpital de la Salpêtrière, Paris, France. MEG recording was performed using a whole-head MEG system (CTF Systems, Canada) with 151 radial gradiometers over the scalp and 29 reference gradiometers and magnetometers for ambient field correction. Eye movements were monitored with four ocular electrodes (Viasys Healthcare). The EOG was calibrated prior to testing using a simple saccade task. Any trials on which an eye movement was apparent, based on visual inspection of the four EOG traces, were excluded from the analysis.

Signals were digitized at a sampling rate of 1250 Hz (0–200 Hz bandwidth) during epochs lasting 5 s, beginning 1 s prior to stimulus onset. Trials were rejected off-line for eye blink, eye movement, head movement, muscle, or electromagnetic artifacts. A wavelet transform was applied to each trial at each sensor, using complex morlet wavelets (details of these methods are fully described elsewhere; see Tallon-Baudry, Bertrand et al., 1996), resulting in an estimate of power at each sample in time and at each frequency between 8 and

130 Hz. The resulting time–frequency (TF) data were then averaged across trials within each condition (correct/aware, correct/unaware, incorrect/aware, incorrect/unaware). We defined two time windows referenced to the time of stimulus onset, which we call “pre” (–500 to –100 ms) and “post” (+100 to +500 ms). For each frequency, the average power during the pre-stimulus time window was used as a baseline. The data were log transformed to approach a normal distribution (henceforth, any mention of spectral power refers to the log-transformed data) prior to performing a two-factor ANOVA, with factors “accuracy” (correct, incorrect) and “awareness” (aware, unaware). Data pre-processing and wavelet analysis were performed using in-house software.

3. Results

3.1. Behavioral

GY's accuracy on the orientation discrimination task, although low, was significantly greater than expected by chance whether or not he reported awareness of the stimulus: 211/366 (57.7%) correct when aware ($p < 0.005$ binomial, two-tailed), 86/147 (58.5%) correct when unaware ($p < 0.05$ binomial, two-tailed). There was no significant difference in accuracy between the aware mode and the unaware mode of responding ($\chi^2 = 0.0083$, $p = 0.93$). There was, however, a substantial effect of awareness on reaction time in the orientation-discrimination task, GY's responses arriving, on an average, approximately 130 ms earlier overall (189 ms earlier for correct responses and 64 ms earlier for incorrect responses) when he reported awareness (see Table 1). A two-factor ANOVA with factors “accuracy” (correct/incorrect) and “awareness” (aware/unaware) revealed a highly significant main effect of awareness ($p < 0.001$). The main effect of accuracy ($p = 0.12$) and the interaction ($p = 0.092$) did not reach significance.

Due to the documented inhomogeneity of GY's blind hemifield (sensitivity is not the same everywhere; see Kentridge, Heywood & Weiskrantz, 1997), we suspected that one stimulus orientation might have been more or less likely than the other to provoke reports of awareness. Recall that two orientations were used, which we refer to as top-leaning-left (TLL: \) and top-leaning-right (TLR: /). There was a significant difference in the proportion of “aware” responses between TLL (23.3% aware, 61/259) and TLR (34.8% aware, 89/254) stimuli ($\chi^2 = 8.25$, $p < 0.005$), suggesting that GY's reports of awareness were indeed connected to the presence of the stimulus. Accuracy, on the other hand, was not significantly different between the two orientations, with 54.7% correct (142/259) for TLL, and 60.9% correct (155/254) for TLR stimuli ($\chi^2 = 2.02$, $p > 0.15$). This is another argument for a relative independence between accuracy and awareness. Note that the observed difference in the proportion of aware responses is unlikely to have

Table 1
Response time, in milliseconds, for the four conditions tested

	AWARE		UNAWARE	
	Correct	Error	Correct	Error
Mean	807	927	996	991
Standard deviation	381	363	372	380
<i>n</i>	86	61	211	155

¹ This target proportion was chosen based on the assumption that GY might gradually drift toward a higher proportion of “aware” responses as the experiment progressed.

been due to an intrusion of the stimulus into the sighted hemifield for two reasons: (1) of the two, TLL would be the most likely to intrude (being nearer to GY’s region of macular sparing), but this produced the smaller proportion of aware responses, and (2) the nearest edge of either stimulus to fixation was beyond 4.5° eccentricity, which is well outside of GY’s region of macular sparing.

3.2. MEG

After artifact rejection, there remained 108 trials in the “aware” condition (46 error, 62 correct) and 254 trials in the “unaware” condition (104 error, 150 correct). Comparison of the TF data from left occipito-parietal sensors after baseline subtraction revealed a difference in gamma-band activity (44–66 Hz) during the 500 ms immediately following stimulus onset (Fig. 2A and B). Topographical plots of the average power between 44 and 66 Hz and +100 to +500 ms post-stimulus revealed a roughly circular “region of interest” (ROI) spanning an array of 14 sensors over left occipito-parietal cortex (Fig. 2C). The mean 44–66 Hz power was averaged across these 14 sensors during two separate time windows: –500 to –100 ms (“pre”) and +100 to +500 ms (“post”) relative to stimulus onset. The ANOVA (accuracy × awareness), applied to the baseline-corrected data, revealed a significant main effect of awareness ($F(1,358) = 4.898, p < 0.03$, Fig. 2D). There was no

Table 2

Effect of the factors “accuracy” and “awareness”, and their interaction, on the log-transformed power in the range 44–66 Hz (γ-band) during two time windows, “pre” (–500 to –100 ms) and “post” (+100 to +500 ms), and for the ratio post/pre

Source	Post/pre		Pre		Post	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Accuracy	0.068	0.7950	0.014	0.9069	0.178	0.6731
Awareness	4.898	*0.0275	2.255	0.1341	1.091	0.2970
Accuracy × awareness	0.398	0.5285	0.095	0.7586	0.177	0.6742

Spectral power was averaged across an ROI comprising 14 sensors (see Fig. 2). For the *F* scores, d.f. = (1358).

significant difference between correct and incorrect responses ($F(1,358) = 0.068, p = 0.79$) nor was there a significant interaction effect ($F(1,358) = 0.398, p = 0.53$). The same test applied to the average power in the alpha band (8–12 Hz) in the same ROI revealed no significant effects. There were no significant differences in gamma power between conditions during the pre-stimulus period alone or the post-stimulus period alone (see Table 2). We also tested for a correlation between response time and baseline-corrected power in the gamma band, but no correlation was detected ($r^2 = 0.005, p = 0.48$; see Fig. 3).

Although the analysis of variance is well known for being robust against violations of assumptions, the test becomes much more susceptible to heterogeneity of variance with noticeably

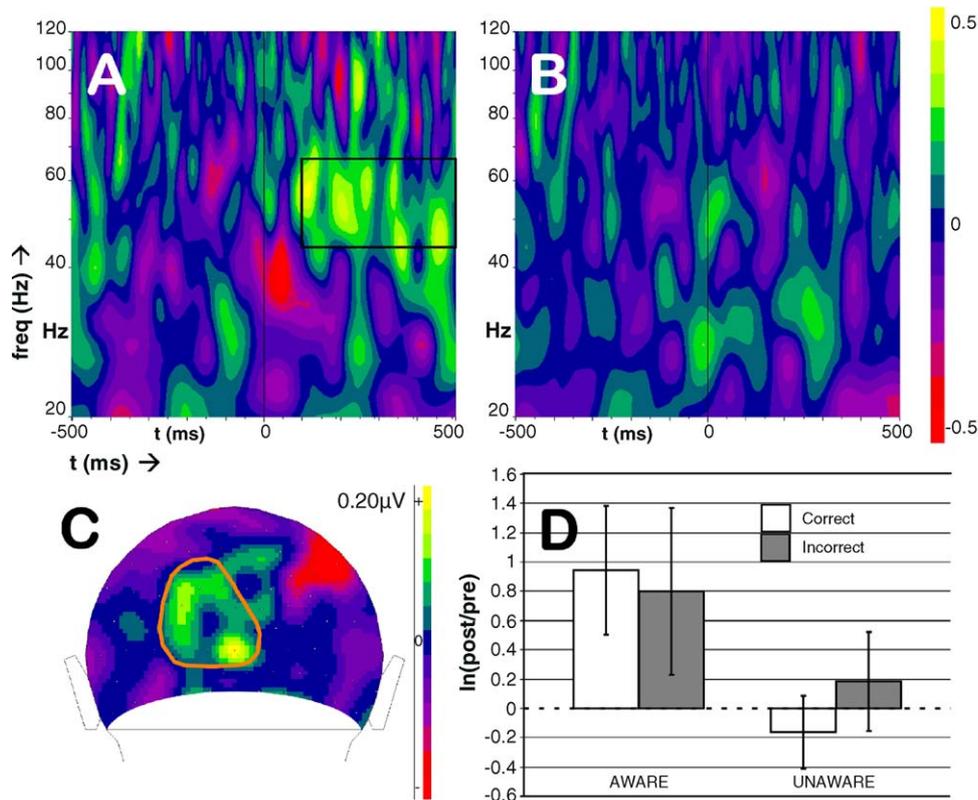


Fig. 2. Comparison of gamma-band activity for “aware” and “unaware” trials. (A) Time–frequency plot showing the baseline-corrected, log-transformed power averaged over (A) aware and (B) unaware trials, for maximally responding sensor MZ001 (151-channel MEG, CTF systems, Canada), which can be seen in the lower right area of the region of interest outlined in orange in (C). (C) Topography of the average [ln(post) – ln(pre)] in the window +100 to +500 ms, 44–66 Hz. (D) Bar graph showing baseline-corrected gamma-power for all four combinations of the two factors used in the analysis (aw, aware; un, unaware; co, correct response; in, incorrect response). Error bars are standard error of the mean.

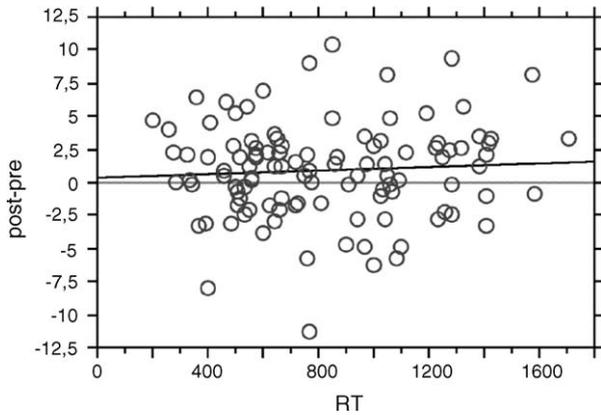


Fig. 3. Scatter plot of normalized gamma power [$\ln(\text{post}) - \ln(\text{pre})$, no unit] as a function of reaction time (ms). The regression line ($Y = 0.001X + 0.3$) is shown in black. $R^2 = 0.005$, $p = 0.48$.

unequal sample sizes. Hence, we also performed an F test on the equality of variance (Levene's test) on the mean baseline-corrected gamma power. This test revealed no significant differences ($p > 0.13$). We conducted two resampling tests in order to rule out the possibility of a false positive due to unequal sample sizes: (I) we performed 1000 ANOVAs on resampled data, randomly allocating data to one of the four cells, but maintaining the same N in each cell as originally obtained. Only 24 of the F values thus obtained were larger than the F value obtained on the original data, thereby showing that our results are significant with a p value of 0.024, which is consistent with the significance level obtained from the original ANOVA. (II) In order to estimate what would have been the result had the number of samples been equated, we considered the original 108 data points from the AWARE condition and compared them to 108 randomly selected data points from the UNAWARE condition (without replacement), computed the corresponding t -value, and repeated this procedure 1000 times. The mean (i.e. expected) t -score across these 1000 tests was 1.9535 (d.f. = 214), which indicates a significant difference at $p = 0.026$ (very similar to what we obtained on the ANOVA and the first permutation test). Altogether, the results indicate that gamma power is indeed larger in the aware than in the unaware condition, irrespective of sample size.

4. Discussion

In response to near-threshold (luminance contrast) stimuli, GY sometimes reported awareness and sometimes did not. On an orientation discrimination task, GY's accuracy was significantly greater than expected by chance but no different, whether he reported awareness of the stimulus or not. There was a significant effect of awareness on GY's reaction times: he was approximately 190 ms faster to respond correctly to stimuli of which he reported being aware (64 ms faster for incorrect responses). Gamma-band oscillations in the left occipito-parietal region correlated significantly with awareness, but neither with accuracy nor reaction times. Although it is very difficult to infer the localization of a neural source from the scalp topography using MEG, the observed dorsal topography of induced gamma band activity in our study is consistent with previous functional imaging

studies of this same patient (Barbur, Watson et al., 1993; Baseler, Morland et al., 1999; Sahraie, Weiskrantz et al., 1997; Zeki & Ffytche, 1998).

It seems reasonable to entertain the idea that GY's blind-field awareness ("that something happened") may be unlike anything experienced in normal vision, and this may appear to limit the generality of our findings. However, the generalization of our results may not depend on what that awareness "is like". What we will assert is that, during the experiment described here, somewhere in GY's brain there existed neural activity that at some times was outside of awareness (not directly reportable) and at some other times was within awareness (directly reportable). We are looking for electrophysiological markers that, for a given content, *whatever that content may be*, tend to co-occur with that content being reportable. That is, we are looking for the signature of a mechanism or process that is independent of the particular content. From this standpoint, our results should generalize, and evidence from previous studies supports this claim – in normal subjects gamma-band activity has been found to correlate with awareness (Burgess & Ali, 2002; Summerfield, Jack et al., 2002).

With regard to the behavioral results, it should be emphasized that GY's accuracy on the orientation discrimination task *with* awareness was not different from his accuracy *without* awareness. This is important to our aim of measuring correlates of awareness while maintaining a constant above-chance level of accuracy, following the suggestion by Weiskrantz, Barbur et al. (1995). Note, however, that the level of performance obtained in our study (~58% correct), even though highly significant, is lower than the performance of this same patient on similar tasks in previous studies (Kentridge, Heywood et al., 2004). We attribute GY's comparatively low (though still significant) accuracy to two factors. First, we used a random checkerboard pattern instead of a solid bar of high luminance contrast, as has commonly been used in the past. Second, we used oblique orientations (45° and 135°) instead of 0° and 90°, again differing from previous studies, in order to make sure that the medial edge of both tilted stimuli was the same distance from the vertical mid-line.

It could be argued that what we have labeled "awareness" in our study may actually be a response-criterion artifact. However, the response time data argue against this interpretation. The substantial overall mean difference of approximately 130 ms between "aware" and "unaware" trials (190 ms for correct responses) is large enough to suggest a qualitative difference between these two modes of responding. This last point, however, raises the issue of a possible confound between awareness and faster responding. It remains logically possible that the enhanced gamma-band activity during "aware" trials reflects neural dynamics that favor faster responding, independent of or interacting with awareness.

Recent studies (Gonzalez Andino, Michel et al., 2005; Kilner, Bott et al., 2005; Schoffelen, Oostenveld et al., 2005) provide evidence that enhanced gamma-band activity, during the period leading up to a cue to respond, is a predictor of subsequent response speed. Note, however, that the enhancement of gamma-band activity reported in these studies appears *before* the onset of

the cue to respond (as ought to be the case if the phenomena are causally related). As previously mentioned, in the present study we found no evidence of an absolute difference in the gamma band during either the pre-stimulus period or post-stimulus period alone. This is inconsistent with an explanation of our data based on reaction time, which instead would predict a significant *absolute* difference in gamma-band activity sometime before the subject's response. In addition, the foci of gamma-band activity identified in these two studies were frontal and/or parietal (more consistent with motor-related processing) whereas in the present study the focus was occipito-parietal (more consistent with visual sensory-related processing). Lastly, we found no evidence in our data of a correlation between response time and gamma-band activity in either the baseline-corrected data (*post-pre*) or the *pre* or *post* periods alone (see Fig. 3).

Although GY can be assumed, based on prior studies, to be a highly reliable subject (e.g. Weiskrantz, Barbur et al., 1995), it is reasonable to question whether or not his awareness reports are connected to the appearance of the stimulus. In addition to the significant effect of stimulus orientation on reported awareness (see Section 3.1), this question can in part be addressed by referring back to the contrast titration procedure. If GY's aware/unaware responses were unreliable and/or unrelated to the appearance of a visual stimulus, then this would have been clearly evident during the staircase procedure, and the staircase would likely have not converged on a stable contrast setting. It is reassuring to note that the proportion of aware and unaware trials obtained during the first four blocks of the experiment (34%/66%) is nearly the same as that observed during the latter half of the contrast titration procedure (35%/65%), both of which are consistent with the target of the staircase (40%/60%). The proportion of aware responses declined somewhat during the latter four blocks of the experiment (after the break) resulting in an overall proportion of 29% aware/71% unaware.

Our main finding of a significant difference in the level of induced gamma-band activity between "aware" and "unaware" trials confirms previous results (Burgess & Ali, 2002; Summerfield, Jack et al., 2002) increasing our confidence in induced gamma-band activity as a reliable and specific correlate of sensory awareness. We would like to propose that induced gamma-band oscillations might herald the "entry" of an active neural representation (in this case the feeling that "something happened") into the "dominant focus" (Kinsbourne, 1993) of ongoing global neural activity,² which can be thought of metaphorically as the "arena" for awareness. At the same time it is possible for local information processing to continue in parallel and influence the behavioral outcome without entering awareness, as evinced by GY's comparable above-chance accuracy on both aware and unaware trials. In light of this we take note of the apparent difference in information content between GY's subjective experience of events in his blind field and his above-chance guesses. According to GY's verbal commentaries between blocks, when he responded "aware", it was simply an

awareness "that something happened", devoid of any sensation of an object or an orientation. This is corroborated by the fact that GY was no more accurate (in fact slightly less so) at guessing the orientation of the bar when he reported awareness compared to when he reported no awareness. The ability to guess accurately regarding a stimulus *feature* of which one is unaware, even though there may be an awareness of the *presence* of the stimulus, has been called *Type II* blindsight by Weiskrantz (Sahraie, Weiskrantz et al., 2002).

One important question is whether or not sensory awareness may be determined by the state of background activity – by factors that are independent of and precede the arrival of the stimulus – as opposed to involving an interaction between the stimulus and ongoing activity, as we would like to argue. In an attempt to address this question, we note that the significant difference in gamma-band activity between "aware" and "unaware" trials in our study is revealed only in the ratio between the post- and pre-stimulus periods. Comparison of "aware" versus "unaware" trials for either the pre- or post-stimulus period alone did not reveal any significant difference in the gamma band. This is suggestive of an interaction between ongoing and stimulus-evoked activity, perhaps reflecting the entry of a neural representation into the global neuronal coalition (Maia & Cleeremans, 2005) whose activity constitutes a conscious state. It is theoretically possible for this state of affairs to arise simply as a result of having relatively large between-trial variability in the overall level of gamma energy, compared to the between-trial variability in the difference *post – pre* (a *within*-trial subtraction). This is highly unlikely in our case, however, because the variance across trials of the difference *post – pre* was actually *larger* than the variance across trials for either *pre* or *post* alone.

Linkenkaer-Hansen, Nikulin et al. (2004) found evidence of a non-linear relationship between pre-stimulus energy in the alpha, beta, and gamma bands and accuracy in the detection of near-threshold somatosensory stimuli. The fact that we do not find an effect of accuracy (or awareness) in the pre- or post-stimulus gamma-band energy in our data using a linear measure (the ANOVA) does not preclude the possibility of there being a non-linear relationship, which we did not test for in the present analysis.

The dissociation between awareness and accuracy in patient GY, noted first by Weiskrantz, Barbur et al. (1995) and later revisited by Zeki and Ffytche (1998), might seem to pose a problem for "uncentered" theories of awareness, like those of Kinsbourne (1993) or Tononi and Edelman (1998). One defining feature of such theories is that awareness is not uniquely associated with any *particular* cortical region or functional network and is not dissociable from the neural activity that carries its content: the area(s) that discriminate(s) e.g. faces from other objects is necessary for awareness of an object *as being a face*. This implies that a transition from unawareness to awareness of a sensory/perceptual object must be accompanied by a change in neural information processing in areas of the brain that normally respond to that sort of object. And a change in information processing along a certain stimulus dimension should be accompanied by a change in discrimination accuracy along that same dimension. So, how can it be that GY's awareness can vary

² Similar notions are the "global workspace" of Baars (2002) and the "dynamic core" of Tononi and Edelman (1998).

distinctly, without any detectable variation in his discrimination accuracy? The answer lies hidden in the fact that the (reported) content of GY's awareness ("something happened") is not informative as to the stimulus dimension along which GY is being asked to make a discrimination (orientation). What would be problematic for "uncentered" theories of awareness, and quite remarkable, would be for the same dissociation to be realized in the context of a stimulus *detection* paradigm, but this is not the case here. Instead, what we report is a dissociation between awareness of an event and discrimination of an orientation, which is also remarkable, but not at all the same thing.

Visual feature binding (Treisman, 1998) is a specific instance of what we refer to more broadly as "perceptual integration". It has been argued that feature binding may be necessary for visual awareness (Treisman, 2003). Evidence from the phenomenon of illusory conjunctions (Treisman & Schmidt, 1982; Wolfe & Cave, 1999), for example, suggests that neural representations (in vision at least) must be "bound", even if incorrectly, if they are to be experienced consciously. In the context of GY's blind visual field it is difficult to conceive of what "binding" might mean: GY may indeed report a *feeling* in response to visual stimuli presented in his blind field – and it would seem that there is nothing to bind this "feeling" to. If feature binding is necessary for visual awareness, then GY's experience that "something happened" in his blind visual field is not a true "visual" experience (see Zeki & Ffytche, 1998 for a different opinion). Otherwise it must be the case that binding is not strictly necessary for visual awareness, and what is experienced by GY represents the only known instance of an unbound visual percept.

It is important to note that GY probably does not experience his blind visual hemifield as a "dark area", as intuition might lead one to suppose. Rather, the way GY experiences his blind visual hemifield (as a whole) is probably more like the way normally sighted individuals experience what is behind them – it is simply outside of their visual field. This is consistent with GY's insistence that his experiences in response to blind-field stimuli do not feel "visual" to him, and his descriptions seem to evoke the sense of an orienting response. Previous accounts, however, differ in terms of the way in which GY describes his experiences (visual versus non-visual) in response to blind-field stimuli, alluding either to a non-visual "feeling", as we report (de Gelder, Pourtois et al., 2001; Sahraie, Weiskrantz et al., 1997; Zeki & Ffytche, 1998), or a true, though obviously impoverished, "visual" experience (Barbur, Ruddock et al., 1980; Finlay, Jones et al., 1997; Stoerig & Barth, 2001; Zeki & Ffytche, 1998). Gauging subjective experience is a complicated matter, and one for which there exists no commonly accepted methodology. Therefore it is perhaps not surprising to find variation among different paradigms and experimenters. Nevertheless, even if GY has had unusual visual experiences during previous studies, he did not report having any such experience during the present study.

One possible function of neural synchrony (oscillatory or otherwise) might simply be to impart greater downstream efficacy upon the activity in an ensemble of neurons (Fries, Reynolds et al., 2001; Schoffelen, Oostenveld et al., 2005). In this way, neural synchrony could serve as an attentional biasing mechanism and might be only indirectly related to awareness. In

this case one might expect anticipatory effects of attention to appear as an enhancement of local (as opposed to long-range) synchrony (Borgers, Epstein et al., 2005; Fries, Reynolds et al., 2001; Tallon-Baudry, Bertrand et al., 2004). Tallon-Baudry (2003) has argued that oscillatory activity in MEG is more likely to reflect local (intra-areal) synchrony because of its similarity to patterns of local synchrony obtained from intracranial recordings: sustained time course, more focal topography, and greater frequency variability within the gamma range. Thus, it is equally possible that our results reflect local biasing effects related to exogenously driven visuo-spatial attention, which has been shown behaviorally to operate even in GY's blind visual field (Kentridge, Heywood et al., 1999a,b; Kentridge, Heywood et al., 2004).

It could be argued that the blind-field stimulus engages exogenous attentional processes, perhaps via the superior colliculus, which yield the observed increase in local gamma-band activity and, often, an accompanying awareness. Assuming that attention is necessary (even if not sufficient) for awareness, then it is impossible to say whether the observed pattern of activity correlates *uniquely* with awareness, in our study or any other. For example, in studies involving the attentional blink phenomenon (e.g. Gross, Schmitz et al., 2004), it is unclear how to label the phenomenon under investigation: is it attention, or awareness? Whether this distinction is an empirical one or a conceptual one remains an important open question.

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References

- Baars, B. J. (2002). The conscious access hypothesis: Origins and recent evidence. *TICS*, 6(1), 47–52.
- Barbur, J. L., Ruddock, K. H., et al. (1980). Human visual responses in the absence of the geniculocalcarine projection. *Brain*, 103, 905–928.
- Barbur, J. L., Watson, J. D. G., et al. (1993). Conscious visual-perception without V1. *Brain*, 116, 1293–1302.
- Baseler, H. A., Morland, A. B., et al. (1999). Topographic organization of human visual areas in the absence of input from the primary cortex. *Journal of Neuroscience*, 19, 2619–2627.
- Borgers, C., Epstein, S., et al. (2005). Background gamma rhythmicity and attention in cortical local circuits: A computational study. *PNAS*, 102(19), 7002–7007.

- Bullier, J. (2001). Feedback connections and conscious vision. *TICS*, 5(9), 369–370.
- Burgess, A. P., & Ali, L. (2002). Functional connectivity of gamma EEG activity is modulated at low frequency during conscious recollection. *International Journal of Psychophysiology*, 46(2), 91–100.
- Cowey, A. (2004). The 30th Sir Frederick Bartlett Lecture. Fact, artefact, and myth about blindsight. *The Quarterly Journal of Experimental Psychology*, 57A(4), 577–609.
- Cowey, A., & Walsh, V. (2000). Magnetically induced phosphenes in sighted, blind and blindsighted observers. *Neuroreport*, 11(14), 3269–3273.
- de Gelder, B., Pourtois, G., et al. (2001). Unseen stimuli modulate conscious visual experience: Evidence from interhemispheric summation. *Neuroreport*, 12(2), 385–391.
- Dehaene, S., Sergent, C., et al. (2003). A neuronal network model linking subjective reports and objective physiological data during conscious perception. *PNAS*, 100(14), 8520–8525.
- Engel, A. K., Roelfsema, P. R., et al. (1997). Role of the temporal domain for response selection and perceptual binding. *Cerebral Cortex*, 7(6), 571–582.
- Engel, A. K., & Singer, W. (2001). Temporal binding and the neural correlates of sensory awareness. *TICS*, 5(1), 16–25.
- Finlay, A. L., Jones, S. R., et al. (1997). Movement in the normal visual hemifield induces a percept in the 'blind' hemifield of a human hemianope. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, 264(1379), 267–275.
- Fries, P., Reynolds, J. H., et al. (2001). Modulation of oscillatory neuronal synchronization by selective visual attention. *Science*, 291(5508), 1560–1563.
- Gonzalez Andino, S. L., Michel, C. M., et al. (2005). Prediction of response speed by anticipatory high-frequency (Gamma-Band) oscillations in the human brain. *HBM*, 24, 50–58.
- Gross, J., Schmitz, F., et al. (2004). Modulation of long-range neural synchrony reflects temporal limitations of visual attention in humans. *PNAS*, 101(35), 13050–13055.
- Herrmann, C. S., Munk, M. H. J., et al. (2004). Cognitive functions of gamma-band activity: Memory match and utilization. *TICS*, 8(8), 347–355.
- Hochstein, S., & Ahissar, M. (2002). View from the top: Hierarchies and reverse hierarchies in the visual system. *Neuron*, 36(5), 791–804.
- Kaiser, J., & Lutzenberger, W. (2003). Induced gamma-band activity and human brain function. *Neuroscientist*, 9(6), 475–484.
- Kentridge, R. W., Heywood, C. A., et al. (1999a). Residual vision in multiple retinal locations within a scotoma: Implications for blindsight. *Journal of Cognitive Neuroscience*, 9(2), 191–202.
- Kentridge, R. W., Heywood, C. A., et al. (1999b). Attention without awareness in blindsight. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, 266(1430), 1805–1811.
- Kentridge, R. W., Heywood, C. A., et al. (2004). Spatial attention speeds discrimination without awareness in blindsight. *Neuropsychologia*, 42(6), 831–835.
- Kentridge, R. W., Heywood, C. A., & Weiskrantz, L. (1997). Residual vision in multiple retinal locations within a scotoma: Implications for blindsight. *Journal of Cognitive Neuroscience*, 9(2), 191–202.
- Kilner, J., Bott, L., et al. (2005). Modulations in the degree of synchronization during ongoing oscillatory activity in the human brain. *European Journal of Neuroscience*, 21, 2547–2554.
- Kinsbourne, M. (1993). Integrated cortical field model of consciousness. *Ciba Foundation Symposium*, 174, 43–50, discussion 51–60.
- Kinsbourne, M. (1997). In J. D. Cohen & J. W. Schooler (Eds.), *What qualifies a representation for a role in consciousness? Scientific approaches to consciousness* pp. 335–355. Hillsdale, NJ: Lawrence Erlbaum Associates Inc.
- Lamme, V. A., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *TINS*, 23(11), 571–579.
- Lee, K.-H., Williams, L. M., et al. (2003). Synchronous Gamma activity: A review and contribution to an integrative neuroscience model of schizophrenia. *Brain Research Reviews*, 41(1), 57–78.
- Linkenkaer-Hansen, K., Nikulin, V. V., et al. (2004). Prestimulus oscillations enhance psychophysical performance in humans. *Journal of Neuroscience*, 24(45), 10186–10190.
- Maia, T. V., & Cleeremans, A. (2005). Consciousness: Converging insights from connectionist modeling and neuroscience. *TICS*, 9(8), 397–404.
- Pascual-Leone, A., & Walsh, V. (2001). Fast backprojections from the motion to the primary visual area necessary for visual awareness. *Science*, 292(5516), 510–512.
- Pollen, D. A. (2003). Explicit neural representations, recursive neural networks and conscious visual perception. *Cerebral Cortex*, 13(8), 807–814.
- Sahraie, A., Weiskrantz, L., et al. (1997). Pattern of neuronal activity associated with conscious and unconscious processing of visual signals. *PNAS*, 94(17), 9406–9411.
- Sahraie, A., Weiskrantz, L., et al. (2002). Psychophysical and pupillometric study of spatial channels of visual processing in blindsight. *Experimental Brain Research*, 143(2), 249–256.
- Sauve, K. (1999). Gamma-band synchronous oscillations: Recent evidence regarding their functional significance. *Conscious Cognition*, 8(2), 213–224.
- Schoffelen, J. M., Oostenveld, R., et al. (2005). Neuronal coherence as a mechanism of effective corticospinal interaction. *Science*, 308(5718), 111–113.
- Singer, W., & Gray, C. M. (1995). Visual feature integration and the temporal correlation hypothesis. *Annual Review of Neuroscience*, 18, 555–586.
- Stoerig, P., & Barth, E. (2001). Low-level phenomenal vision despite unilateral destruction of primary visual cortex. *Conscious Cognition*, 10(4), 574–587.
- Stoerig, P., & Cowey, A. (1997). Blindsight in man and monkey. *Brain*, 120(Pt. 3), 535–559.
- Summerfield, C., Jack, A. I., et al. (2002). Induced gamma activity is associated with conscious awareness of pattern masked nouns. *International Journal of Psychophysiology*, 44(2), 93–100.
- Tallon-Baudry, C. (2003). Oscillatory synchrony and human visual cognition. *Journal of Physiol-Paris*, 97(2–3), 355–363.
- Tallon-Baudry, C., & Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in object representation. *TICS*, 3(4), 151–162.
- Tallon-Baudry, C., Bertrand, O., et al. (1996). Stimulus specificity of phase-locked and non-phase-locked 40 Hz visual responses in human. *Journal of Neuroscience*, 16(13), 4140–4249.
- Tallon-Baudry, C., Bertrand, O., et al. (2004). Attention modulates gamma-band oscillations differently in the human lateral occipital cortex and Fusiform Gyrus. *Cerebral Cortex*.
- Taylor, M., & Creelman, C. (1967). PEST: Efficient estimates on probability functions. *The Journal of Acoustical Society of America*, 41, 782–787.
- Tononi, G., & Edelman, G. M. (1998). Neuroscience—Consciousness and complexity. *Science*, 282(5395), 1846–1851.
- Tononi, G., Edelman, G. M., et al. (1998). Complexity and coherency: Integrating information in the brain. *TICS*, 2(12), 474–484.
- Treisman, A. (1998). Feature binding, attention and object perception. *Philosophical Transactions of the Royal Society of London. Series B Biological Sciences*, 353(1373), 1295–1306.
- Treisman, A. (2003). Consciousness and perceptual binding. In *The unity of consciousness binding, integration, and dissociation*. A. Cleeremans. Oxford: Oxford University Press.
- Treisman, A., & Schmidt, H. (1982). Illusory conjunctions in the perception of objects. *Cognitive Psychology*, 14(1), 107–141.
- Varela, F., Lachaux, J. P., et al. (2001). The brainweb: Phase synchronization and large-scale integration. *Nature Reviews. Neuroscience*, 2(4), 229–239.
- Weiskrantz, L., Barbur, J. L., et al. (1995). Parameters affecting conscious versus unconscious visual-discrimination with damage to the visual-cortex (V1). *PNAS*, 92(13), 6122–6126.
- Weiskrantz, L., Harlow, A., et al. (1991). Factors affecting visual sensitivity in a hemianopic subject. *Brain*, 114(Pt. 5), 2269–2282.
- Wolfe, J. M., & Cave, K. R. (1999). The psychophysical evidence for a binding problem in human vision. *Neuron*, 24(1), 11–17.
- Zeki, S., & Ffytche, D. H. (1998). The Riddoch syndrome: Insights into the neurobiology of conscious vision. *Brain*, 121, 25–45.