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Bandpass characteristics of high-frequency sensitivity and visual experience in blindsight

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ABSTRACT

Patient RP suffers a unilateral right homonymous quadrant anopia but demonstrates better than chance discrimination for stimuli presented in the blind field at temporal frequencies between 33 and 47 Hz (all significant at $p < .05$, binomial). Examination of her reports of visual experience during blind-field discrimination suggests a more complex picture in which experiences particular to correct discrimination are not found at low-mid-gamma frequencies, but are significantly more likely than average (76%, $p < .001$) at a lower frequency (22 Hz) at which blindsight is not observed. We believe that visual experience may serve to support blindsight if discrimination tasks are generally impaired at frequencies outside of the low-mid-gamma band. If this is so, although generally experienced as non-specific and unstructured light, the visual experience that accompanies discrimination performance must be based upon a neural representation which includes information on the visual features present in the stimulus.

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1. Introduction

Damage to primary visual cortex or to the optic radiation results in clinical blindness across circumscribed areas of the patient's visual field. In spite of this, cortically blind patients often show above-chance performance detecting, discriminating or localizing stimuli presented in their blind field (Pöppel, Frost, & Held, 1973; Weiskrantz, Warrington, Sanders, & Marshall, 1974). Referred to as 'blindsight' (Weiskrantz et al., 1974) a special sensitivity to transient, as compared with static stimuli has been described in the literature since the first studies of residual visual capability following induced blindness. Described in terms of a stato-kinetic dissociation (Riddoch, 1917) it is suggested that sensitivity to transient stimuli is brought about by a particular *temporal* visual channel transmitting kinetic as opposed to static visual information (Schiller et al., 2006). This temporal channel may be responsible for a wide range of detection and localization abilities in the blind field, including the detection of light/dark onsets (Teuber, Battersby, & Bender, 1960), flicker (Weiskrantz, 1986) and an enhanced ability to localize in space a flickering relative to static stimulus (Perenin, Ruel, & Hécaen, 1980).

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The existence of a temporal channel with a particular bandpass characteristic of between approximately 10 and 33 Hz with peak performance at 20 Hz was originally reported in patient GY by Barbur, Harlow, and Weiskrantz (1994). More recently and using a larger group of patients, Sahraie, Weiskrantz, Trevethan, Cruce, and Murray (2002) have shown enhanced discrimination for gratings with luminance repeatedly modulated at a rate of 10 Hz, as compared with static gratings that simply switched on or off, while in a follow-up study Trevethan and Sahraie (2003) found a very similar pattern of performance over frequency between GY and a second patient VN who also demonstrated enhanced blindsight while detecting stimuli of relatively low spatial frequencies between 1 and 3.5 cycles/, and presented at 10–33 Hz (with peak performance at 20 Hz). In a third study Sahraie, Trevethan, and MacLeod (2008) examined eight cortically blind patients reporting, on the average, peak performance across a 5–20 Hz bandwidth. However and significantly, consideration of the individual data from these eight patients reveals fluctuations in detection performance at frequencies either side of peak performance at 10 Hz, with performance in some cases differing in the order of 30% and 40% within 5 Hz of peak performance. These data would tend to suggest that the temporal channel can be relatively narrowly tuned within the individual.

There is controversy in deciding the precise anatomical correlates with blindsight, with some theorists suggesting a subcortical tectopulvinar route (Brown, Kroliczak, Demonet, & Goodale, 2008) as opposed to the idea that enhanced performance in blindsight may be brought about by koniocellular projections to extrastriate cortex and from there to motion coding mechanisms in middle temporal visual area (MT, see the review by Vakalopoulos, 2008). fMRI evidence supports the role of extrastriate cortex during blindsight (Goebel, Muckli, Zanella, Singer, & Stoerig, 2001) while Vakalopoulos argues that direct koniocellular projections to MT explain residual motion sensitivity, in spite of damage to primary visual cortex. Thus it seems plausible that extrastriate activity correlates with the particular sensitivity to temporally modulated stimuli found in blindsight. The likely involvement of extrastriate also suggests that it may be possible to identify a second bandwidth of relevance to blindsight, one related to limited form-from-motion coding at mid-gamma-band frequencies of between 30 and 50 Hz. This expectation arises from consideration of a variety of evidence linking extrastriate neuronal responses, which have been reported at frequencies in the broader gamma band (30–80 Hz) with the binding of different elements of a moving stimulus (e.g. Engel, Kreiter, König, & Singer, 1991; Kreiter & Singer, 1992). In a second line of evidence Elliott and colleagues (Elliott & Müller, 1998, 2000) have shown that a masked grouping embedded in a flickering display will prime detection of a subsequent grouping only if the masked grouping is embedded within 40 Hz flicker. Further examination of the temporal specificity of these effects was reported by Elliott and Müller (2004) who showed several specific bandpass characteristics located at 32 Hz, between 37 and 40 Hz and between 46 and 47 Hz. Similar to the data reported by Sahraie et al. (2008), sensitivity to temporal frequencies was consistent across studies and was very narrowly tuned with, for example, a 20 ms priming effect at 40 Hz reducing to 0 ms (i.e. no priming) at 41 Hz. Comparable differences are also evident either side of priming effects at 32 and 46–47 Hz.

Frequency-specific priming at 40 Hz appears in the EEG as the concurrent activation at high frequency of a neural assembly recorded over left anterior regions of cortex with a second recorded over the left occipito-parietal region (see, Conci, Elliott, Müller, Wendt, & Becker, 2004; Elliott, Conci, & Müller, 2003). Anatomically, this pattern of effects compares well with a report of high frequency left occipito-parietal activity recorded in an EEG study of blindsight patient GY, although in this case EEG activity corresponded better with his reports of a non-specific visual experience rather than with his blindsight performance (Schurger, Cowey, & Tallon-Baudry, 2006). Visual detection and discrimination ability in the blind visual field can occur accompanied by visual experiences and when it does, it is referred to as Type II blindsight (Weiskrantz, 1997). Patients who experience Type II blindsight do not describe their phenomenal impression as one of 'seeing' but rather as a kind of 'feeling' or impression that something appeared or has moved within their blind field. A link between motion coding, blindsight and visual experience is also indicated by reports that GY can experience visual phosphenes in his blind field when induced via bilateral transcranial magnetic stimulation (TMS) applied to both ipsilesional and contralesional cortices over the extrastriate areas V5/MT (Silvanto, Cowey, Lavie, & Walsh, 2007). However and in spite of a similarity between the brain areas implicated in Type II blindsight, with the areas activated by 40-Hz priming neither Schurger et al., nor Silvanto et al., employed transient stimuli in their experiments.

Accordingly, given the existence and anatomical similarities between the narrowly tuned temporal channels in blindsight and those supporting frequency-specific priming in normal vision, we sought to establish whether or not blindsight could be induced by stimuli modulated at around 40-Hz. Detailed examination of this band has not been possible previously because of the use of conventional CRT monitors which are limited in temporal frequency to multiples of $\frac{1}{f}$ of the horizontal refresh rate. Instead, in both Experiments 1 and 2 we employed an oscilloscopic monitor with extremely high temporal-frequency resolution capable of measurement at temporal frequencies that are unavailable using conventional CRTs (see Bach, Meigen, & Strasburger, 1997). In Experiment 1, patient RP who has shown some evidence of blindsight performance was presented with a discrimination task in which she was asked to report the orientation of gratings presented statically and at various frequencies in the range 33–47 Hz. In Experiment 2, we examined the relationship between temporally induced blindsight and visual experience. We considered it possible that the type of non-specific visual experience reported in blindsight may be reported more often at the temporal frequencies found in previous studies, that is to say at around 20 Hz. Our expectation was based upon other findings in which hallucinatory visual experiences both structured and unstructured are readily induced by stimulus flicker at around 20 Hz (Becker & Elliott, 2006; Becker, Gramman, Müller, & Elliott, 2009). If a non-specific Type II blindsight were found to accompany flicker at 20 Hz, the visual experiences accompanying blindsight might be best characterized in terms of transient hallucinations rather than in terms of the visual experience of stimulus events.

2. Methods

2.1. Participant information

RP (Female, aged 57 years) suffered an upper right homonymous quadranopia (see Fig. 1a) resulting from a stroke at the age of 54 with resulting damage to her left occipital lobe. She was of average intelligence (Lehrl, 2005), did not suffer from visuo-spatial neglect (Wilson, Cockburn, & Halligan, 1987), or problems maintaining vigilance or making a decision. She suffered no other neurological damage and was perfectly able to discriminate all stimuli presented in her intact visual field.

2.2. Stimuli and apparatus

RP undertook two near identical experimental procedures. In both, stimulus gratings comprised a triad of elongated bars each representing a Gaussian weighted increase and decrease in luminance along the width of the bar. These gratings were presented horizontally, vertically or to the right or left oriented diagonal. Bars were presented at of $2.3° \times 0.9°$ and were set at approximately 1 cycle/° of visual angle and so within the 3.5 cycle/° limit already identified as the maximum spatial resolution for successful blindsight performance (Trevethan & Sahraie, 2003). Overall stimulus dimensions were $2.9° \times 2.7°$. In the case of the left and right tilted diagonal at angles of ±45° to the meridian. Gratings were presented within the absolute blind field at an eccentricity of $+10.7° \times +9.6°$ of visual angle relative to a colored fixation point attached to the screen surrounding the monitor.

Gratings were presented on a GBM 2211 FOCUS-oscilloscope monitor screen ($15.2\ cm \times 12.4\ cm$) with a fast P4 phosphor which ensured illuminated pixels reduced to 10% of full luminance within 200 microseconds (µs) of image termination. Stimulus image frame generation, event timing and data collection were controlled by an IBM compatible PC running custom made software programmed in Assembler and C, which also controlled oscilloscopic image presentation through an Interactive Electronics Systems point plotter buffer with 4 Mb frame store memory (Finley, 1985). Unlike conventional CRT monitors point plotters are pixel addressable with timing easily achievable at sub millisecond resolution. Timing was controlled by plotting exactly 999 pixels to ensure image frame control with millisecond resolution. Although the plotter was capable of a plot rate of 1 MHz, the desirability for fine-scaled temporal with good image resolution lead to a trade-off between temporal resolution and the number of illuminated pixels. This compromise was achieved with each image frame comprising 799 illuminated pixels, which, with a cascading phosphor decay rate of 200 µs per pixel, gave an overall plot time of 999 µs and thereby a plot rate closely approximating 1 kHz. Stimuli were presented in a dimly lit room under controlled lighting conditions (mean screen surround luminance 13 cd/m^{-2}, with stimulus luminance maintained at 3.05 cd/m^{-2}). In Experiment 1 stimuli were presented as static (i.e. at the background 1-kHz plot frequency) or flickered in square wave at 33, 40, and 48 Hz, while in Experiment 2 stimuli were presented as static or flickered at 20, 22, 25, 28, 33, 38, 50, 71 and 100 Hz. In Experiment 1, we examined the hypothesis that successful discrimination would be found across the lower-mid-gamma band (i.e. 30–50 Hz). The major aim of Experiment 2 was to extend upon Experiment 1 but at the same time examining for any effects of flicker frequency on the incidence and quality of visual experiences that accompany blindsight. In this experiment the flicker frequencies employed were decided upon given two related considerations: firstly and while desirable, a better frequency resolution across the 10–50-Hz band would necessitate a substantial increase in the number of experimental trials. However, because of her neurological damage, RP was unable to undertake extensive testing. Our aim was to examine across as wide a bandwidth as possible and with previous studies in mind, we expected data in support
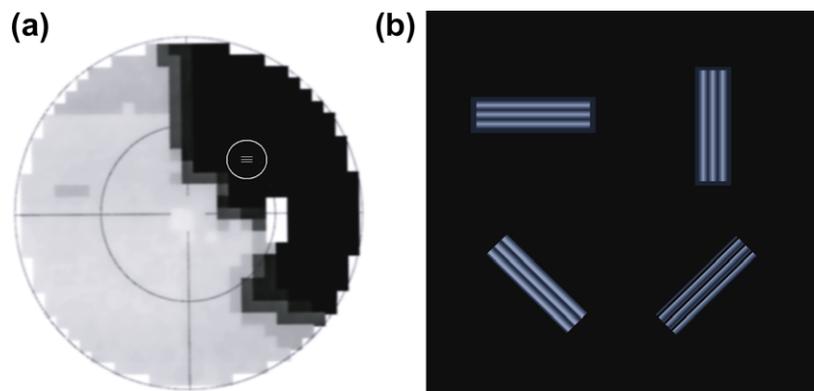
Fig. 1. In 1 (a) static perimetry (Interzeag OCTOPUS-perimeter 101 and compatible OCTOPUS Examination Software for patient RP) in which each rectangle represents 2° squared of visual angle, white rectangles signify the intact fields, gray relative blind and the black rectangles the absolute blind field(s). The small white bar inside the white circle indicates the exact position and size of the stimuli, within the central 15° region of the visual field. Patient RP has an upper right homonymous quadrant Anopia, which overlaps into the lower right quadrant. Macular sparing of 14.25° squared of visual angle to the right upper quadrant from fixation point is evident. The appearance of stimuli at the four orientations used in Experiments 1 and 2 is shown in 1(b).

Table 1
Experiment 1 – %-correct discrimination performance by flicker frequency.

Frequency (Hz)	0	33	40	48
	28	33	39	45
	ns	$p < .05$	$p < .005$	$p < .001$

of Experiment 1, i.e. demonstrating blindsight performance at around 40 Hz, while replicating previous studies which have also found blindsight at 20 Hz. However, we were unsure as to how well tuned the effect at 20 Hz would prove to be. Consequently, and given the finding of a broad ceiling in effect size between 10 and 20 Hz (e.g. Barbur et al., 1994; Sahraie et al., 2008; Trevethan & Sahraie, 2003) it was decided to sample across a number of frequencies slightly higher than 20 Hz with a view to identifying whether or not, and if so how blindsight is distributed across a range of higher neighboring frequencies.

2.3. Procedure

Two experiments were carried out, both involving an identical discrimination task with four response alternatives but with the difference that in Experiment 2, RP was also asked to describe any attendant visual experiences she had. For both experiments and on each trial, a grating was presented on the oscilloscopic monitor screen, appearing in one of four orientations: vertical, horizontal, and left and right tilted diagonal. The discrimination task involved reporting the orientation of the grating (and in Experiment 2 to describe any visual experiences). A discrimination task was chosen over a stimulus detection task both to minimize the influence of straylight (stimuli were presented on each trial) and because discrimination requires an identity judgment to be made which may in turn more likely involve the oscillatory mechanisms concerned with visual-feature (i.e. orientation) coding.

RP sat in front of the oscilloscope monitor with retinal size maintained by controlling monitor – eye distance using a chin rest. She was instructed to avoid eye-movements while maintaining fixation on the colored fixation point on the screen surrounding the monitor. Trials in which fixation was not maintained were noted and rejected offline. Her oral responses were recorded by the experimenter (to avoided RP shifting fixation from the fixation point to the computer keyboard) who also transcribed her descriptions.

Stimuli were presented for 2000 ms, following manual key press, a 250 ms computer generated tone and a randomized delay of 200–300 ms (to avoid any effects of contingent negative variation in the brain response). Experiment 1 consisted of 360 trials divided into 9 × 40 trial blocks. Experiment 2 consisted 20 blocks of 40 trials each (800 trials). In both experiments blocks were separated by breaks of >10 s. In both experiments a training block of 40 randomized practice trials was presented prior to the experimental blocks. and all stimulus conditions (orientations and flicker frequencies) were varied multifactorially and pseudo-randomly to reduce the influence of order effects.

3. Results

3.1. Experiment 1

Since there were four different independent stimulus conditions, a correct response has a probability of $p = 25\%$ while an incorrect response has a probability of $p = 75\%$. The corresponding distribution is the Binomial distribution. The probability of having, out of n trials up to k correct is:

$$P_k = \sum_{1}^{k} \binom{n}{k} p^k (1-p)^{n-k} \tag{1}$$

RP undertook 80 trials per frequency condition and on this basis the percentage of correct responses needed to be equal to or higher than 33% in order to be considered significantly above-chance performance. Although RP did not show evidence for blindsight when the gratings were presented statically, significant discrimination performance was achieved when the gratings were flickered at 33 Hz, 40 Hz, and 48 Hz (33%, $p < .05$; 39%, $p < .005$; 45%, $p < .001$, respectively, all tested against the binomial distribution detailed above, see Table 1).

3.2. Experiment 2

Using the same criterion as employed for Experiment 1, on the whole discrimination performance was found to be non-significantly different from random guessing. Although inconsistent with previous findings of a sensitivity across the 20–33 Hz band, consistent with Experiment 1 RP discriminated the orientation of the gratings significantly often when flickered at 38 Hz (34%, $p < .05$ binomial, see Table 2). She was also close to significance in orientation discrimination when the gratings were presented statically (32%).

RP reported visual experience relatively infrequently on 23% of trials overall, with reports almost always describing an experience of unstructured diffuse light appearing somewhere in the blind field. Fig. 2a shows some patterning in the

Table 2
Experiment 2 – %-correct discrimination performance by flicker frequency.

Frequency (Hz)	0	22	25	28	33	38	50	71	100
	32	24	16	21	28	34	17	32	28
	ns	ns	ns	ns	ns	$p < .05$	ns	ns	ns

relationship between visual experience and frequency, with reportage increasing overall between 20 and 38 Hz, and with peak reportage also evident at the higher frequencies of 71 and 100 Hz. However, for the most part this appears to be a function of frequency and unrelated to blindsight given almost equivalent patterns for both correct and incorrect discrimination trials and an absence of any particular difference between the frequency of experiences for incorrect and correct discriminations at 38 Hz, the only frequency at which discrimination was achieved with greater than chance probability. Overall, visual experiences were as frequently reported on incorrect (44%) as they were on correct (49%) response trials.
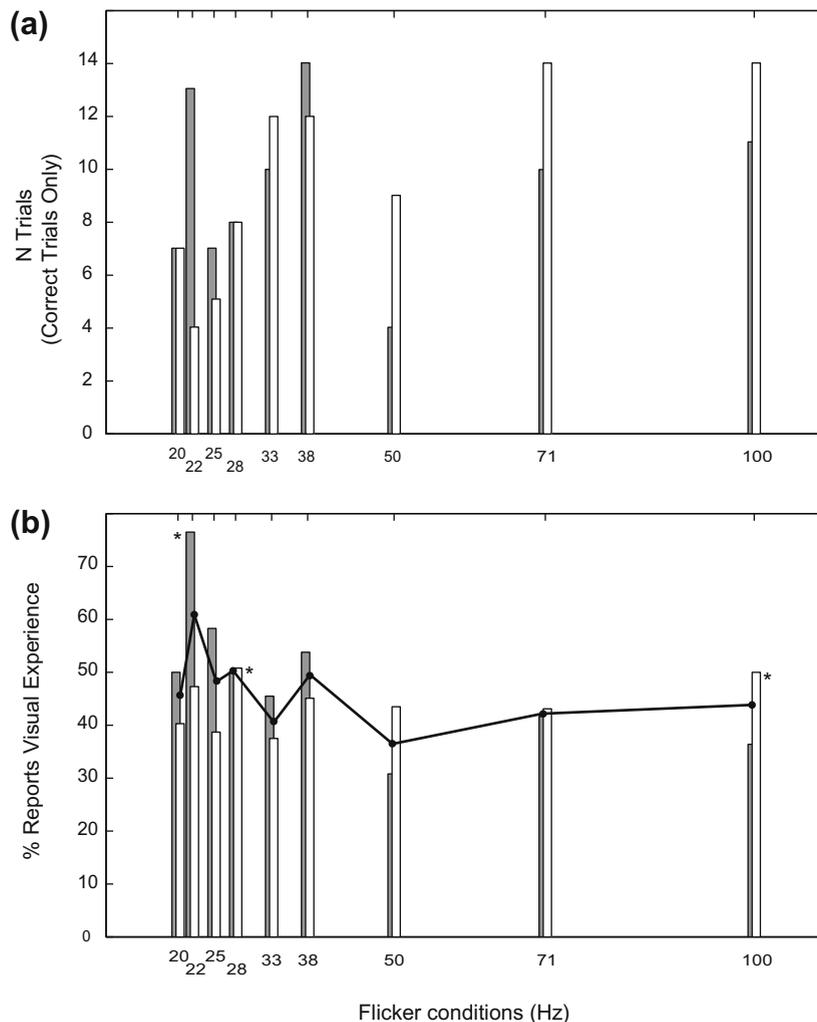
Fig. 2. In (a) are the number of trials upon which reports of visual experience (gray bars) is compared against the number of trials on which no reports were given (white bars) for correct discrimination performance over frequency. For static presentations (not presented here across frequency) RP reported visual experience on 14 occasions when incorrect and 11 occasions when correct. In (b) the percentage of reports of visual experience over frequency is denoted by the gray bars for correct discrimination performance and by the white bars for incorrect discriminations. The average percentage of these reports is denoted by the connected black circles. Percentages that differ significantly from the average percentage of reports for the correct and incorrect discriminations are indicated by stars to the left of the gray or to the right of the white bars for correct and incorrect discriminations, respectively. Visual experiences accompanied correct discriminations significantly more often than average at when stimuli were flickered at 22 Hz and incorrect responses when stimuli flickered at 28 and 100 Hz. For static presentations, visual experiences were reported on 44% of correct and 51% of incorrect discriminations. Neither of these values differed significantly from average reportage.

However inspection of Fig. 2b indicates that visual experience is quite differently distributed across flicker frequencies when the correct and incorrect trials are considered separately. To evaluate these differences, the percentage of reports was square-root transformed separately for the incorrect and correct discriminations, with each value compared against the respective mean of these transformed values across all frequencies. For incorrect discriminations, reports of visual experience were significantly higher than average when stimuli flickered at 28 Hz ($t(9) = 4.2$, $p < .005$) and 100 Hz ($t(9) = 3.7$, $p < .005$). For correct discriminations, and generally consistent with the expectation of effects close to 20 Hz, visual experiences were reported significantly more often than average when stimuli flickered at 22 Hz ($t(9) = 5.8$, $p < .001$), at which frequency 76% of correct reports were accompanied by visual experience. The fact that at 20 Hz there was neither significant report of visual experience, nor substantial evidence for blindsight indicates the effects at 22 Hz to rely upon a fairly well circumscribed bandwidth. Although close, the difference in frequencies associated with peak reportage on incorrect and correct trials suggests the existence at least two different, and relatively narrow temporal channels that mediate functionally different types of flicker-induced visual experience. To develop this idea further, frequencies with peak reportage were considered alongside those at which visual experiences were reported significantly less frequently than on average. The presence of frequencies at which visual experiences were reported relatively infrequently suggests one consequence of flicker to be interactions in phase with endogenous rhythms, with occasional and frequency specific effects arising due to the alignment of stimulus and endogenous rhythms at particular, functionally relevant phases. For incorrect trials, low reportage was found at 25 Hz ($t(9) = 3.42$, $p < .01$) and 33 Hz ($t(9) = 4.3$, $p < .001$) and for correct response trials at 50 Hz ($t(9) = 4.5$, $p < .001$). These frequencies, when considered in the time domain indicate a separation between low and low phases of ∼10 ms which characterizes visual experience over frequency for the incorrect discrimination trials. These are separated from the frequency of correct discrimination trials by 25 ms, suggesting an endogenous frequency of 50 ms period duration, i.e. of around 20 Hz.

4. Discussion

By employing technology capable of presenting stimuli with fine-scaled temporal resolution, sensitivity to the orientation of a grating presented with the blind field can be demonstrated across a band of frequencies in the low-mid-gamma band (i.e. 33–47 Hz, Experiment 1). Examination of a wider range of temporal frequencies, including those previously found to enhance stimulus detection in the blind field (Experiment 2) reveals a similar pattern of effects but only partially replicates previous findings (e.g. Barbur et al., 1994; Sahraie et al., 2008; Trevethan & Sahraie, 2003). Specifically and consistent with those studies, while there appears to be no enhancement of blindsight at high temporal frequencies (i.e. ⩾50 Hz) and small effects at mid-gamma frequencies (38 Hz), the peak effects previously reported at around 20 Hz were not found. This should not be taken as counterfactual with respects to previous findings but rather an extension to them given that the different tasks involved likely require the engagement of different brain mechanisms with different temporal characteristics (see also Weiskrantz, 1961 for a related argument). For example, these data are suggestive of the idea that enhanced blindsight is not mediated by a single wide-band temporal channel from retina to cortex but by several, task-specific temporal channels. However given that the effects reported here are found clustered around a subharmonic of the temporal channels (e.g. 10 and 20 Hz) reported previously, it seems more likely that the temporal channel is more sensitive to higher frequencies than previously thought and does different things with the temporal code it is given dependent upon task. Thus, while detection performance is enhanced at 10 and 20 Hz, successful discrimination, which requires an identity code to be computed, is better achieved at the higher frequencies around 40 Hz, i.e. those more commonly associated with feature binding and perceptual organization.

This argument requires modification when one takes into consideration the relationship between discrimination performance when gratings were static and when they flickered. In both Experiments 1 and 2, enhanced discrimination relative to static presentation is only found at mid-gamma frequencies, while for almost all other frequencies discrimination performance is less accurate. In addition performance at mid-gamma frequencies is comparable with performance given static presentations, which in turn is more likely to promote correct responses than the other frequency conditions. This suggests that discrimination at gamma frequencies is not enhanced but rather preserved relative to temporal presentation at other frequencies, which in turn implies that embedding a stimulus within a temporal envelope may impede discrimination performance if temporal frequency is not considered carefully. One putative reason for this is that the temporal frequency of stimulus presentation promotes discrimination in blindsight only when it interacts in phase with an existing endogenous rhythm and not when it induces or alters that rhythm. There is some evidence to suggest the priming results of Elliott and Müller (1998, 2004) may be explained in a similar way (cf. Kompass & Elliott, 2001) although much more evidence is required to corroborate this explanation.

Examination of visual experience in blindsight proves a little less straightforward to explain. On the one hand, while visual experiences were more often reported at higher temporal frequencies (⩾38 Hz) this cannot be claimed to relate to blindsight because enhanced discrimination was observed at only one frequency while the likelihood of visual experience was either equivalent between correct and incorrect discrimination trials and/or indistinguishable from the average incidence of reportage across all (correct or incorrect) trials. On the other hand although correct discrimination was at chance for frequencies around 20 Hz, when RP judged orientation correctly at 22 Hz, she very often reported visual experience, in fact significantly more often than on the average and much more frequently than on incorrect trials. This pattern of effects is consistent with expectations that visual experiences would be more likely to accompany correct discrimination at around

20 Hz than at mid-gamma frequencies. It also suggests against the possibility that visual experiences are simply artefacts of the temporal code and not specific to correct discrimination. However, at the same time correct discrimination at 22 Hz cannot be claimed with any degree of confidence to be other than random guessing (note also the results reported by Schurger et al., for whom occipito-parietal activity correlated with reports of visual experience that were themselves unrelated to blindsight performance).

One possible resolution to this puzzle appeals to the idea that discrimination in blindsight may be impaired when stimuli are temporally modulated. Consideration of the very substantial percentage of trials upon which visual reports are given at 22 Hz might indicate that a tendency to experience visual phenomena acts in support of discrimination performance, attenuating the negative effects of flicker and reducing the attendant downward trend in correct discrimination. This explanation assumes, as our hypothesis assumed, that visual experience would be bandpass-specific at around 20 Hz and it is consistent with the type of narrow tuning observed in other studies. If correct, it implies the type of visual phenomena experienced during Type II blindsight are stimulus related and while degraded and without defined form, can support discrimination of basic visual features such as orientation.

How this is brought about at a brain systems level remains to be resolved. One potential problem is the presence of visual awareness without the involvement of primary visual cortex although one recent review identifies activation in extrastriate areas, if supported by activation in other brain areas, as sufficient for the generation of visual experience (Silvanto, 2008). Critical to this argument is the idea that key functions of primary visual cortex, and perhaps more particularly the fine-scale rendering of visual structure may be absent but not necessary for some, seemingly non-specific experience. How this relates then to the discrimination of feature attributes such as orientation remains to be resolved. In this respect it is known that the major projections to extrastriate cortex via koniocellular pathways are insensitive to orientation and, while pulvinar neurons are orientation selective, tectal neurons located on the tectopulvinar pathway are not (Vakalopoulos, 2008). Vakalopoulos argues that blindsight can only be understood by consideration of wider cortical networks, which may include more than one bottom-up pathway interacting with descending connections to orientation-specific neurons in the pulvinar. Evidence that oscillatory priming at 40 Hz varies in magnitude as a function of the relative complexity and predictability of the masked prime (Shi & Elliott, 2007) provides some evidence that related visual-form processing, without awareness, is subject to top-down influences.

In conclusion, discrimination in the blind field may be generally impaired rather than enhanced by temporal stimulus presentation although and if this is the case; correct discrimination (blindsight) is preserved when stimuli are presented at temporal frequencies between 33 and 47 Hz (and not at lower or higher frequencies). Examination of visual experience during discrimination (Type II blindsight) suggests a more complex picture in which experiences particular to correct discrimination are not found at low-mid-gamma frequencies, but are found instead at lower frequencies at which blindsight is not observed. Under these conditions, blindsight might be considered an explanation for discrimination performance only if discrimination is assumed to be generally impaired by temporal stimulus presentation, but supported by the presence of visual experience. If this is so, although generally experienced as non-specific and unstructured light, the visual experiences accompanying blindsight must be based upon a neural representation which includes information on the visual features present in the stimulus.

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