

Attention without awareness in blindsight

R. W. Kentridge^{1*}, C. A. Heywood¹ and L. Weiskrantz²

¹Department of Psychology, Science Laboratories, University of Durham, South Road, Durham DH1 3LE, UK ²Department of Experimental Psychology, University of Oxford, South Parks Road, Oxford OX1 3UD, UK

The act of attending has frequently been equated with visual awareness. We examined this relationship in 'blindsight'—a condition in which the latter is absent or diminished as a result of damage to the primary visual cortex. Spatially selective visual attention is demonstrated when information that stimuli are likely to appear at a specific location enhances the speed or accuracy of detection of stimuli subsequently presented at that location. In a blindsight subject, we showed that attention can confer an advantage in processing stimuli presented at an attended location, without those stimuli entering consciousness. Attention could be directed both by symbolic cues in the subject's spared field of vision or cues presented in his blind field. Cues in his blind field were even effective in directing his attention to a second location remote from that at which the cue was presented. These indirect cues were effective whether or not they themselves elicited non-visual awareness. We concluded that the spatial selection of information by an attentional mechanism and its entry into conscious experience cannot be one and the same process.

Keywords: attention; consciousness; blindsight; human vision; striate cortex; spatial orientating

1. INTRODUCTION

Shifts of attention within the visual field can be overt or covert, where the latter are not accompanied by orientating movements (Posner 1980). Covert attention to a peripheral location facilitates the detection of, and responses to, targets presented at that location. It has long been assumed that attention and awareness are inextricably linked (James 1890) and the assumption is implicit in many contemporary theories of consciousness (Velmans 1996). Mack & Rock (1998) showed that when we do not attend to stimuli we are unaware of them. However, it has not previously been possible to test whether attending to a stimulus necessarily gives rise to awareness. It is quite possible that attention and awareness are only coupled together when attention is voluntarily directed, rather than automatically captured by stimuli (Posner 1994). They may also only be coupled when attention is directed in the service of object recognition, rather than simply being directed to a particular spatial location (Milner & Goodale 1996).

'Blindsight' subjects with a damaged striate cortex detect, discriminate and localize visual stimuli presented in their blind fields despite a denial of acknowledged awareness (Sanders et al. 1974; Weiskrantz 1997). The existence of the phenomenon and its neural bases have been the subject of considerable debate (Campion et al. 1983; Fendrich et al. 1992). However, there is evidence to show that it is not, as has been suggested, an artefact resulting from light scatter (King et al. 1996) or simply a result of changes in the subject's willingness to report detection of stimuli (a change in response bias; Azzopardi & Cowey 1997; Kentridge et al. 1999) or, at least in the subject of

the present study, an effect mediated by isolated patches of undamaged striate cortex (Kentridge *et al.* 1997). To examine the question of whether attention and awareness are inextricably linked or whether the operation of selective attention is demonstrable in the absence of awareness, we tested the ability of a blindsight patient, G.Y., to switch attention to locations in his 'blind' field. We measured the effect of cues indicating the probable location of stimuli on his reaction time (RT) to those stimuli.

2. THE SUBJECT

G.Y., a 41-year-old man, has been fully reported on elsewhere (Barbur et al. 1980, 1993; Blythe et al. 1987). He suffered unilateral damage to his left striate cortex, which was confirmed by computerized tomography (Blythe et al. 1987) and magnetic resonance imaging (Barbur et al. 1980), as a result of a car accident at the age of eight years. He has a right homonymous hemianopia but retains around 3° of macular sparing, consistent with the damage revealed by neuroimaging. G.Y. gave informed consent to participate in the experiments.

3. METHODS

(a) Central cueing experiment

The ability to direct spatial attention is typically assessed by presenting a target preceded by a cue which may or may not indicate the correct location of the subsequent target (Posner 1980). Valid cues produce more rapid responses to targets than misleading cues, which in turn may produce slower responses than a neutral condition. We adapted this method for use in blindsight. An auditory tone was preceded by a visual cue that signalled the probable target location. The subject's task on each trial was to report, using a button press, whether or not a visual

^{*}Author for correspondence (robert.kentridge@durham.ac.uk).

1806

target accompanied the presentation of the auditory tone. His RTs were measured. After making the response, indicating whether or not a target had been presented, the subject was then required to make a second 'commentary' response indicating whether he had had any awareness of a target.

Stimuli were generated using a Cambridge Research Systems VSG2/3 and displayed against a $67.5 \, cd \, m^{-2}$ background on an Eizo F784T colour monitor. Each trial began with the presentation of a black 1.0° fixation cross for 0.5 s. This was then replaced by a smaller 0.17° cross; after a further $0.5\,s$ a 1.0° arrow pointing towards one of two possible target locations was superimposed for 0.6 s (each location was indicated with equal probability within a block of trials). The possible target locations were both at an eccentricity of 9° from fixation; one was 10° (polar) to the right of the vertical meridian and the other 15° below the horizontal. At the offset of the arrow cue there was a 0.5 s interval with just the small fixation cross present (a stimulus onset asynchrony typical in this type of attentional cueing study), followed by a 0.016s tone signalling the start of the target period. A target, if present, was a 1° diameter disc. The disc was decremented in luminance with a Gaussian profile over a period of 0.5 s, starting and finishing two standard deviations away from the peak contrast of -17% (a minimum luminance of $47.5 \,\mathrm{cd}\,\mathrm{m}^{-2}$) which was reached after $0.25 \,\mathrm{s}$. We used a gradual temporal modulation, rather than one with abrupt onset or offset, as the latter have been shown to contribute strongly to awareness of stimuli (Macknik & Livingstone 1998). In 50% of the trials no target was presented. In 68.75% of the trials where a target was present it was in the location indicated by the cue, while in the other 31.25% it was presented at the other location (see figure 1a). In order to permit analyses of the accuracy of target detection in valid and misleading cue conditions, trials in which no target was presented were allocated randomly to these two conditions, again in the proportions 68.75% and 31.25%. The subject was seated $57\,\mathrm{cm}$ from the screen and used a combined chin and forehead rest. The subject's eye position was monitored throughout the experiment by one of the experimenters using a remote video system which provided a continuous magnified image of G.Y.'s eyes. All trials in which an eye movement was detected were discarded from the analysis. Before the start of the experiment the subject was given written instructions indicating the two possible target locations and describing the sequence of events in each trial. These instructions indicated that a target, if presented, was more than twice as likely to appear at the location indicated by the arrow than at the other location and that targets would appear in 50% of the trials. As targets were indeed more likely to appear in the valid than misleading location, the cue-target contingency could, in principle, be learned even if the subject's explicit knowledge of the contingency was unavailable to the systems mediating blindsight. The subject was instructed to respond rapidly on a button box to report whether or not a target (in either location) had accompanied the tone in each trial, guessing if necessary and then to make a second response indicating whether he had had any experience whatsoever, including non-visual experiences such as 'feeling something was there' accompanying the tone. Testing was conducted in ten blocks of 128 trials. The subject was given no feedback on his performance.

(b) Direct peripheral cueing

The methods were the same as those used in the previous experiment with the following exceptions. Instead of an arrow,

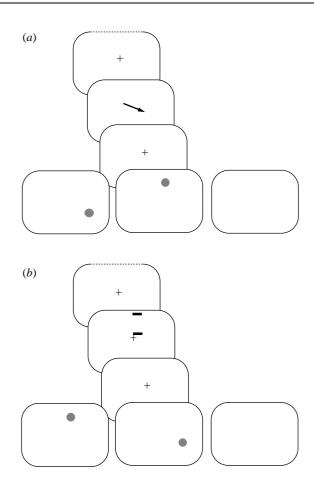


Figure 1. Stimulus sequences used in each trial. (a) The sequence used in the central-cueing experiment. In this example the arrow is cueing the lower of the two possible target locations. The left frame at the bottom illustrates a trial where the target was presented at the location indicated by the cue, the middle frame one where it was presented at the other, misleading location, and the right frame one where no target was presented. (b) The sequences used in the other experiments. In this example the upper location is directly cued by the peripherally presented bars and the lower left, middle and right frames again illustrate the valid, misleadingly cued and target-absent trials, respectively.

the cue consisted of two bars, 2° above and below one of the target locations. Each bar was 1° wide and 0.196° high and decremented in luminance with a Gaussian profile over a period of 0.5 s, starting and finishing two standard deviations away from the minimum luminance of $40.0 \, \mathrm{cd} \, \mathrm{m}^{-2}$ (reached at $0.25 \, \mathrm{s}$), which yielded a -26% Michelson contrast. The gap between the end of cue presentation and that of target presentation was reduced to $0.1 \, \mathrm{s}$. The target was modulated in luminance over a $0.2 \, \mathrm{s}$ period rather than the $0.5 \, \mathrm{s}$ period used in experiment l; its peak contrast remained at -17% (see figure 1b). The subject was presented with written instructions explaining the new procedure.

(c) Indirect peripheral cueing

The methods were identical to those of the previous experiment (see $\S3(b)$) with the exception of the contingency between cue and target locations. Instead of cues signalling that a subsequently appearing target would occur at the same location as the cue with 68.75% probability, cues now indicated that there was a 68.75% probability of targets appearing at the other

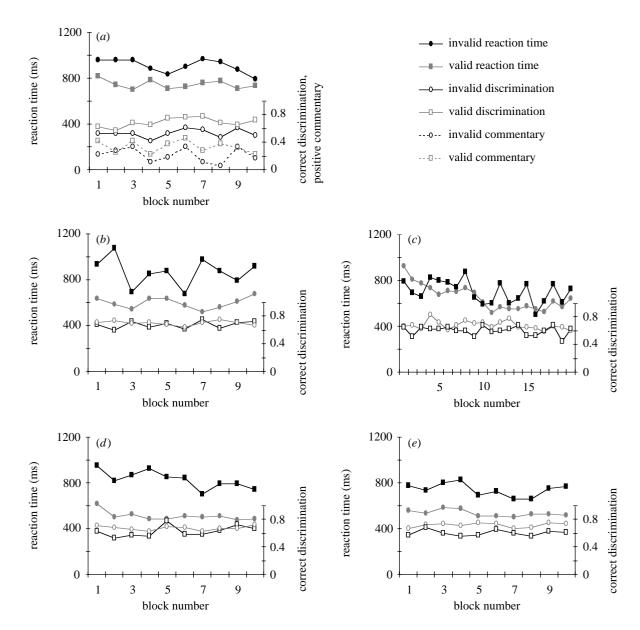


Figure 2. Effects of cue validity on RT and target detection accuracy. The mean RTs for correct responses to present targets and the proportion of correctly detected targets in the valid and misleading cueing conditions are shown for each block of 128 trials. (a) The results using centrally presented arrow cues. In addition to showing the RT and accuracy results it also shows the proportion of trials in which G.Y. reported target awareness. The short right-hand ordinate indicates both the scale for the proportion of correct responses in each condition and the proportion of responses in which awareness of the target was reported. For all other panels target awareness was reported as zero throughout. (b) Mean RT and detection accuracy results for direct, and (ϵ) indirect, indications of target locations by low-contrast peripheral cues. (d) Mean RT and detection accuracy results for direct, and (ϵ) indirect, indications of target locations by high-contrast peripheral cues.

location. The subject was informed of the changed contingency before testing. There were 20 blocks of 128 trials.

(d) Direct peripheral cueing with high-contrast cues

The methods replicated those of the direct peripheral cueing experiment (see $\S 3(b)$), with the exception of the peak contrast of the cue, which was now -93% (minimum luminance $2.5 \, \text{cd m}^{-2}$).

(e) Indirect peripheral cueing with high-contrast cues

The methods replicated those of the indirect peripheral cueing experiment (see $\S3(c)$), again with the exception of the higher -93% peak contrast of the cue. In addition, ten rather than 20 blocks of testing were conducted.

4. RESULTS AND DISCUSSION

(a) Central cueing experiment

Figure 2a shows that G.Y. was quicker to detect targets when the cue accurately disclosed their location. Statistical analyses were conducted on the RTs for each cueing condition for all trials in which a target was correctly identified as being present, after discarding trials in which there were anticipatory responses (RT < 150 ms) and mishits of the buttons (RT > 1500 ms) and trials in which G.Y. moved his eyes away from fixation. Only seven trials (0.55%) were discarded. The proportion of trials discarded in all of the experiments reported in this paper never exceeded 0.7%. An independent samples

t-test comparing the RTs for conditions where the cue correctly and incorrectly predicted the subsequent target location shows a significant effect of cue validity $(t_{101.78} = 7.47 \text{ and } p < 0.001;$ all t-tests use a pooled variance estimate of t and a corrected d.f. for inhomogeneity of variance as provided by the Statistical Package for the Social Sciences (SPSS) when Levene's test indicates it is appropriate).

Figure 2a also shows that G.Y. was more accurate in reporting whether or not a target had been presented when the cue correctly indicated its location ($\chi_1^2 = 28.79$ and p < 0.001). Binomial tests of his performance in each cueing condition showed that his ability to detect a target was significantly better than chance for trials with a valid cue (632 out of 915 (69% correct) and p < 0.001) but not for ones with a misleading cue (190 out of 358 (53% correct) and n.s.). As his discrimination performance is better in the validly cued condition the RTs advantage in this condition cannot be attributed to a trade-off between the speed and accuracy of judgements.

G.Y.'s correct responses were significantly slower than his incorrect ones when a target was present in the trials with misleading cues ($t_{176} = 7.94$ and p < 0.001). The RTs of these incorrect responses did not differ from those of trials in which no target was presented ($t_{734} = 1.24$ and n.s.). This indicates that the difference between correct RTs to targets in the two cueing conditions was due to an effect of cue validity on the speed of response to targets, rather than the slowing of response one might expect to find in the misleading condition if all of G.Y.'s responses in that condition were random and uninfluenced by the presence of a target. This then is evidence for an effect of attention on the processing of visual stimuli in G.Y.'s blind field. However, the key question that concerns us is whether evidence can be found for attentionally selective processing of stimuli in the absence of awareness of those stimuli. G.Y. demonstrate two modes of perception within his scotoma (Weiskrantz et al. 1995), one in which he reports no awareness of stimuli but was nevertheless capable of discriminating their properties in forcedchoice tasks and the other in which he reports awareness of stimuli, although he still denies having normal phenomenal visual experience of them. Transient, highcontrast or moving stimuli are particularly likely to elicit awareness. We monitored G.Y.'s awareness of targets using a commentary paradigm in which he was asked to report whether he had had any awareness of a target after each trial (figure 2a). Analysis of these commentary responses showed that validly cued trials are significantly more likely to give rise to experience than ones with misleading cues ($\chi_1^2 = 8.84$ and p < 0.005). Attention has already been reported to give rise to phenomenal experience in a case of the auditory analogue of blindsight: 'deaf-hearing' (Silbersweig & Stern 1998). We were also able to analyse separately trials in which G.Y. reported no awareness of the target and still found a significant effect of cue validity on RT (valid cue RT, mean = 766 ms, s.d. = 153 ms and n = 40 observations, and misleading cue RT, mean = $853 \,\text{ms}$, s.d. = $191 \,\text{ms}$ and $n = 153 \,\text{observa}$ tions; $t_{52.63} = 2.65$ and p < 0.05). This evidence in favour of attention without awareness encouraged us to use less salient target stimuli in subsequent experiments directed at the question of whether it is possible to direct spatial

attention in blindsight using cues presented within the scotoma, when a subject is unaware of either cue or target.

(b) Direct peripheral cueing

Although the peripheral cues had a slightly higher contrast than the targets, preliminary tests had indicated that G.Y. was rarely aware of them when they were presented without targets. Figure 2b shows that G.Y.'s RT was faster when the cue and target locations coincided than when they differed $(t_{146.88} = 9.08 \text{ and } p < 0.001)$. There was no difference between his ability to detect targets in the valid and misleading cueing conditions $(\chi_1^2 = 0.646$ and n.s.); in both cases his performance was significantly better than chance (624 out of 917 (70%) and p < 0.001 in the valid condition, and 241 out of 356 (68%) and p < 0.001 in the misleading condition). Although G.Y. made trial-by-trial commentary responses throughout the experiment, he did not report awareness of a single target. He was also asked after each block of trials whether he had had any experience of the cues; his responses indicated that he did not. For example, 'I would be none the wiser if you were not putting any cues up just to confuse me' and 'I just listen for the beep and press a button'. These results suggest that attention can be directed to locations cued within G.Y.'s scotoma. However, it may be argued that these results can simply be explained in terms of temporal and spatial summation of the cue and target energy leading to a more readily detectable target in the valid condition. The indirect peripheral cueing experiment tests whether this is the case.

(c) Indirect peripheral cueing

Successful use of the information conveyed by a cue in this experiment requires interpretation of the cue in light of the rule relating cue and target locations—sometimes characterized as executively, as opposed to automatically, controlled attention (Posner 1994). Simple summation of cue and target energy or the automatic capture of attention by cues would both lead to an RT advantage for targets presented at the same location as the cue—in this experiment that is the less likely misleading location. Figure 2c shows the pattern of results obtained over extended testing. Over the first three blocks of testing (384 trials) G.Y. responded more quickly to targets in the misleading condition, that is, targets which appear in the same place as the preceding cue. His pattern of results then changed and, although there is considerable variability between blocks, he now showed RT advantages in the valid condition. He became quicker at detecting targets that appeared at the location remote from the cue than he was at detecting targets presented at the same location as the cue. A *t*-test using all trials (including the first three blocks) shows this RT advantage to be statistically significant $(t_{829} = 2.50 \text{ and } p < 0.05)$. We also found a difference in his ability to detect the presence of targets between conditions $(\chi_1^2 = 15.59 \text{ and } p < 0.001)$; in both cases his performance was significantly better than chance (1191 out of 1750 (68%) and p < 0.001 in the valid condition, and 476 out of 793 (62%) and p < 0.001 in the misleading condition). As G.Y.'s accuracy was better in the valid than in the misleading condition, his RT advantage cannot be attributed to a speed-error trade-off. G.Y. continued to give trial-by-trial commentary on his awareness of targets and

again he did not report awareness of a single target. His remarks upon being questioned after each test block indicated that he had no awareness of cues either: 'No awareness of cues', 'No experience of anything', 'Still nothing there'. These results confirm that G.Y. can direct attention within his blind field using cues of which he is unaware. Further, they show that the direction of this selective attention, as revealed by an RT advantage in detecting stimuli presented at attended locations, does not give rise to awareness of those stimuli even when the relationship between cue and target location is not a simple identity. In isolation one might explain the results of this experiment in terms of forward masking of the target by the cue in the misleading condition or the phenomenon of 'inhibition of return' (Posner et al. 1985) rather than attentional cueing. However, neither of these alternative explanations is consistent with the results of both this experiment and the preceding one.

Finally, we went on to investigate whether the direction of attention by cues in the blind field, of which G.Y. was nevertheless aware, would give rise to awareness of targets. G.Y. has reported a form of awareness for moving or transient stimuli of high contrast presented within his scotoma, although he characterizes it as being a nonvisual experience (Weiskrantz et al. 1995). We therefore repeated the preceding pair of experiments but used cues of the highest contrast achievable with our monitor.

(d) Direct peripheral cueing with high-contrast cues

Figure 2d shows a highly significant effect of cue validity on RT ($t_{151.19} = 14.50$ and p < 0.001). There was no difference in G.Y.'s accuracy in detecting targets between cueing conditions ($\chi_1^2 = 2.617$ and n.s.) and in both cases his performance was significantly better than chance (618 out of 919 (67%) and p < 0.001 in the valid condition, and 223 out of 357 (62%) and p < 0.001 in the misleading condition). G.Y. never reported any awareness of the targets, but his responses to questioning at the end of each block indicate that he was aware of the high-contrast cues and also that this awareness gave him some knowledge of cue location as these examples illustrate: 'I am aware of the top cue most of the time and the right one occasionally' and 'I could not describe what I experience, but I definitely know where the top one [cue] is; the other one does not seem as far below the midline as I expected. No experience of the targets at all though'. The pattern of results is broadly similar to that found with low-contrast cues. The absence of awareness of targets in the attended location occurs whether or not G.Y. is aware of the cues indicating that location.

(e) Indirect peripheral cueing with high-contrast cues

Figure 2e shows a highly significant effect of cue validity on RT ($t_{125.1}$ =7.80 and p < 0.001). G.Y. was more accurate at detecting targets on validly cued trials (χ_1^2 =16.413 and p < 0.001), but in both conditions his performance was significantly better than chance (629 out of 879 (72%) and p < 0.001 in the valid condition, and 240 out of 399 (60%) and p < 0.001 in the misleading condition). G.Y. did not report awareness of a single target. His responses to questioning at the end of each block indicated that he was still aware of the high-

contrast cues and their location, although this awareness was decreasing: 'I am aware of all of them at the top but virtually none at the bottom' and '25-35% aware—it starts well but degrades very quickly'. As we found with low-contrast cues, G.Y. was capable of directing attention to a location remote from the cue without becoming aware of the stimuli attended to at that location. There is, however, an important difference between the pattern of results obtained with the high- and low-contrast cues. Prior to both of the indirect cueing experiments G.Y. had been performing tasks where the cues directly indicated the probable target location. Even though the instructions given to him explicitly explained that the contingency between cue location and probable target location was reversed, in the low-contrast indirect peripheral cueing experiment (see §§ 3(c), 4(c)) G.Y. nevertheless initially showed an RT advantage in the misleading condition; in other words when targets were presented in the same location as the cue they followed. In both indirect cueing experiments, the targets only appeared at the same location as cues in a small minority of trials. This misleading condition did, however, correspond to the direct cuetarget contingency of the preceding experiment. It appears that G.Y. was still behaving as if the direct contingency was still operating for the first three blocks of the low-contrast indirect cueing experiment (see $\S 4(c)$). In the present experiment, however, the reversed contingency was effective in speeding his RT from the first block. It is also apparent that in the low-contrast experiment there was a great deal of variability in the effect of cue validity which was often small and sometimes even negative, whereas the effect found in the current experiment was larger and more consistent. G.Y. summed up what may be the crux of these differences during one of the post-test debriefings in the present experiment: 'When I am aware [of the cue] I can try to attend to the other [i.e. valid] location...when I was not aware of any of the cues [during low-contrast cue experiments] I could not try to switch my attention'. In other words, G.Y. could only voluntarily direct his attention when he had awareness of the cue location.

5. GENERAL DISCUSSSION

In all the experiments we report in this paper, G.Y. showed faster RTs in his detection of targets when those targets were preceded by cues which correctly predicted a target's location than he did when the cues provided misleading indications of a target's location. These RT advantages were never accompanied by a reduction in G.Y.'s accuracy in discriminating between the presence and absence of targets. Furthermore, his discrimination accuracy was always significantly better than would be expected if he were simply guessing. These findings confirm the observation that topographic information is processed in the blind hemifield and is available to a variety of neural mechanisms controlling responses such as eye movements (Blythe et al. 1987; Barbur et al. 1988), pointing (Weiskrantz 1989) and verbal responses (Barbur et al. 1980). The present results provide compelling evidence that topographic information is also available to mechanisms which allow G.Y. to direct attention to locations in his blind field selectively.

The central cueing experiment (see §§ 3(a), 4(a)) showed that, with a sufficiently salient target, G.Y. was more likely to be aware of stimuli presented at the location to which he was attending. In other words, attention can modulate awareness. The remaining experiments showed, however, that attention can be directed towards a location and confer an advantage in processing stimuli presented at that location, without those stimuli entering consciousness. Therefore, the spatial selection of information by an attentional mechanism and its entry into conscious experience cannot be one and the same process.

We had expected that the direction of attention might be restricted to situations in which G.Y. was aware of the cue and, hence, could act voluntarily and to situations in which the cue could automatically direct attention by virtue of being in the same location as the target. Using cues near the threshold of detectability, McCormick (1997) found that normal subjects could direct their attention to directly cued locations without cue awareness but could only direct their attention to locations indirectly indicated by a cue if they were aware of that cue. Neither McCormick's (1997) results or Posner's (1994) hypothesis that the executive control of attention involves awareness at first appear consistent with our finding that cues of which G.Y. was unaware could direct his attention to arbitrary remote locations. An indirect cue-target location contingency appears to require voluntary as opposed to automatic control of attention. Direct and indirect cueing differ from one another in two ways; indirect cueing requires the application of an arbitrary rule relating the cue and target locations and the suppression of automatic orientating to the cue location. Our smoothly temporally modulated stimuli may have had a relatively weak capacity to orientate attention automatically (Jonides & Yantis 1988). In Posner's (1994) model, the application of an attentional rule is expected to involve activation of frontal brain areas mediating working memory and language. However, there is also the possibility that a consistent relationship between the cue and target positions may be encoded in the eye-movement system. Glimcher & Sparks (1992) showed that the activity of prelude burst cells in the superior colliculus, which precedes and predicts eyemovement direction, can be modulated by indirect cues to a target's location. Kustov & Robinson (1996) also showed that indirect relationships between cue and target locations can be encoded within brain systems involved in eye-movement control and that these indirect relationships modulate attention as well as eye-movement initiation. Finally, Basso & Wurtz (1997) showed that changes in the probability that a target will appear at a particular location modulate the activity of collicular cells firing in the build-up to an eye movement. Taken together, these findings suggest that a simple cue-target contingency may be encoded in the collicular-parietal, eye-movement control system and may not necessarily require the involvement of frontal language and memory systems. We suggest that the slower development of a valid cue RT advantage, where G.Y. was unaware of cues, in comparison to the corresponding high-contrast cue experiment where he was aware of cues and reported that he was voluntarily attempting to shift his attention, may reflect differences between the relatively slow, non-conscious acquisition of the cue-target location contingency and its

voluntary use. McCormick's (1997) subjects may have failed to acquire an indirect contingency with cues of which they were unaware as a consequence of the comparatively short periods of testing he used. The suggestion that cue-target relationships can be learnt implicitly is supported by recent findings by Lambert et al. (1999) that arbitrary relationships between peripheral cues and the target locations most likely to follow them are effective in orientating the attention of normal subjects, even when they are unaware of the contingency, unaware of the peripheral cues or unaware of both. In G.Y. it appears to be the case that explicit knowledge of a cue-target relationship can only be used voluntarily when the cue gives rise to awareness. When he remained unaware of the cue he could only make use of it after a period during which, we suggest, implicit learning takes place.

We focus on the eye-movement system as having a potential role in mediating non-conscious, attentional processes in G.Y. since recent functional magnetic resonance imaging of G.Y. showed that, during trials in which he reported awareness of visual stimuli, there was activation in the dorsolateral prefrontal cortex but, in trials where his discrimination was correct but he reported no awareness, the activity was primarily subcortical, notably in the superior colliculus (Sahraie et al. 1997). Willed action (Frith et al. 1991), spatial memory (Ungerleider et al. 1998) and the suppression of habitual responses (Jahanshahi et al. 1998) have all been associated with activity in the dorsolateral pre-frontal cortex, as has the voluntary direction of attention (Posner 1994). When G.Y. directs his attention voluntarily, the cue can be immediately interpreted in the light of the remembered rule relating cue and target positions. We note, however, that when G.Y. reported awareness of stimuli he still denied normal visual experience of them. Although awareness of visual cues may be mediated by activity reaching the dorsolateral pre-frontal cortex by a route that bypasses the striate cortex, the experience of visual qualia is apparently severely compromised without the striate cortex.

In conclusion, we present evidence that attending to a stimulus at a particular location is not synonymous with being aware of it. This is consistent with Milner & Goodale's (1996) proposal that 'there is more than one substrate supporting selective visual attention and that only one of these substrates is linked with conscious experience' (p. 183) and builds on our own recent finding that prior information about the time at which a target will appear also improves performance in blindsight (Kentridge et al. 1999). Our present results, showing that peripheral cues could orientate attention indirectly without awareness of either cue or target, may appear to pose problems for Posner's (1994) hypotheses about the relationship between voluntary attention and awareness. In light of the differences between the patterns of results obtained with highand low-contrast peripheral cues, we are currently addressing the question of whether prolonged practice in the use of indirect spatial cues below the threshold of awareness in normal subjects results in the implicit acquisition of an attentional contingency. However, it is clear that, while the direction of attention towards a stimulus may be necessary if it is to reach awareness (Mack & Rock 1998), attention is not sufficient for awareness.

We thank I. Gilchrist for helpful discussion. C.A.H. gratefully acknowledges receipt of a University of Durham Sir Derman Christopherson Foundation Fellowship.

REFERENCES

- Azzopardi, P. & Cowey, A. 1997 Is blindsight like normal nearthreshold vision? *Proc. Natl Acad. Sci. USA* 94, 14190–14194.
- Barbur, J. L., Ruddock, K. & Waterfield, V. A. 1980 Human visual responses in the absence of the geniculo-calcarine projection. *Brain* 103, 905–928.
- Barbur, J. L., Forsyth, P. M. & Findlay, J. M. 1988 Human saccadic eye movements in the absence of the geniculocalcarine projection. *Brain* 111, 63–82.
- Barbur, J. L., Watson, J. D. G., Frakowiak, R. S. J. & Zeki, S. 1993 Conscious visual perception without Vl. Brain 116, 1293–1302.
- Basso, M. A. & Wurtz, R. H. 1997 Modulation of neuronal activity by target uncertainty. *Nature* 389, 66–69.
- Blythe, I. M., Kennard, C. & Ruddock, K. H. 1987 Residual vision in patients with retrogeniculate lesions of the visual pathways. *Brain* 110, 887–894.
- Campion, J., Latto, R. & Smith, Y. M. 1983 Is blindsight an effect of scattered light, spared-cortex and near-threshold vision? *Behav. Brain Sci.* 6, 423–486.
- Fendrich, R., Wessinger, C. M. & Gazzaniga, M. 1992 Residual vision in a scotoma: implications for blindsight. *Science* 258, 1489–1491.
- Frith, C. D., Friston, K., Liddle, P. F. & Frackowiak, R. S. 1991 Willed action and the prefrontal cortex in man: a study with PET. Proc. R. Soc. Lond. B 244, 241–246.
- Glimcher, P. W. & Sparks, D. L. 1992 Movement selection in advance of action in the superior colliculus. *Nature* **355**, 549–545
- Jahanshahi, M., Profice, P., Brown, R. G., Ridding, M. C., Dirnberger, G. & Rothwell, J. C. 1998 The effects of transcranial magnetic stimulation over the dorsolateral prefrontal cortex on suppression of habitual counting during random number generation. *Brain* 121, 1533–1544.
- James, W. 1890 Principles of psychology. London: Macmillan.
- Jonides, J. & Yantis, S. 1988 Uniqueness of abrupt visual onset in capturing attention. *Percept. Psychophys.* 43, 346–354.
- Kentridge, R. W., Heywood, C. A. & Weiskrantz, L. 1997 Residual vision in multiple retinal locations within a scotoma: implications for blindsight. J. Cogn. Neurosci. 9, 191–202.
- Kentridge, R. W., Heywood, C. A. & Weiskrantz, L. 1999 Effects of temporal cueing on residual visual discrimination in blindsight. *Neuropsychologia* 37, 479–483.
- King, S. M., Azzopardi, P., Cowey, A., Oxbury, J. & Oxbury, S. 1996 The role of light scatter in the residual visual sensitivity of patients with complete cerebral hemispherectomy. *Visual Neurosci.* 13, 1–13.

- Kustov, A. A. & Robinson, D. L. 1996 Shared neuronal control of attentional shifts and eye movements. *Nature* 384, 74–77.
- Lambert, A., Naikar, N., McLachlan, K. & Aitken, V. 1999 A new component of visual orientating: implicit effects of peripheral information and subthreshold cues on covert attention. J. Exp. Psychol. Hum. Percept. Perform. 25, 321–340.
- McCormick, P. A. 1997 Orienting attention without awareness. *J. Exp. Psychol. Hum. Percept. Perform.* 23, 168–180.
- Mack, A. & Rock, I. 1998 Inattentional blindness. Cambridge, MA: MIT Press.
- Macknik, S. L. & Livingstone, M. S. 1998 Neuronal correlates of visibility and invisibility in the primate visual system. *Nature Neurosci.* **1**, 144–149.
- Milner, A. D. & Goodale, M. A. 1996 The visual brain in action. Oxford University Press.
- Posner, M. I. 1980 Orienting of attention. Q. J. Exp. Psychol. 32, 3–95
- Posner, M. I. 1994 Attention: the mechanisms of consciousness. Proc. Natl Acad. Sci. USA 91, 7398-7403.
- Posner, M. I., Rafal, R. D., Choate, L. S. & Vaughan, J. 1985 Inhibition of return: neural basis and function. Cogn. Neuropsychol. 2, 211–228.
- Sahraie, A., Weiskrantz, L., Barbur, J. L., Simmons, A. & Williams, S. C. R. 1997 Pattern of neuronal activity associated with conscious and unconscious processing of visual signals. *Proc. Natl Acad. Sci. USA* **94**, 9406–9411.
- Sanders, M. D., Warrington, E. K., Marshall, J. & Weiskrantz, L. 1974 'Blindsight': vision in a field defect. *Lancet* **20**, 707–708.
- Silbersweig, D. A. & Stern, E. 1998 Towards a functional neuroanatomy of conscious perception and its modulation by volition: implications of human auditory neuroimaging studies. *Phil. Trans. R. Soc. Lond.* B 353, 1883–1888.
- Ungerleider, L. G., Courtney, S. M. & Haxby, J. V. 1998 A neural system for human visual working memory. *Proc. Natl Acad. Sci. USA* 95, 883–890.
- Velmans, M. 1996 An introduction to the science of consciousness. In *The science of consciousness: psychological, neuropsychological and clinical reviews* (ed. M. Velmans), pp. 1–22. London: Routledge.
- Weiskrantz, L. 1989 The Ferrier Lecture. Outlooks for blindsight: explicit methodologies for implicit processes. Proc. R. Soc. Lond. B 239, 247–278.
- Weiskrantz, L. 1997 Consciousness lost and found. Oxford University Press.
- Weiskrantz, L., Barbur, J. L. & Sahraie, A. 1995 Parameters affecting conscious versus unconscious visual discrimination with damage to the visual cortex (V1). *Proc. Natl Acad. Sci. USA* **92**, 6122–6126.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.