

Towards a unified model of vision and attention: Effects of visual landmarks and identity cues on covert and overt attention movements.

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ABSTRACT

To what extent are shifts of attention driven by encoding of *visual-spatial landmarks*, associated with useful locations, or by encoding of environmental cues that act as *symbolic representations*, providing information about where to look next? In Experiments 1-3 we found that when cues were presented with a long exposure time (300ms) attention shifts were driven by the symbolic identity of cue stimuli, independently of their visual-spatial (landmark) features; but when cues were exposed very briefly, (66ms), attention shifts were independent of symbolic information, and were driven instead by visual landmark features. This unexpected finding was interpreted in terms of the transient and sustained response characteristics of the M-cell and P-cell inputs to the dorsal and ventral visual streams, respectively, and informed our theoretical proposal that attentional effects elicited by visual-spatial landmarks may be driven by dorsal stream (*'where pathway'*) encoding; while attentional effects driven by the symbolic identity of cues may be driven by ventral stream (*'what pathway'*) encoding. Detailed predictions derived from this proposal, and based on distinct physiological properties of the two visual streams were tested and confirmed in Experiments 4-6. Our results suggest that a two-process view of attention shifting can be integrated with dual-stream models of vision. According to this unified theory:

- (1) Landmarks associated with visually useful locations elicit rapid, non-conscious shifts of attention, via non-semantic, dorsal visual stream encoding of their features and spatial relationships;
- (2) Slower, endogenous shifts of attention are elicited by ventral visual stream encoding of symbolic-semantic information.

Keywords: attention; vision; consciousness; awareness; dorsal visual stream; ventral visual stream; visual orienting; visual perception; eye movements; spatial cueing

While the distinguished philosopher, Karl Popper, championed the idea that scientific theory should be at least *potentially* vulnerable to falsification (Popper, 1959), in his most recent book, the philosopher of cognitive science, Daniel Dennett, reminds his readers of the scientific value of hypotheses which are not merely vulnerable to falsification, but which really do turn out to be based on mistaken ideas. According to Dennett, “Mistakes are not just opportunities for learning; they are, in an important sense, the *only* (italics in original) opportunity for learning or making something truly new.” (Dennett, 2013, p.21).

Consequently, Dennett enjoins his readers: “Try to acquire the weird practice of savoring your mistakes, delighting in uncovering the strange quirks that led you astray. Then, once you have sucked out all the goodness to be gained from having made them, you can cheerfully set them behind you and go on to the next big opportunity.” (Dennett, 2013, p.23). While the pages of published research articles are typically replete with accounts of bold hypotheses neatly confirmed by data, research outcomes of the opposite variety, where well-formulated hypotheses *fail* in response to experimental challenge, can be just as informative. The initial aim of the programme of work described below was to resolve an important and troubling discrepancy in previous literature regarding effects of environmental cues on movements of visual attention. The two most promising hypotheses for resolving this discrepancy were soundly disconfirmed by data from the first two experiments, leading us to consider a third possibility in Experiment 3, which had been dismissed as relatively unlikely when the work began. Findings from our third experiment indicated that this least favoured of the three hypotheses was in fact, the correct one. This unanticipated result led to the development of a model which integrates a two-process view of visual attention (Chica, Bartolomeo and Lupiáñez, 2013; Corbetta & Shulman 2002; Posner, 1978,1980; Posner, Snyder & Davidson, 1980) with dual-stream models of vision (Milner & Goodale, 2006; Ungerleider & Mishkin,

1982). Predictions generated from this model were tested, and confirmed in Experiments 4, 5 and 6.

The problem that troubled us was this: Work carried out in our own laboratory (Lambert, Roser, Wells and Heffer, 2006; Shin, Marrett & Lambert, 2011) showed that when letters presented in central vision, were used as spatial cues in a visual orienting paradigm, attentional effects were driven by visual-spatial properties of the cue stimuli, rather than by their semantic-symbolic properties; but other work, notably that reported by Fischer, Castel, Dodd & Pratt (2003) employing number stimuli as cues, has supported the opposite conclusion - that orienting behaviour can be driven by semantic-symbolic properties of cue stimuli, irrespective of their low-level visual-spatial features (see also Hommel, Pratt, Colzato & Godijn, 2001).

To foreshadow the story that will unfold below, in our first experiment we tested a prediction, derived from the *spatial correspondence hypothesis* (Lambert, Roser Wells & Heffer, 2006; Shin, Marrett & Lambert, 2011) that when numbers are used as cues in a spatial orienting task, attentional effects will be affected by the presence or absence of *visual landmarks* – features of the cue stimuli that are predictively associated with the location of a target object. This prediction was roundly disconfirmed, leading us to test, in Experiment 2, a prediction, derived from the idea that spatial cognition and numerical cognition may recruit overlapping neural circuits in parietal cortex (Hubbard, Piazza, Pinel & Dehaene, 2005). Evidence that there may be closer neurocognitive links between numerical and spatial cognition, than between verbal and spatial cognition led us to predict that stronger effects on spatial attention would be observed when numbers were used as cues, compared to a condition employing letters as cues. The results of Experiment 2 showed that this prediction was also false. Consequently, we were forced to examine, in Experiments 3 & 4, a hypothesis considered

unlikely at the outset – that the exposure duration of the cue stimulus, which differed in the studies of Fischer *et al.* (2003) and those of Lambert *et al.* (2006) and Shin *et al.* (2011) may be an important factor that modulates whether visual orienting effects in response to precues are driven by visual-spatial (landmark) properties of cue stimuli, as we have claimed (Lambert *et al.*, 2006; Shin *et al.*, 2011); or by semantic-symbolic properties of the cues, as others have claimed (Fischer *et al.*, 2003; Hommel *et al.*, 2001). In the second part of the paper, we ‘suck the goodness’ from both our failed (Experiments 1 & 2) and successful hypotheses (Experiments 3-6), in tandem with an overview of previous evidence, by developing a new model of the neurocognitive mechanisms and pathways responsible for controlling moment to moment changes in the direction of visual attention.

As indicated in the brief overview above, our initial aim was to adjudicate between two competing, and apparently incompatible claims regarding effects of precues on covert shifts of attention. The first claim, developed in a series of papers from our own laboratory, is that phasic orienting of covert visual attention in response to environmental cues depends upon visual and spatial features of the cue, and is not driven directly by the meaning of the cue (Lambert & Duddy, 2002; Lambert, Roser, Wells & Heffer, 2006; Marrett, de-Wit, Roser, Kentridge, Milner & Lambert, 2011; Shin, Marrett & Lambert, 2011). Key evidence for this claim emerged from a series of experiments in which participants were instructed to shift attention in response to letter cues presented in central vision. The ability of participants to shift attention in response to these cues was found to depend critically upon visual and spatial features of the letter; and was not driven directly by the symbolic meaning of the letters, in terms of their designation as signals for left and right targets (Lambert *et al.*, 2006; Shin *et al.*, 2011). Lambert *et al.* (2006) reported two experiments in which single, centrally presented letters cued the likely location of a target object. Participants were able to shift attention to the left or right in response to single cue letters that possessed the visual feature

of left-right asymmetry, such as ‘d’ and ‘b’; but, letter cues that were visually symmetric, such as X, T, v and o, failed to elicit any change at all in the orientation of attention – even with relatively long delays between cue and target onset, where participants had 400-500ms to prepare and execute a shift of attention in response to the information conveyed by the cue. Shin *et al.* (2011) also found that orienting effects were driven by visual-spatial features of the cue display, and that single, visually symmetric letter cues had no effect on spatial attention.

The situation investigated in these studies (Lambert *et al.*, 2006; Shin *et al.*, 2011) is, as many readers will recognise, a close variant of the widely used endogenous cueing paradigm, pioneered by Michael Posner and colleagues (Posner, 1980; Posner *et al.*, 1980), in which participants shift attention in response to a centrally presented cue, typically an arrow, or arrow-head stimulus (Chica, Bartolomeo & Lupianez, 2013; Chica, Martin-Arevalo, Botta & Lupianez, 2014; Wright & Ward, 2008). The ability of participants to shift attention in this paradigm has been widely interpreted as reflecting an endogenous form of orienting in which participants encode the symbolic meaning of the cue stimulus, and then shift attention in accord with that encoding (Chica *et al.*, 2013; Klein, 2004; Pratt, Radulescu, Guo & Hommel, 2010). However, in the experiments described by Lambert *et al.* (2006), the symbolic meaning carried by visually symmetric and asymmetric letters was identical, and very simple (i.e. one letter indicated that the next target would probably appear on the left, while a second letter indicated that the next target would probably appear on the right). Nevertheless, participants conspicuously failed to shift attention in response to cue stimuli lacking the visual feature of spatial asymmetry (see also Shin *et al.*, 2011). Moreover, the stimuli typically used as central cues in the Posner cueing paradigm, such as arrow figures, are strongly asymmetric (e.g. see Kincade, Abrams, Astafiev, Shulman & Corbetta, 2005). In light of this, we proposed that attentional behaviour in paradigms employing central cues is

not driven by *symbolic* encoding of the cue stimulus, followed by a matching shift of attention, but instead involves a simple kind of learning which is sensitive to predictive associations between *visual-spatial* features of the cue display and target location. The leftward and rightward facing components of stimuli such as arrow shapes, or the letters ‘d’ and ‘b’ provide participants with *visual landmarks*, that are predictively associated with target location. We suggested that participants may learn the predictive utility of these spatial correspondence associations (Lambert *et al.*, 2006), perhaps non-consciously (Lambert, Naikar, McLachlan & Aitken, 1999; Risko & Stolz, 2010). However, learning of this kind is not possible when cue stimuli are spatially symmetric (e.g. X,T,v,o).

This *spatial correspondence hypothesis* also accounted for an earlier set of findings, in which we explored effects of peripherally presented bilateral letter cues on visual orienting behaviour (Lambert & Duddy, 2002). When the location of a target tended to correspond with the location of a particular cue letter, participants oriented rapidly and effectively. In these cases, rather than learning correspondences between target location and specific visual elements of a central cue, orienting was driven by correspondence between target location and the side of presentation (left or right) of a particular cue stimulus (Lambert & Duddy, 2002; Lambert, Norris, Naikar & Aitken, 2000; Shin *et al.*, 2011). That is, the visual landmark comprised a complete stimulus located on the left or right, rather than visual elements within a centrally located cue.

Thus, according to the spatial correspondence hypothesis visual orienting in response to environmental cues is driven by a simple form of associative learning, which is sensitive to predictive links between landmark features of stimuli in the environment and the location of objects of interest. Spatial correspondence learning provided a simple, one-process explanation of visual orienting in response to both central and peripheral spatial cues –

behaviour that had hitherto been explained in terms of a two-process model, in which central and peripheral cues were thought to elicit two distinct types of orienting, variously termed endogenous vs. exogenous (Chica *et al.*, 2013; Klein, 2004), or goal-directed vs. stimulus driven (Corbetta & Shulman, 2002), or symbolic vs. direct (Wright & Ward, 2008), or voluntary vs. reflexive (Muller & Rabbitt, 1989).

Spatial correspondence learning provided a good account of results from an extensive series of experiments performed in our own laboratory (Lambert & Duddy, 2002; Lambert, Naikar, McLachlan & Aitken, 1999; Lambert, Norris, Naikar & Aitken, 2000; Lambert, *et al.*, 2006; Lambert & Shin, 2010; Shin *et al.*, 2011), and was also able to explain a wide array of earlier findings from research employing visually asymmetric cue displays, including paradigms employing unilateral peripheral cues or object onsets, and paradigms employing visually asymmetric central cues (for recent reviews of the literature on spatial cueing see Chica *et al.*, 2013,2014; Wright & Ward, 2008). However, a salient feature of the spatial correspondence hypothesis is that it is vulnerable to falsification by any demonstration of visual orienting in response to visually symmetric cue stimuli. Moreover, the extensive literature on attentional cueing does include a number of studies where participants have appeared able to shift attention in response to the *symbolic meaning* of visually symmetric cue stimuli presented in central vision (Hommel, Pratt, Colzato & Godijn, 2001; Pratt *et al.*, 2010; Fischer, Castel, Dodd & Pratt, 2003). A striking example of this concerns shifts of attention elicited in response to numbers presented in central vision (Fischer *et al.*, 2003; Ristic, Wright & Kingstone, 2006). Attentional orienting in response to number cues appears to be a robust phenomenon, and empirical explorations of number cueing effects were prompted in large part by the demonstration by Fischer *et al.* (2003) that presentation of a high-value digit in central vision (8 or 9) tended to elicit an ostensibly automatic shift of attention to the right, while presentation of a low-value digit (1 or 2) tended to elicit a shift of attention to the left.

These results were interpreted as arising from a tight coupling between attention to external space, and the internal representation of numbers in spatial terms, with low numbers being represented on the left and high numbers on the right, of a mental number-line. For present purposes the important point is that the study of Fischer *et al.* (2003), and the further explorations of number cueing effects that followed (Galfano, Rusconi & Umiltà, 2006; Ristic *et al.*, 2006) demonstrated that numerical stimuli are potent stimuli for eliciting shifts of spatial attention. Moreover, two of the stimuli used by Fischer *et al.* (2003), namely 1 and 8, were either nearly, or completely visually symmetric. These findings posed a serious problem for the spatial correspondence hypothesis.

Thus, the literature on visual orienting in response to central precues includes two apparently contradictory sets of findings. Lambert *et al.* (2006) reported that when letters were used as central cues, shifts of attention were elicited in response to visually asymmetric stimuli, but symmetric letters failed to elicit attention shifts (see also Shin *et al.*, 2011). In contrast, when numbers have been used as spatial cues, robust shifts of attention have been observed, even though the stimulus-set included the visually symmetric characters 1 and 8. This empirical discrepancy has important theoretical implications, because the former finding has been interpreted as supporting an interpretation of attentional cueing effects in terms of spatial correspondence learning (Lambert *et al.*, 2006), whereas the latter is consistent with the more widely held view that symbolic and semantic encoding plays an important role in spatial orienting in response to central cues (Chica *et al.*, 2013, 2014; Pratt *et al.*, 2010).

Experiments 1-3, described below, aimed to resolve this empirical discrepancy, and to adjudicate between the competing theoretical interpretations just described, regarding visual orienting in response to spatial cues.

EXPERIMENT ONE

Experiment One aimed to resolve the empirical discrepancy between our findings (Lambert *et al.*, 2006; Shin *et al.*, 2011) and those of others (Fischer *et al.*, 2003; Galfano *et al.*, 2006; Ristic *et al.*, 2006), and thereby to adjudicate between the competing theoretical accounts described above. This aim was realised by evaluating experimentally, the relative contributions of symbolic encoding and spatial correspondence learning, to visual orienting in response to centrally presented number cues. In order to assess spatial correspondence learning, we departed somewhat from the design employed by Fischer *et al.* (2003), and rendered the number cues spatially informative, rather than uninformative. Participants were presented with a number in central vision, and then made a simple detection response to target objects that could appear on the left or right of the display. Participants were informed that the semantic value of the central number predicted the likely location of the target. For one group of participants, low numbers were usually followed by a target on the left, while high numbers were usually followed by a target on the right; this contingency was reversed for a second group of participants. These two conditions are referred to below as the ‘*Normal number-line*’ and ‘*Reversed number-line*’ conditions respectively. Previous work has shown that number cueing effects are plastic, and can be modified by top-down control: Ristic *et al.* (2006) found that the effect described by Fischer *et al.* (2003) could be reversed by asking participants to imagine a reversed number line, with high numbers represented on the left and low numbers represented on the right.

A key feature of the stimuli employed in this experiment was that two of the four numbers employed as cues (1 & 8) were rendered as perfectly symmetric characters, while the other two cues (2 and 7) were laterally asymmetric. If visual orienting in this situation is driven primarily or exclusively by symbolic-semantic encoding, then visually symmetric and

asymmetric cues should elicit attention shifts that are comparable in magnitude. Arguably, one might expect the visually symmetric cues 1 and 8 to elicit somewhat larger attentional effects, because of the slightly greater symbolic distance between the numbers 1 and 8, compared with the symbolic distance between 2 and 7.

In contrast, if visual orienting is driven primarily or exclusively by spatial correspondence learning, based on the association between target location and landmark features of the cue stimuli, then clear attentional effects should be observed in response to the visually asymmetric cue stimuli 2 and 7; and visual orienting in response to the visually symmetric cue stimuli 1 and 8 should be significantly reduced, or entirely absent. In the former case, spatial correspondence learning could be based upon predictive associations between target location and lateral asymmetry in the angular and curved portions of the characters ‘2’ and ‘7’, which provide visual landmark information; but, in the case of visually symmetric characters (‘1’ and ‘8’), such learning is not possible.

METHOD

Participants: Thirty two adult volunteers were recruited to take part, with sixteen completing a ‘normal’ number line condition and sixteen completing a ‘reversed’ number line condition. Volunteers for this study were drawn from the student population of Auckland University.

Apparatus: The experiment was conducted using a Tobii T120 eye-tracker in a well-lit room, and stimuli were displayed on the Tobii screen measuring 33.7cm x 27cm, with a screen resolution of 640 x 350 pixels.

E-Prime was used to write the software to control the presentation and timing of visual stimuli. A chin-rest was used to prevent any unnecessary head movements and to maintain the head at a distance of approximately 60cm from the Tobii computer screen and eye monitor.

Display and stimuli: All stimuli were presented in black against a white background. A fixation cross subtending 3mm x 3mm was presented in the centre of the screen. The cue stimuli, also presented at the centre of the screen, were the numbers 1, 2, 7, 8 subtending 4mm (width) x 7mm (height). The cue stimuli '1' and '8' were rendered as perfectly symmetric characters (i.e. '1' was rendered as a single vertical line). The target stimulus, an asterisk (*) subtending 4mm x 4mm, was presented either to the left or to the right of the fixation cross. The centre of each target was 8.1cm from the centre of the fixation cross.

Procedure: Each experimental session began with a procedure that calibrated the assessment of eye movements by the Tobii T120 eye tracker. Participants were required to follow a red circle with their eyes as it moved to between different locations on the Tobii screen.

Following the calibration, the experimental task was explained to participants. Each trial began with presentation of a central fixation cross for 1,000ms., followed by a blank screen for 100ms, followed by re-presentation of the fixation cross for 1,000ms. Hence, the fixation cross 'blinked' for 100ms. The aim of this was to ensure that participants were attending to the centre of the screen at the beginning of every trial. A central cue was then presented for 300ms, and after a variable delay a target asterisk would be presented on either the left or right of the screen. Participants were told that the target would usually occur in the location cued by the value of the central number, but on some occasions it may not appear where expected. They were instructed to press the spacebar as soon as they detected the target on

the left or right of the screen and to keep their eyes fixated on the central fixation cross throughout the experiment.

The experiment contained two number line conditions; normal and reversed. Half the participants were told to imagine a normal number line where low numbers (1, 2) are found on the left-hand side and high numbers (7, 8) are found on the right-hand side. The other half were told to imagine a reversed number line where low numbers (1, 2) are on the right and high numbers (7, 8) are on the left. Participants were told to use the number cues in order to predict the probable location of the target, but were warned that the target asterisk may not always appear where cued.

The stimulus onset asynchrony (SOA – the delay between onset of the number cue and onset of the target) was either brief (150ms) or relatively long (700ms). In the case of the brief SOA the target asterisk appeared while the number cue was still present on the screen. (i.e. There was an overlap of 150ms where the number cue and target asterisk were both presented on the screen). In the long SOA condition the target appeared 400ms after offset of the number cue.

Seventeen percent of trials were catch trials, where a number cue was presented but there was no target stimulus. On catch trials there was an interval that varied randomly between 2.1s and 2.6s between offset of the letter cues and the “blink” of the central cross signalling the start of the next trial. Participants were told to press the space bar only when they saw the target asterisk and to refrain from pressing the space bar when there was no target. The message “Catch trial error” was displayed in centre of the screen for 2s, if participants responded on a catch trial.

Design: At the beginning of the testing session, participants were presented with 20 practice trials to familiarize themselves with the task. Participants then performed three blocks of 96

experimental trials. Each block of trials contained 16 catch trials, 64 valid trial and 16 invalid trials. On valid trials, the target appeared at the location cued by the number, while on invalid trials, the target appeared at the opposite location. The length of the SOA (150ms or 700ms), the location of the target asterisk (left or right), and the symmetry of the number cues (Symmetric: 1, 8 or Asymmetric: 2, 7) varied randomly from trial to trial, with equal numbers of trials in each of these conditions.

RESULTS

Response times less than 100ms or more than 1000ms were excluded from analysis. Trials with response times less than 100ms were categorized as anticipatory, and one participant who made an excessive number of these anticipatory errors, was excluded from further analysis. The rate of anticipations (1.8%) and catch trial errors (1.1%) for the remaining 31 participants was acceptably low. Thus, response time data from 16 and 15 participants in the normal and reversed number line conditions respectively were analysed. These results are summarised in Figure 1.

Figure 1

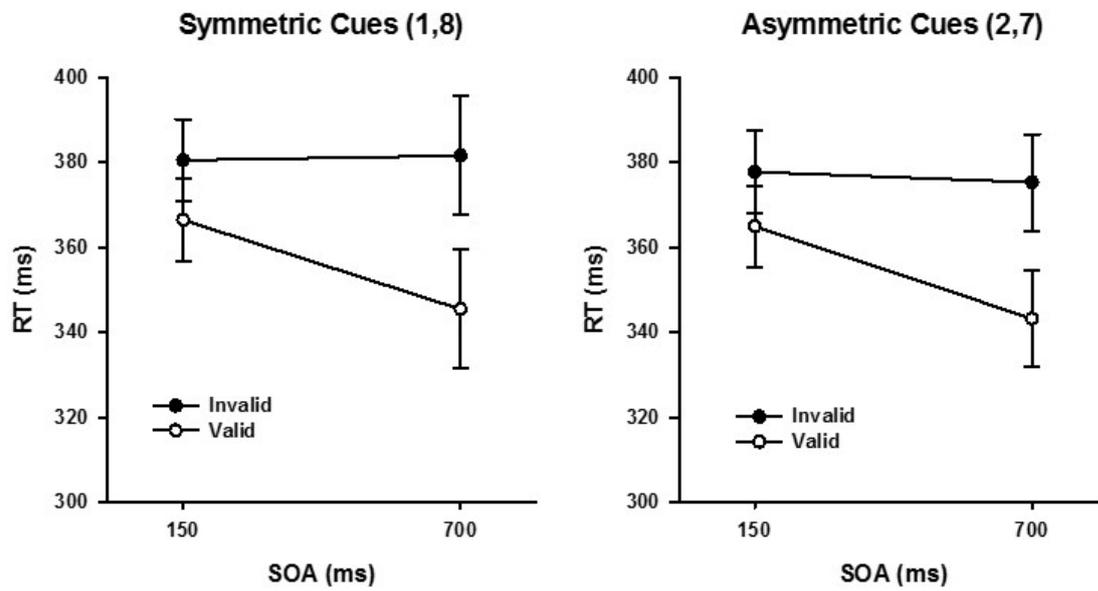


Figure 1. Mean response times in Experiment 1. Error bars represent the standard error of the difference in response times between valid and invalid trials.

Data were analysed using a 2 x 2 x 2 x 2 analysis of variance, with three within subject factors; SOA (150ms, 700ms), Cue Symmetry (Symmetric, Asymmetric), Validity (Valid, Invalid) and one between subjects factor: number line condition (Normal, Reversed). This analysis revealed a main effect of validity $F(1,29) = 5.54, p = 0.026, \eta^2_p = .16$, which was qualified by a significant interaction between validity and SOA, $F(1,29) = 18.37, p < 0.001, \eta^2_p = .39$, (see Figure 1). Further analysis of this interaction showed that in the SOA 700ms condition mean response times were reliably quicker in the valid (344ms) compared to invalid (378ms) condition, $F(1,29) = 8.74, p = .006, \eta^2_p = .23$; but in the SOA 150ms condition response times in the valid (366ms) and invalid (379ms) conditions did not differ reliably, $F(1,29) = 2.19, n.s.$

If attention shifting in this situation is influenced by visual-spatial features of the cue stimuli, then the difference between valid and invalid trials should vary as a function of cue symmetry. Contrary to this prediction, the interaction between trial validity and cue symmetry was non-significant ($F < 1$), and neither of the higher-order interactions that included the factors validity and cue symmetry approached significance (both $F < 1$). As Figure 1 illustrates, validity effects in the symmetric and asymmetric cue conditions were closely similar.

No other significant effects were observed. The interaction between validity and number line condition was non-significant, $F(1,29) = 2.09, n.s.$: attentional effects in the normal and reversed number line conditions were of comparable magnitude.

A further analysis was performed in order to ascertain whether results from the experiment reflected covert shifts of attention shifts (i.e. attention shifts that occur in the absence of overt changes in the direction of gaze). Although participants were instructed to maintain fixation, it was possible that manual response times may have been influenced by the presence of eye

movements. Although eye tracking data were not available for one participant, the remaining 30 participants were divided into two groups, based on their eye-movement behaviour. Eye movements greater than 1° in magnitude were made on fewer than 5% of trials in the ‘Eyes Still’ group (N=17), while participants in the ‘Eyes moved’ group made eye movements of 1° or more on greater than 5% of trials (N=13). This analysis revealed the same overall pattern as the primary analysis. More importantly, none of the interaction terms involving validity and eye movement group approached significance (all $p > .25$). Moreover, a separate analysis of data from the ‘Eyes still’ group revealed the same overall pattern as the primary analysis, i.e. a significant main effect of validity, $F(1,15) = 15.86, p = .001, \eta^2_p = .51$, qualified by the presence of a significant interaction between validity and SOA, $F(1,15) = 5.22, p = .037, \eta^2_p = .26$; and no other effects.

DISCUSSION

Results from Experiment One were clear-cut. Contrary to the prediction of the spatial correspondence hypothesis, attentional effects of number cues were unaffected by visual-spatial features of the cue stimulus – the presence of visual landmarks. Effect sizes for the interaction between trial validity and cue symmetry, and higher-order interactions involving these factors, were minuscule. Hence, the data are consistent with the view that visual orienting in response to centrally presented cue stimuli is driven primarily by symbolic-semantic encoding of the cue stimulus (Fischer *et al.*, 2003; Ristic *et al.*, 2006). That is, participants encoded the symbolic identity of the centrally presented number, and then shifted attention covertly to the left or right, on the basis of that encoding.

Although data from Experiment 1 were unequivocal, they contrast with earlier findings, showing that when letters were used as cues, visual orienting was influenced by visual-spatial

features of the cue stimulus (Lambert *et al.*, 2006; Shin *et al.*, 2011). This suggested the possibility that numbers and letters may exert quite different effects on attention in spatial cueing paradigms. The idea that numerical stimuli may enjoy a special status, with regard to their effects on attention, is consistent with evidence that numerical cognition and spatial cognition may enjoy an especially close neurocognitive association. Numerical cognition and spatial cognition have both been linked with processing in parietal cortex (Hubbard, Piazza, Pinel & Dehaene, 2005), whereas processing of letter stimuli has, in contrast, been associated with temporal cortical areas (Kronbichler *et al.*, 2008; Seghier *et al.*, 2012). Hubbard *et al.* (2005) propose that “numerical-spatial interactions arise from common parietal circuits for attention to external space and internal representations of numbers.” (p. 435).

EXPERIMENT TWO

Experiment Two tested the hypothesis that numeric and alphabetic stimuli may exert different effects on attention when used as spatial cues, as a consequence of the closer neurocognitive relationship between numerical cognition and spatial cognition (Hubbard *et al.*, 2005). One group of participants shifted attention in response to centrally presented numbers (1 or 8), while a second group shifted attention in response to centrally presented letters (I or X). The visual features of the number ‘1’ and the letter ‘I’, as presented to participants, were identical and comprised a single vertical line. This design feature enabled us to assess effects of cue category, independently of low-level visual features of the cue.

The attentional effects of number cues showed no influence of visual symmetry in Experiment One, so we predicted that the laterally symmetric number cues (‘1’ and ‘8’) employed in Experiment 2 would elicit similarly clear effects on attention. However, in our earlier work with letter cues, laterally symmetric cues, such as ‘I’ and ‘X’ stimuli failed to

elicit shifts of attention (Lambert *et al.*, 2006; Shin *et al.*, 2011). If this empirical discrepancy occurs because number stimuli have a stronger neurocognitive association with spatial cognition than letter stimuli, then in Experiment Two, participants will be able to shift attention in response to number cues, but not in response to letter cues. More specifically, this hypothesis predicts that participants will orient appropriately in response to a vertical line cue, when this stimulus is encoded as a number ('1'), but will fail to shift attention when the same stimulus is encoded as a letter ('I').

METHOD

Participants: Forty eight adult volunteers, drawn from the student population of the University of Auckland, took part. Of these, 24 shifted attention in response to number cues (number cue condition), and 24 shifted attention in response to letters (letter cue condition).

Apparatus & stimuli: In Experiment 1, the pattern of results was uninfluenced by eye movements. Therefore eye-tracking was not included in Experiment 2, which was performed using a suite of Dell Optiplex-990 PCs. Stimulus dimensions and timing of the cue and target stimuli were the same as for Experiment 1.

Procedure: This was similar to Experiment 1. In the number cue condition, 12 participants were instructed that the target would usually appear on the left following the number '1' and on the right following the number '8', as in the normal number line condition of Experiment 1; for the other 12 participants, '1' cued a right target and '8' cued a left target, as in the reversed number line condition of Experiment 1. In the letter cue condition, 12 participants were instructed that the target would usually appear on the left following the cue 'I' (which was physically identical to the stimulus for '1', employed in the number

condition), and would usually appear on the right following the cue 'X'. For the other 12 participants in this condition, 'I' cued a right target and 'X' cued a left target.

Design: Participants performed 20 practice trials, followed by two blocks of 96 experimental trials. Within each block, the distribution of valid, invalid, and catch trials was the same as for Experiment 1.

RESULTS

The rates of anticipation errors (1.4%) and catch trial errors (3.8%) were both acceptably low in Experiment Two. Results are summarised in Figure 2. Response time data were entered into a 2x2x2 mixed-model analysis of variance, with two within subjects factors, namely SOA (150ms, 700ms) and validity (valid, invalid), and one between subjects factor, cue category (number, letter). This revealed a main effect of validity, $F(1,46) = 12.90$, $p < .001$, $\eta^2_p = .22$, with shorter mean response times on valid (344ms) compared to invalid (361ms) trials. However, as in Experiment One, this effect was qualified by a significant interaction with SOA, $F(1,46) = 7.71$, $p = .008$, $\eta^2_p = .14$. As Figure 2 illustrates, a stronger advantage for valid compared to invalid trials was observed in the SOA 700ms condition.

Figure 2

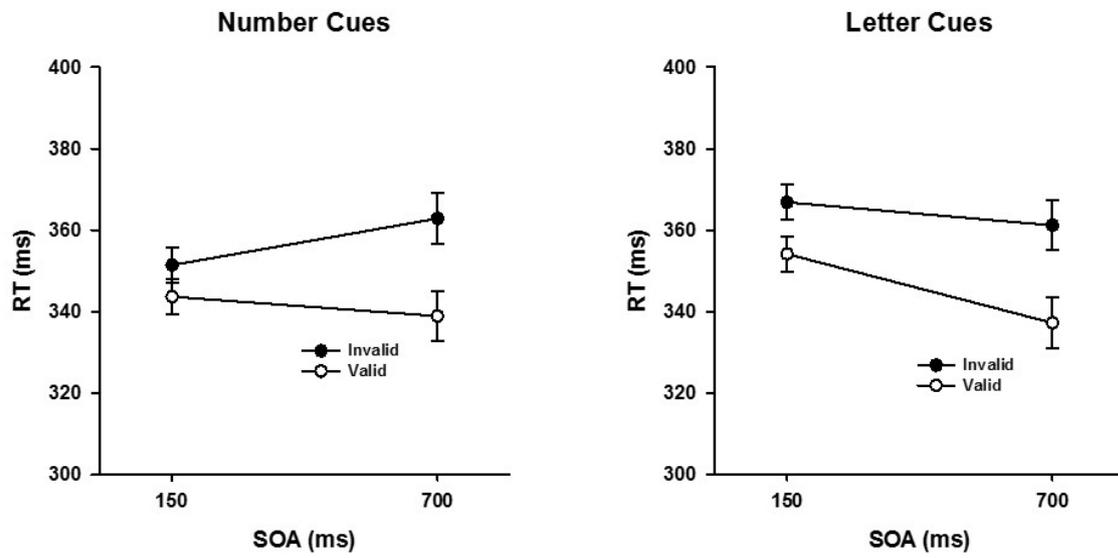


Figure 2. Mean response times in Experiment 2. Error bars represent the standard error of the difference in response times between valid and invalid trials.

The key outcome of this analysis was that, contrary to prediction, there was no evidence of any variation in the magnitude of visual orienting effects, in response to number and letter cues. No interaction was observed between cue category and validity ($F < 1$, $\eta^2_p = .001$), and the three-way interaction between cue category, validity and SOA was also non-significant ($F < 1$, $\eta^2_p = .005$).

A further analysis was also performed, focusing specifically on trials where participants shifted attention in response to the vertical line stimulus, which represented a number and a letter to participants in the number cue and letter cue groups respectively. This analysis produced the same outcome as the primary analysis. That is, there was a main effect of validity, $F(1,46) = 8.19$, $p = .006$, $\eta^2_p = .15$ and an interaction between validity and SOA, $F(1,46) = 13.07$, $p < .001$, $\eta^2_p = .22$. As in the primary analysis, there was no interaction between cue category and validity ($F < 1$), and the three-way interaction between cue category, validity and SOA was also non-significant ($F < 1$).

DISCUSSION

The results of Experiment Two, like those of the first experiment, were clear-cut: Contrary to prediction, visual orienting behaviour did not vary as a function of whether participants shifted attention in response to a centrally presented letter or a centrally presented number. Effect sizes for the interactions between trial validity and cue category were minuscule. Critically, when the laterally symmetric letters 'I' and 'X' were presented centrally, as cues for attention, clear visual orienting effects were observed. This finding appears to conflict directly with results reported by Lambert *et al.* (2006) and Shin *et al.* (2011), in which laterally symmetric letter cues failed to elicit shifts of attention. This unexpected and

troubling discrepancy in our data led us to develop a further hypothesis, regarding factors that may modulate effects of spatial cues on visual attention.

Although the design of Experiment 1 departed from the procedure employed by Fischer *et al.* (2003) in using number cues that were spatially informative, rather than uninformative, other features of their method were incorporated into our study. A notable feature of their design was that central number stimuli were displayed for 300ms, which is considerably longer than the exposure time of 66ms that was employed in the letter cueing studies of Lambert *et al.* (2006). Therefore, the studies of Fischer *et al.* (2003) and Lambert *et al.* (2006) differed not only with respect to cue category (numbers vs. letters), but also with respect to cue exposure time.

The hypothesis that cue exposure time may be an important factor modulating the attentional effects of cue stimuli was considered unlikely at the outset of this project, leading us to test the ostensibly more plausible hypotheses examined in Experiments 1 and 2. However, both these hypotheses were disconfirmed roundly by the data, prompting us to reconsider the possibility that cue exposure time may play an important role. The cue items employed in this paradigm were drawn from a (very) small stimulus set, were easily discriminable, and were presented in central vision. Under these conditions, there is no doubt that participants' would be able to encode the identity of the cues with essentially 100% accuracy, regardless of cue exposure time. While it is clear from several decades of work using this paradigm, including data from Experiments 1 and 2, that the SOA between cue onset and target onset is a powerful factor modulating the magnitude of covert orienting in response to spatial cues, effects of cue exposure time, in conditions where highly accurate encoding of central cues can be assumed, have not, to our knowledge, been reported previously. Nevertheless, the pattern of discrepancies and concordances that we have described, between the results of

Experiments 1 and 2, and previous findings reported by Lambert *et al.* (2006), Shin *et al.* (2011) and by Fischer *et al.* (2003) led us, on purely empirical grounds, to consider the hypothesis that visual orienting effects may be modulated by cue exposure duration. Although the design of Experiment 3 was prompted by purely empirical considerations, the results that were obtained had, as will be seen, important theoretical implications with regard to the control of visual orienting by environmental cues.

EXPERIMENT THREE

The design of Experiment 3 was closely similar to that employed in the normal number line conditions of Experiments 1 and 2, except with respect to this feature: the exposure time of the number cues was the same (66ms) as that employed in the letter cueing experiments of Lambert *et al.* (2006). If cue exposure time is an important factor that modulates visual orienting effects, then two predictions can be made: (1) Results from Experiment 3 will resemble those reported by Lambert *et al.* (2006) with briefly presented letters. That is, visually asymmetric number cues will elicit clear attention shifts, but the attentional effects of visually symmetric numbers will be absent, or reliably weaker; (2) The attentional effects of visually symmetric numbers presented with a brief exposure time in Experiment 3 will be reliably weaker than those observed in Experiment 2, where visually symmetric numbers were presented under identical experimental conditions, aside from the use of a longer exposure time.

METHOD

Participants: Sixteen adult volunteers, drawn from the student population of the University of Auckland, took part.

Apparatus & stimuli: The apparatus used for this experiment was the same as for Experiment 2. The numerical stimuli employed as cues were the same as those employed in Experiment 1, and in the number condition of Experiment 2.

Procedure: This was similar to the normal number line conditions of Experiments 1 and 2.

Design: Participants performed 20 practice trials, followed by three blocks of 96 experimental trials. Within each block, the distribution of valid, invalid, and catch trials was the same as for Experiments 1 and 2.

RESULTS

The rates of anticipation errors (1.1%) and catch trial errors (2.7%) were both acceptably low. Results from the experiment are summarised in Figure 3. Mean response time data were entered into analysis of variance, with three repeated measures factors: cue symmetry (asymmetric vs. symmetric), SOA (150ms vs. 700ms), and validity (valid vs. invalid). As in Experiments 1 and 2, the interaction between SOA and validity was reliable, $F(1,15) = 7.48$, $p = .015$, $\eta^2_p = .33$. In addition, the predicted interaction between cue symmetry and validity was significant, $F(1,15) = 6.46$, $p = .023$, $\eta^2_p = .30$. Both of these interactions are illustrated in Figure 3. Further analysis showed that in the SOA 150ms condition the response time difference between valid and invalid trials was reliable neither with visually symmetric, nor with asymmetric number cues; however, in the SOA 700ms condition, the difference between

valid and invalid trials was reliable when participants were presented with visually asymmetric cues ($t(15) = 3.01, p = .009, \eta_p^2 = .38$), but not when presented with visually symmetric cues ($t(15) = 1.03, n.s., \eta_p^2 = .07$).

Figure 3.

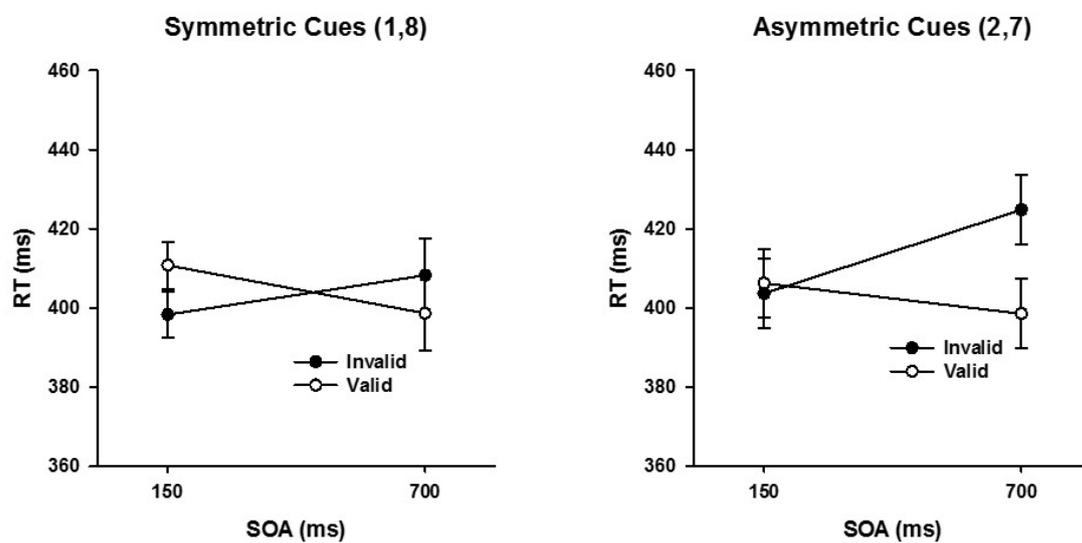


Figure 3. Mean response times in Experiment 3. Error bars represent the standard error of the difference in response times between valid and invalid trials.

Effects of cue exposure time

The experimental conditions encountered by participants in Experiments 2 and 3 were identical, enabling us to perform a direct comparison, assessing attentional effects of visually symmetric number cues presented with long (300ms – Experiment 2) and short (66ms – Experiment 3) exposure times. This analysis revealed a significant interaction between cue exposure time and validity, $F(1,26) = 8.13, p = .008, \eta^2_p = .24$, in which response times were reliably quicker on valid compared to invalid trials when visually symmetric cues were presented with a long (300ms) exposure time (Valid RT = 335ms; Invalid RT = 359ms; Invalid minus valid RT difference = 24ms, $p = .002, \eta^2_p = .60$), but not when they were presented with a brief (66ms) exposure time (Valid RT = 405ms; Invalid RT = 403ms; Invalid minus valid RT difference = -2ms, n.s., $\eta^2_p = .004$).

DISCUSSION

Results from Experiment 3 showed that when number cues were displayed to participants with the same brief exposure time (66ms) as employed in the study of Lambert *et al.* (2006) with letter cues, the same pattern of results was observed. When the cue stimuli were visually asymmetric, affording an opportunity for spatial correspondence learning to occur, based on visual landmarks, participants shifted attention to the location cued by these visual-spatial features. However, when the cues were visually symmetric, affording no opportunity for spatial correspondence learning, participants failed to shift attention. Moreover, the influence of cue symmetry on visual orienting observed in this experiment ($\eta^2_p = .30$) would be classified as a large effect, according to broadly accepted guidelines (Cohen, 1988; Bakeman, 2005). The magnitude of this effect was clearly larger (by a factor of 50) than the negligible effect of cue symmetry on orienting ($\eta^2_p = .006$) observed in Experiment 1.

Hence, the results of Experiment 3 suggest an empirical regularity that accounts for the discrepancy between our own findings, where attentional effects were dominated by encoding visual-spatial (landmark) features of cue stimuli, and those of others, where attentional effects were driven by encoding symbolic-semantic features of precues. That is, when environmental cues were presented very briefly, as in Experiment 3, visual orienting effects were independent of the symbolic information conveyed by the cue, and were driven instead by visual-spatial features of the cue and spatial correspondence learning, as described earlier (Lambert *et al.*, 2006; Shin *et al.*, 2011). This contrasts with the pattern observed in Experiments 1 and 2, and in other studies where attentional cues were presented with a longer exposure time (Fischer *et al.*, 2003). Here, visual orienting effects were independent of low-level visual-spatial features, and were driven by the symbolic information carried by stimuli designated as left and right cues. Consistent with the classic theoretical conception of endogenous orienting (Chica *et al.*, 2013; Klein, 2004; Wright & Ward, 2008), attention shifts in these experiments appear to have been driven by symbolic-semantic encoding – that is, by whether the meaning assigned to the cue, via experimental instructions, signifies that the next target will probably be on the left or right of the display.

To be of value, this empirical regularity does, of course, require a theoretical explanation that generates novel predictions and provides insight into the neurocognitive mechanisms of visual attention. Converging evidence from several sources supports the proposal that attention shifts driven by learning spatial correspondences between cue and target location rely on dorsal stream encoding of the visual landmarks provided by cue stimuli. For example, Marrett *et al.* (2011) investigated whether patient DF, who sustained bilateral damage to area LO, part of the ventral stream, was able to shift attention in response to spatial correspondence cues (a bilateral pair of letters). DF performed very poorly when asked to discriminate consciously between these bilateral letters, but was nevertheless able to shift

attention appropriately in response to them, when they predicted the location of a simple target stimulus (Marrett *et al.*, 2011). Moreover, electrophysiological evidence has shown that peripheral stimuli which predict target location, and consequently trigger a shift of attention, are associated with early activation of the dorsal stream; while peripheral stimuli that demand a conscious, perceptual discrimination response are associated with activation of the ventral stream that exhibits a somewhat slower time-course (Lambert, Wootton, Ryckman & Wilkie, 2014; Lambert & Wootton, 2016; Marrett *et al.*, 2011 see General Discussion).

The proposal that key functions of the ventral and dorsal visual streams are to encode the identity of visual stimuli and to encode the spatial relationships between them, respectively, was championed several decades ago, by Ungerleider and Mishkin (1982), in their classic work examining effects of visual stream lesions in rhesus monkeys. Lesions to the ventral stream, but not those applied to the dorsal stream, impaired perceptual discrimination. Conversely, lesions to the dorsal stream, but not those applied to the ventral stream, impaired performance of a visual landmark task, where monkeys were rewarded for choosing a covered food-well that was close to a landmark object, such as a striped cylinder. There are clear parallels between the landmark learning task of Ungerleider & Mishkin (1982), and the spatial correspondence learning task used in our studies of visual attention: in both cases the location of an object of interest is predicted by a landmark stimulus. The observation that patient DF is able to shift attention in response to peripheral letter cues that predict target location (Marrett *et al.*, 2011), and the finding that processing of these cues is associated with an electrophysiological index of dorsal stream activation (Lambert & Wootton, 2016; Marrett *et al.*, 2011), is consistent with the view that spatial correspondence learning in humans and landmark learning in monkeys recruit similar processes, and that both rely on the dorsal visual stream. Accordingly, the term *landmark cueing* is used below, to refer to experimental paradigms where the location of a target object is predicted, either by the location of a

landmark object (Lambert & Duddy, 2002; Marrett *et al.*, 2011), or by the spatial arrangement of landmark features, such as arrow-shapes or other asymmetric elements, within a cue stimulus (Lambert *et al.*, 2006).

While processing visual-spatial (landmark) properties of environmental stimuli is associated with the dorsal visual stream, encoding of symbolic-semantic properties is associated with ventral visual stream processing (Carlson, Simmons, Kriegskorte & Slevc, 2014; Peelen & Caramazza, 2012). This suggests that in Experiments 1 and 2, and in previous work (Fischer *et al.*, 2003; Hommel *et al.*, 2001), where attention shifting was driven by symbolic-semantic properties of cue stimuli, independently of their visual-spatial features, cue encoding is likely to have relied on the ventral visual stream. Hence, there may be a simple, one-to-one correspondence between landmark cueing and symbolic cueing on the one hand, and the functional specialisation of the dorsal and ventral streams, for processing visual-spatial relationships, and symbolic attributes respectively, of environmental stimuli.

Why are symbolic and landmark cueing effects influenced by the exposure duration of the cue?

In addition to following distinct anatomical routes, from V1 to posterior parietal cortex and from V1 to inferior temporal cortex respectively, the dorsal and ventral streams exhibit different physiological characteristics. The vast majority of fibres in the dorsal stream carry signals that originate from the two magnocellular (M-cell) layers of LGN, while the ventral stream is the main target of fibres originating from the four parvocellular (P-cell) layers of LGN (Merigan & Maunsell, 1993). In addition to its P-cell input, the ventral stream also receives substantial M-cell input (Merigan and Maunsell, 1993). P-cell and M-cell derived fibres have distinct properties. Notably, M-cell derived channels exhibit a transient response

to visual stimulation (Livingstone & Hubel, 1988; Robson & Kulikowski, 2012). That is, the onset, or offset of a stimulus elicits a transient response in these cells, after which firing rates return to a baseline level. In contrast, cells in the parvocellular layers of LGN, which provide the predominant input to the ventral stream, exhibit a sustained response to visual stimulation (Livingstone & Hubel, 1988; Merigan & Maunsell, 1993). That is, their response is sustained for the duration of the visual stimulus. One consequence of these different characteristics is that the M-cell derived fibres of the dorsal stream will respond well, even when stimuli are exposed for a very brief period – because their response is driven primarily by the onset of a stimulus, rather than by its duration. In contrast, activity in the P-cell derived fibres of the ventral stream will be related to stimulus exposure time, and will be greater for those stimuli presented for long, compared to brief periods, because of their sustained response behaviour.

We suggest that the pattern of results observed in Experiments 1-3, and also in earlier work (Fischer *et al.*, 2003; Lambert *et al.*, 2006; Shin *et al.*, 2011) may be related to these response characteristics of cells and fibres in the dorsal and ventral visual streams. Specifically, we propose that briefly exposed stimuli will activate the transient channels that provide input to the dorsal stream, and that this dorsal stream activation plays an important role in encoding the visual-spatial features that elicit rapid attentional orienting towards a likely target location (Lambert & Duddy, 2002; Lambert & Shin, 2010; Marrett *et al.*, 2011). This rapid orienting is driven by the presence of visual landmark features that are predictively associated with target location.

Activation of the ventral stream in response to briefly exposed stimuli will be substantially less than that elicited by stimuli with a lengthy exposure time, due to the sustained response characteristics of the P-cell fibres that comprise the main input to the ventral stream. Data from Experiment 3, together with our earlier findings (Lambert *et al.*, 2006; Shin *et al.*, 2011,

Experiments 1 & 2) indicate that that when cues are presented with a brief exposure time, visual orienting is insensitive to symbolic features of the cue, which in the view of many authors are encoded in the ventral stream, but are beyond the encoding repertoire of the dorsal stream (Peelen & Caramazza, 2012; Milner & Goodale, 2006). That is, when cues were displayed with a brief exposure time, visual orienting was not driven by the meaning assigned, via experimental instructions, to attentional cues, but was driven instead by simple visual-spatial features, together with landmark learning (Experiment 3; Lambert *et al.*, 2006; Shin *et al.*, 2011). A very different pattern was observed in Experiments 1-3, where cues were displayed for a longer duration. In this case, attentional behaviour was freed from dependence on visual and spatial features of the cue, and was instead driven by the meaning assigned to the cue, via experimental instructions. In this case, visual orienting effects of similar magnitude were observed, regardless of whether the cues were visually asymmetric, affording an opportunity for spatial correspondence learning, or visually symmetric, affording no opportunity for spatial correspondence learning. In this situation, where attentional behaviour was determined by symbolic-semantic rather than visual-spatial encoding, we propose that visual orienting is driven by ventral stream encoding of the symbolic identity cue.

EXPERIMENT FOUR

While the interpretation just described provides a competent explanation of previous findings, the ability to generate novel, non-obvious predictions is a key test for any theoretical proposal. According to the account just described, attention shifting based on encoding the symbolic identity of cue stimuli relies on ventral stream encoding, and in particular on the P-cell inputs to the ventral stream; and attention shifting based on encoding the visual-spatial

features of cues relies on dorsal stream encoding, and in particular on the M-cell inputs to the dorsal stream. The aim of Experiment 4 was to test this interpretation, by assessing the effects of cue exposure time in two spatial orienting paradigms.

Figure 4

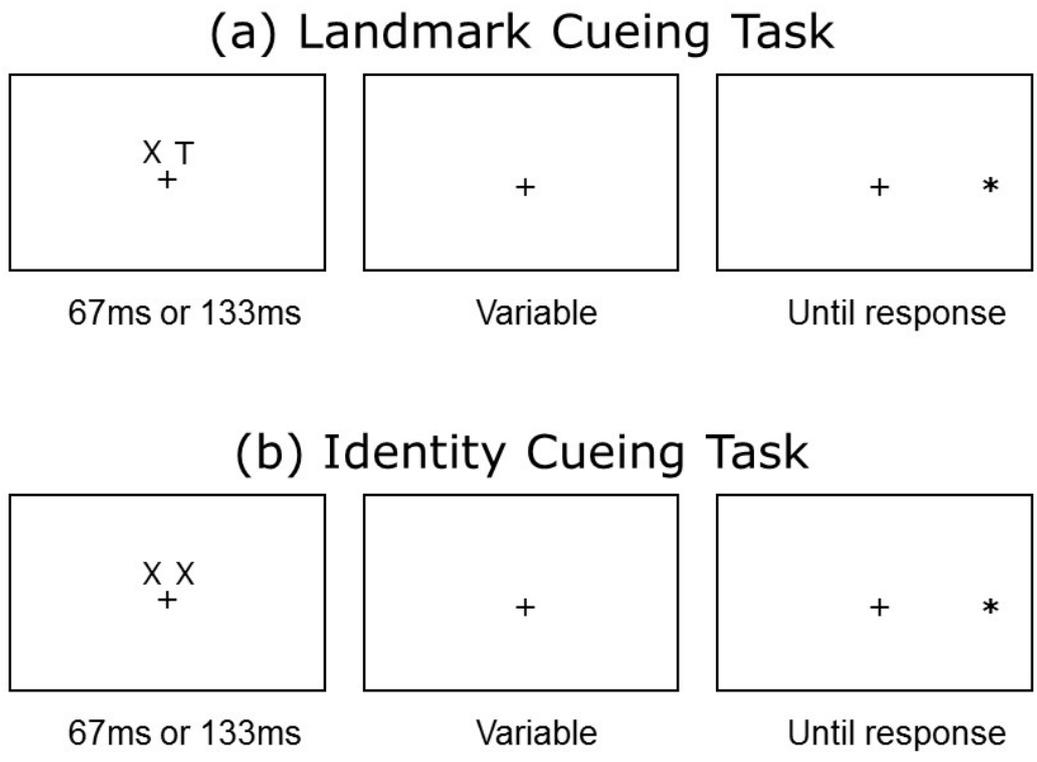


Figure 4. Participants performed two cueing tasks in Experiment 4. The *Landmark Cueing* task is illustrated in the upper panel (a); the *Identity Cueing* task is illustrated in the lower panel (b).

In the *Landmark Cueing* task, illustrated in the upper panel of Figure 4, two cue letters (X and T, or V and O) were presented bilaterally, and participants made a simple detection response to a subsequent target that could appear on the left or right of the screen.

Participants were informed that the target would usually appear on the same side as one of the letters. If visual orienting in this situation is driven by dorsal stream encoding of the spatial relationship between landmark cue letters and target location, then attentional effects will be robust when cues are presented very briefly. Cues were presented for either 67ms (brief exposure time condition) or 133ms (long exposure time condition) in Experiment 4. As explained above, because of the transient response characteristics of M-cell inputs to the dorsal stream, effects mediated by this channel will be triggered by the mere onset (or offset) of a stimulus, and will therefore continue to be observed under conditions of brief exposure time (67ms). Indeed, one might expect such effects to be independent of cue exposure duration. To use a term that has been associated with Ungerleider and Mishkin's (1982) dual-stream model of cortical vision, attentional behaviour in this situation will be driven encoding spatial attributes of cue stimuli within the 'where pathway' (i.e. the dorsal stream).

In the *Identity Cueing* task, illustrated in the lower panel of Figure 4, participants were also presented initially with two letters bilaterally. However, in this case on any individual trial the two letters were always the same (X-X or T-T or V-V or O-O). Aside from their precise spatial arrangement, cue stimuli in the Identity and Landmark Cueing tasks were identical. Participants were informed that the target was likely to appear on the left following one letter pair (e.g. T-T), and on the right following the other cue pair (e.g. X-X). In this situation, there are no spatial correspondences available to participants – with visually symmetric cue displays the target is equally likely to appear on the same or opposite side to either letter. Therefore, in order to programme an appropriate shift of attention, participants must encode the symbolic identity of the cue. If visual orienting in this situation is driven by ventral

stream encoding of cue identity, then attentional effects will collapse in the brief cue exposure time condition. As explained above, because of the sustained response characteristics of P-cell inputs to the ventral visual stream, activity in this channel will be markedly reduced when stimuli are presented very briefly. A relatively powerful design, with a large number of participants was used in this experiment, so that any residual, small magnitude effects of identity cues in the brief exposure time condition could be assessed. Once again, to use a term that has been associated with Ungerleider and Mishkin's (1982) model of vision, we hypothesise that attentional behaviour in this situation will be driven by encoding the identity of cue stimuli within the 'what pathway' (i.e. the ventral stream).

As we acknowledged earlier, the relationship between the dorsal and ventral visual streams and their M-cell and P-cell inputs is not a simple one-to-one correspondence. Although the input signal to the dorsal visual stream originates mainly from the M-cell layers of LGN, the ventral stream receives input from both P-cell *and* M-cell channels. Although our theoretical proposal that attentional effects of landmark cues will be mediated by dorsal visual stream cue encoding leads to the prediction that such effects will mirror properties of the M-cell inputs to the dorsal stream, it is also true that observing this pattern does not *unambiguously* mandate a dorsal visual stream interpretation. However, we maintain that a dorsal stream interpretation is preferable in light of: (i) electrophysiological evidence that landmark cues elicit early activation of the dorsal visual stream (Lambert & Wootton, 2016; Marrett et al., 2011, Experiment 1), (ii) evidence that patient (DF) who has sustained severe ventral stream damage, but in whom the dorsal stream appears to be intact, is able to shift attention normally in response to landmark cues that she claims to be unable to see (Marrett et al., 2011, Experiment 2), and (iii) in light of the conceptual relationship between our landmark cueing task and the landmark learning task of Ungerleider and Mishkin (1982).

METHOD

Participants: Seventy five adult volunteers took part. Two participants made an excessive number of anticipations, and one participant made an excessive number of catch trial errors. Data from these participants were discarded, and three new participants were recruited, to ensure an equal number of participants (18) in each of the four counter-balancing conditions.

Apparatus & stimuli: The experiment was performed using a Dell Inspiron lap-top PC, with a 15" LCD visual display. A chinrest was used to control viewing distance (57cms).

Display and stimuli: Cue stimuli comprised a pair of bilateral letters, presented on either side of the central fixation cross. The dimensions of the letters were approximately 0.45° (width) x 0.6° (height). The inner edge of each letter was presented 0.2° to the left or right of fixation, and the lower edge was 0.4° above central fixation. In the *Landmark Cueing* condition, two different letters, either 'X' and 'T', or 'V' and 'O' were presented on every trial. In the *Identity Cueing* condition, two identical letters ('X', 'T', 'V', 'O') were presented on every trial. The target was an asterisk, subtending 0.4° x 0.4° . The target was aligned with the fixation cross in the vertical-axis, and was presented 7.3° to the left or right of the screen centre.

Procedure: In *Landmark Cueing* blocks, participants were informed that the target would usually appear on the same side as one of the letters. For half the participants, the letters 'X' and 'T' were used as landmark cues; for the other half, the letters 'V' and 'O' were landmark cues. Within each of these groups, the letter used to cue target location was counterbalanced between participants. Hence, counter-balancing this aspect of the design required four groups, with equal numbers of participants shifting attention in response to each of the four letters (X,T,VO).

In *Identity Cueing* blocks, participants were informed that one letter pair signified that the next target would probably be presented on the right of the display, while the other indicated that the next target would probably be on the left. The two letters employed as identity cues were always different to those used as landmark cues. For half the participants, the letter pairs X-X and T-T were used as identity cues, while the letters V-V and O-O were identity cues for the remaining participants. There were four counter-balanced groups, with equal numbers of participants shifting attention left, or right in response to each of the four letters (X,T,V,O).

Cue letters were presented for either 67ms or 133ms, with cue exposure time varying randomly from trial to trial.

Other aspects of the experimental procedure were similar to that used in Experiments 2 and 3.

Design: Each participants performed 10 landmark cueing practice trials, followed by two blocks of 96 landmark cueing experimental trials; and 10 identity cueing practice trials, followed by two blocks of 96 identity cueing experimental trials. The order of participating in the landmark cueing and identity cueing conditions was counter-balanced between participants. Other aspects of the design were similar to that used in Experiments 1-3.

RESULTS

The rate of anticipations (0.4%) and catch-trial errors (0.1%) for the 72 participants in the final data-set were acceptably low. Results from the experiment are illustrated in Figure 5. Mean response times were entered into a four-way, repeated measures analysis of variance with cueing paradigm (Landmark vs. Identity), cue exposure time (67ms vs. 133ms), trial validity (valid vs. invalid), and SOA (150ms vs. 600ms) as factors. The main effect of trial validity, $F(1,71) = 15.27$, $p < .001$, $\eta^2_p = .18$, and the interaction between trial validity and

SOA, $F(1,71) = 8.87$, $p = .004$, $\eta^2_p = .11$, were both significant. This showed that overall, participants responded more rapidly on valid trials, and that the advantage for valid relative to invalid trials was greater in the long SOA condition (Valid RT = 368ms; Invalid RT = 381ms) than in the short SOA condition (Valid RT = 375ms; Invalid RT = 378ms).

Critically, the predicted interaction between cueing paradigm, cue exposure time, and trial validity was reliable statistically, $F(1,71) = 6.41$, $p = .014$, $\eta^2_p = .08$. This complex interaction was analysed further by examining data from the short and long exposure time conditions separately.

Figure 5

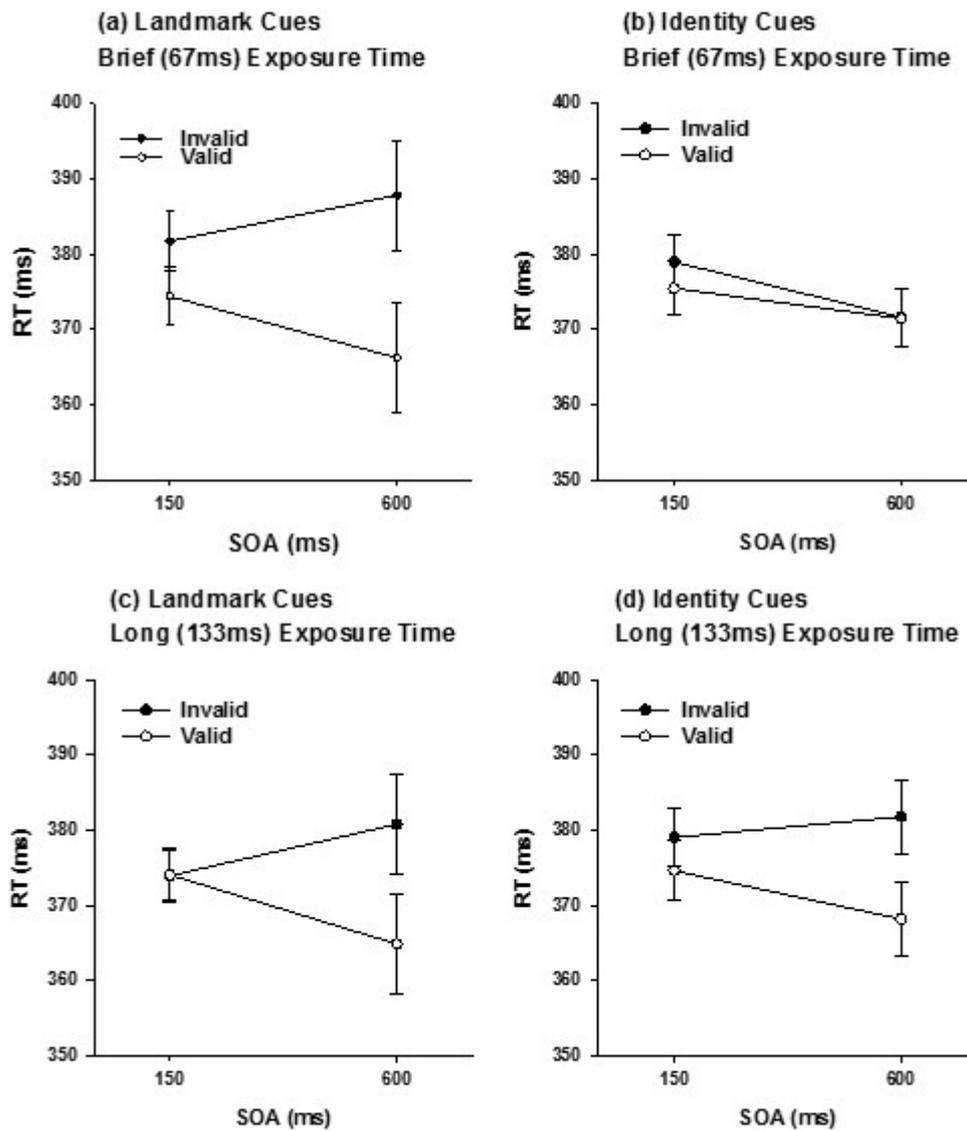


Figure 5. Mean response times in Experiment 4. Error bars represent the standard error of the difference in response times between valid and invalid trials.

The specific prediction that attentional effects of landmark cues would be robust with brief cue exposure times, while effects of identity cues would collapse, was tested by analysing data from the brief cue exposure time condition. The predicted interaction between cueing paradigm and trial validity was significant, $F(1,71) = 6.09$, $p = .016$., $\eta^2_p = .08$ Moreover, in the brief exposure time condition, there were clear effects of landmark cues on attention. Briefly exposed landmark cues elicited a main effect of trial validity, $F(1,71) = 9.62$, $p = .003$, $\eta^2_p = .12$, and an interaction between trial validity and SOA $F(1,71) = 4.00$, $p = .049$, $\eta^2_p = .05$ (see Figure 5, panel a). Despite a relatively powerful experimental design, with 72 participants, briefly exposed identity cues did not appear to influence attention. In the brief exposure time condition with identity cues, the main effect of trial validity ($F < 1$, $\eta^2_p = .009$), and the interaction between validity and SOA ($F < 1$, $\eta^2_p = .005$) were both non-significant (see Figure 5, panel b). Indeed, in the 600ms SOA condition, where participants had more than half a second to prepare and execute a shift of attention in response to the information provided by the cue, response times on valid and invalid trials were essentially identical (see Figure 5, panel b).

In the long exposure time condition the main effect of trial validity $F(1,71) = 10.88$, $p = .002$, $\eta^2_p = .13$ and the interaction between trial validity and SOA, $F(1,71) = 9.54$, $p = .003$, $\eta^2_p = .12$, were both significant, as in the omnibus analysis. Moreover, in the long exposure time condition, attentional effects of precues did not vary as a function of cueing paradigm: the interaction terms between cueing paradigm and trial validity ($F < 1$, $\eta^2_p = .001$), and between cueing paradigm, trial validity and SOA ($F < 1$, $\eta^2_p = .006$) were non-significant (see Figure 5, panels c and d).

As noted earlier, if the attentional effects of landmark cues are driven by transient responses of the M-cell inputs to the dorsal stream, then these effects, indexed by the difference

between valid and invalid trials, may be independent of cue exposure time. Consistent with this, the advantage for valid compared to invalid trials in the landmark condition did not vary reliably according to exposure time, and was at least as large in the brief exposure time condition (Invalid RT (385ms) - Valid RT (370ms) = 15ms; see Figure 5a) compared to the long exposure time condition (Invalid RT (377ms) - Valid RT (369ms) = 8ms; see Figure 5c).

DISCUSSION

Results from Experiment 4 were clear. Reducing cue exposure time had a catastrophic effect on the attentional effects of identity cues. As predicted, identity cueing effects collapsed, and appear to have been completely eliminated when the exposure time of the cue was reduced to 67ms. A radically different pattern was observed in the Landmark cueing condition, where the same visual stimuli, albeit in a different spatial arrangement, were presented. Attentional effects of landmark cues in the brief exposure time condition were at least as large those observed in the long exposure time condition.

As explained in the introduction to this experiment, this pattern is consistent with two theoretical proposals. Firstly, we propose that landmark cueing effects are mediated by the M-cell inputs to the dorsal stream. Because these cells respond transiently to the onset and offset of stimuli, activity in M-cell derived channels will be relatively independent of stimulus exposure time. As Figure 5 illustrates, reducing the exposure time of landmark cues had no impact at all on their attentional effects. Landmark cues exposed for 67ms produced clear effects on the orientation of visual attention (Figure 5a), and these effects were at least as large as those observed in the long exposure time condition (Figure 5c).

Our second proposal is that identity cueing effects are mediated by the P-cell inputs to the ventral stream. Because these cells exhibit sustained responding, activity in this channel will be related directly to stimulus exposure time, so reducing exposure time will reduce channel activity. As Figure 5b illustrates, the attentional effects of identity cues collapsed, and appear to have been eliminated completely, when cue exposure time was reduced to 67ms.

EXPERIMENT FIVE

In addition to differing with respect to their response properties (transient or sustained), the P-cell and M-cell inputs to the dorsal and ventral visual streams differ in their sensitivity to luminance contrast. The M-cell inputs to the dorsal stream exhibit good luminance contrast sensitivity: cells in this channel respond well to low-contrast visual stimuli (Bullier, 2001; Merigan & Maunsell, 1993; Shapley, Kaplan & Soodak, 1981). Therefore, effects mediated by this pathway will remain robust, under conditions of reduced contrast (Bullier, 2001), just as they also remain robust under conditions of reduced exposure time (Experiment Four).

Responses of the P-cell inputs to the ventral stream respond vary substantially with stimulus contrast. These cells respond strongly to stimuli presented with high luminance contrast, but only weakly to low contrast stimuli (Merigan & Maunsell, 1993). This physiological difference enables two further predictions to be made with respect to the attentional effects elicited by spatial cues in the Landmark and Identity cueing procedures. The rationale motivating these predictions, tested in Experiment Five, was directly analogous to that employed in Experiment 4. That is, we propose firstly, that attentional effects elicited by cues in the Landmark procedure will be driven by dorsal visual stream encoding of landmark properties. Because the M-cell inputs to this pathway respond well to low-contrast stimuli, attentional effects of Landmark cues should remain robust under conditions of reduced

contrast. Secondly, if the attentional effects elicited by cues in the Identity Cueing procedure are mediated by the P-cell inputs to the ventral visual stream, then these effects will diminish in magnitude when cue luminance contrast is reduced. The first of these two predictions has been confirmed already in two studies, where rapid orienting effects of similar magnitude were observed, regardless of whether landmark cue letters were presented with low or high luminance contrast (Lambert & Shin, 2010; Shin & Lambert, 2012). However, neither of these studies included the critical comparison between effects of luminance contrast in the landmark and identity cueing procedures. This was remedied in Experiment 5, which provided a direct comparison between effects on attention of high and low contrast cue stimuli, in the Landmark and Identity cueing procedures. As in Experiment 4, our prediction specified the precise form of the expected three-way interaction between cue validity, cueing procedure and cue stimulus contrast. That is, whereas in Experiment 4 we predicted robust cue validity effects under conditions of reduced exposure time in the Landmark cueing procedure, but not in the Identity cueing procedure, in Experiment 5 we predicted robust cue validity effects under conditions of reduced luminance contrast in the Landmark cueing procedure, but not in the Identity cueing procedure.

METHOD

Participants: Twenty adult volunteers (16 females; mean age = 21.5 years) took part. Each received a \$20 voucher as compensation for their time. All participants reported normal or corrected-to-normal vision.

Apparatus and Stimuli: The experimental paradigm was implemented using E-prime 2.0 professional software (Psychology Software Tools Inc., Pittsburgh, Pennsylvania). Stimuli were presented on a Samsung Syncmaster 24 inch screen (Refresh rate: 75Hz; screen resolution: 1920 x 1080 pixels), and participants used a chin rest so they viewed the display from a distance of 57cm. Participants wore a cap containing a high density array of 128 EEG electrodes, and EEG recordings were made as participants performed the two cueing tasks. Electrophysiological data were collected, but are not reported here; these are described separately, as they form part of a broader investigation of effects of normal ageing on visual attention (Sciberras-Lim, 2016).

All stimuli were dark grey in colour and presented against a grey background (Luminance level: 12.91cd/m²). A fixation cross (Weber contrast: 82%) subtending 0.5° by 0.5° was presented in the centre of the screen. Cue stimuli comprised a pair of bilaterally presented letters, presented on both sides of the fixation cross at a distance of 12.4° away from the centre of the screen and 4.2° above the horizontal meridian. Each cue letter was 0.8° by 1°. Half the cue letters were presented in high contrast (2.33 cd/m²; Weber contrast: 82%), while the other half of the cue letters were presented in low contrast (7.62 cd/m²; Weber contrast: 41%). As in Experiment 4, half of the participants were presented with the letters ‘O’ and ‘V’ as landmark cues during the Landmark Cueing Task, and were presented with the letters ‘T’ and ‘X’ as identity cues in the Identity Cueing Task; whilst the other half of the participants were presented with the letters ‘T’ and ‘X’ as landmark cues in the Landmark Cueing Task, and were presented with the letters ‘O’ and ‘V’ as identity cues in the Identity Cueing Task. The target stimulus was always an asterisk (Weber contrast: 41%), subtending 0.5° by 0.5°, presented 12.4° to the left or right of the screen centre, centred on the horizontal meridian.

Procedure: Half of the participants performed the *Landmark Cueing Task* first whilst the other half performed *the Identity Cueing Task* first. Participants were instructed to shift their attention covertly to keep their eyes fixed on centrally presented fixation cross, which remained present throughout the trials.

In the *Landmark Cueing Task*, two different letters, either 'T' and 'X' or 'O' and 'V' were presented for 133ms. After an interval of 467ms (600ms SOA) the target appeared, and participants were required to press the 'spacebar' key as soon as they detected the onset of the target stimulus. If the participants failed to respond to the target within 2s, or made an anticipatory response by pressing the spacebar key prior to the onset of the target stimulus, or within the first 100ms of target stimulus presentation, an error message appear (the message read: Warning! Error!). If the participant made a response during a catch trial (a trial where no target was present) a different error message appeared (the message read: Warning! Catch trial Error!) Each response was followed by an inter-trial interval that lasted between 1s-1.5s. The fixation cross disappeared briefly for 100ms before reappearing, this made the fixation cross appear to blink, providing participants with a warning that the next trial was about to begin. Following this a random interval of between 500ms-800ms elapsed before the presentation of the cues. The inter-trial interval and the time elapsed between the fixation cross reappearance and cue appearance were both randomly jittered. 20% of the trials were catch trials, helping ensure that participants remained alert and were responding to target onsets rather than simply making an anticipatory response. One of the cue letters indicated the likely position of the upcoming target with 75% probability in the non-catch trials. The letter used to cue target location was counterbalanced across participants, so that amongst those whom were presented with the letters 'T' and 'X', half were informed that the letter 'T' indicated the likely position of the upcoming target, while the other half were informed that 'X' indicated the likely position of the upcoming target. This counterbalancing resulted in

equal numbers of participants shifting their attention in response to each of the four cue letters. Participants began with a practice block of 10 trials, followed by 4 blocks of 80 experimental trials each (48 valid trials, 16 invalid trials, and 16 catch trials).

The *Identity Cueing Task*, was identical to the *Landmark Cueing*, save for this feature: two identical letters ('O', 'T', 'V', 'X') were presented for 133ms, and participants were instructed that after one letter pair (e.g. O + O), targets were likely to appear on the right-hand side of the screen; and following presentation of the alternative letter pair (e.g. V + V), targets were likely to appear on the left-hand side of the screen.

RESULTS

Data from four participants were not analysed: One reported feeling unwell during the experiment, one fell asleep, one made an excessive number of eye movements, and one failed to use the chinrest to maintain the correct viewing distance. The rate of anticipations (0.6%) and catch trial errors (2.2%) made by the remaining participants was acceptably low.

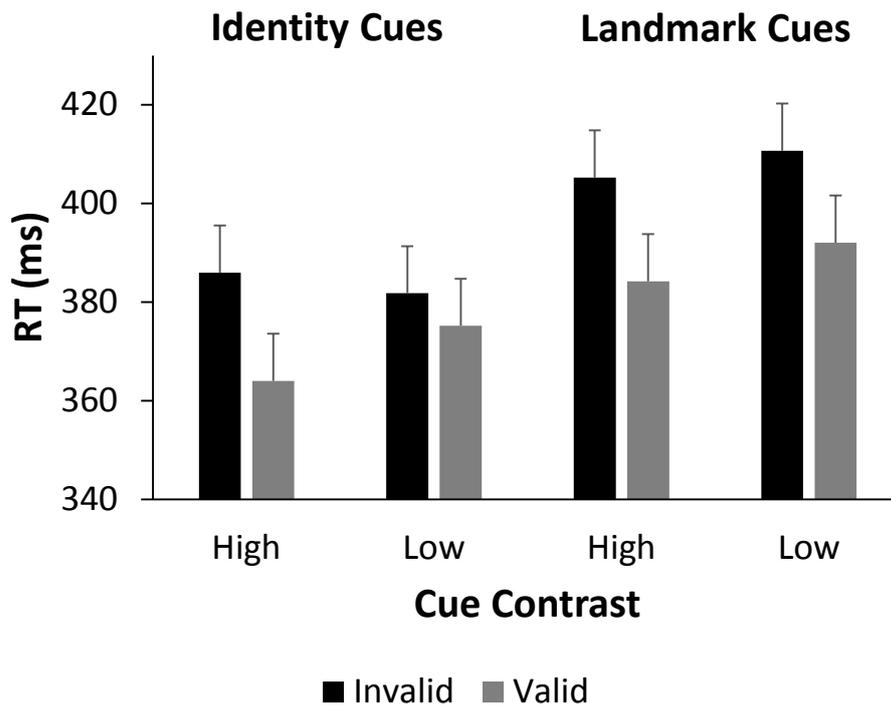


Figure 6. Mean response times in Experiment 5. Error bars represent the standard error of the difference in response times between valid and invalid trials.

Mean response times are illustrated in Figure 6. These data were entered into a three-way, repeated measures analysis of variance with cueing procedure (Landmark vs. Identity), cue contrast (high vs. low) and trial validity (valid vs. invalid) as factors. Overall, participants responded more rapidly in the Identity Cueing (377ms) compared to Landmark Cueing (398ms) condition $F(1,15) = 5.36, p = .035, \eta^2_p = .26$. Critically, the predicted three-way interaction between cueing paradigm, cue contrast and trial validity was reliable statistically, $F(1,15) = 6.12, p = .026, \eta^2_p = .29$. This interaction is illustrated in Figure 6. Further analyses showed that the form of this interaction agreed with prediction. In the Landmark Cueing condition, participants responded more rapidly on valid compared to invalid trials ($F(1,15) = 7.59, p = .015, \eta^2_p = .34$), and the magnitude of this effect did not vary as a function of cue

contrast ($F < 1$; see Figure 6, right). However, in the Identity Cueing condition, trial validity interacted with cue contrast ($F(1,15) = 7.16, p = .017, \eta_p^2 = .32$; see Figure 6, left). Thus, in the Landmark Cueing condition, participants responded more rapidly on valid compared to invalid trials, regardless of cue contrast (both $p < .025$); but, in the Identity Cueing condition participants responded more rapidly on valid compared to invalid trials on trials when the cue was presented with high contrast ($p < .025$), but not on trials where the cue was presented at low contrast ($t < 1$, n.s.).

DISCUSSION

The results of Experiment Five agreed remarkably well with prediction, with the expected three-way interaction revealing a difference between effects of cue contrast on the attentional consequences of landmark and identity cues. In agreement with two earlier reports (Lambert & Shin, 2010; Shin & Lambert, 2012) attentional effects of high contrast and low contrast landmark cues were of similar magnitude. In the identity cueing condition, response times were reliably quicker on valid compared to invalid trials when cues were presented with high contrast, but not when they were presented at low contrast. This is precisely the pattern one would expect to observe if: (1) Attentional effects of landmark cues were mediated by luminance sensitive M-cell channels in the dorsal stream, and (2) Attentional effects of identity cues were mediated by P-cell channels in the ventral stream, which respond weakly to low-contrast stimuli.

Response times were generally quicker in the Identity Cueing relative to Landmark Cueing condition. This effect was not predicted, and it is worth noting that in Experiment Four there was no evidence of an overall difference in response times between the Identity and

Landmark Cueing conditions. In light of this, and in light of the many methodological differences between Experiments Four and Five, it seems unproductive to speculate further at this stage as to why a main effect of cueing condition was observed in the latter experiment, but not the former.

EXPERIMENT SIX

According to the interpretation developed above, attentional effects of landmark cues are mediated primarily by dorsal visual stream encoding while those elicited by identity cues are mediated primarily by ventral visual stream encoding. So far, we have situated this interpretation within Ungerleider and Mishkin's (1982) conception of the dorsal and ventral visual streams as being specialised for encoding spatial relations and stimulus identity, respectively. However, in more recent decades, Ungerleider and Mishkin's (1982) perspective has been to some extent superseded by the theory of Milner and Goodale (1998, 2006), which offers a rather different view of the functional distinction between the dorsal and ventral visual streams. According to Milner and Goodale (2006) the ventral stream delivers '*vision for perception*'. That is, the ventral stream provides visual representations that can become conscious and gain access to working memory. In contrast, the dorsal stream provides '*vision for action*'. According to Milner and Goodale's (2006) framework, visual representations encoded by the dorsal stream play a critical role in rapid, on-line control of visually guided actions. Moreover, Milner (2012) reviewed evidence in support of the proposal that the dorsal stream visual encoding that supports such movements is independent of, and indeed inaccessible to, conscious awareness. Much research attention and effort has been directed towards studying the role of the dorsal stream in visually guided actions of the hand and arm, especially grasping movements (Chen, Sperandio & Goodale, 2015; Milner &

Goodale, 2006). However, movements of the eyes themselves are an especially interesting class of visually guided action. Eye movements, like reaching and grasping movements, are accessible to conscious control: a conscious decision to look up, down, right or left will be generally followed by a corresponding eye movement. Nevertheless, it is also clear that non-conscious processes can influence the onset, dynamics and trajectory of eye movements (Findlay & Gilchrist, 2003). Hence, the aim of Experiment Six was to explore the idea that eye movements can be viewed from the perspective of Milner & Goodale (2006), as *visually guided actions*, influenced by rapid, non-conscious processing in the dorsal visual stream.

In the experiments described so far, we have explored effects of spatial precues on movements of *covert* attention. However, the view that covert shifts of attention and overt movements of the eyes are functionally linked has been widely endorsed (deHaan, Morgan & Rorden, 2008; Rizzolatti *et al.* 1987; Rizzolatti & Craighero, 1998; Smith, Rorden & Jackson, 2004; but see MacLean, Klein & Hilchey, 2015; Smith, Schenk & Rorden, 2012 for contrasting views). Hence, Experiment Six tested the prediction that the constellation of effects observed when landmark cues elicit covert shifts of attention will also be observed when participants shift attention overtly, by moving their eyes. Properties of the M-cell inputs to the dorsal stream, together with our previous findings enabled a highly specific set of predictions to be made regarding effects of landmark cues on eye movements. It was predicted that:

1. Effects of landmark cues on eye movements will be robust under conditions of low luminance contrast. In Experiment Five, landmark cues influenced shifts of covert attention to the same extent, regardless of whether cues were presented with high or low contrast. Experiment 6 tested the hypothesis that effects of landmark cues on overt movements of the eyes will be similarly robust, when cue contrast is reduced.

2. Effects of landmark cues on eye movements will be robust under conditions of brief exposure time. In Experiment Four landmark cues (but not identity cues) influenced shifts of covert attention when the cues were exposed for just 67ms. If attentional effects of landmark cues are driven by transient responses in M-cell channels of the dorsal stream, then such effects should continue to be apparent with even briefer cue exposure times. Accordingly, Experiment 6 tested for effects of landmark cues on overt shifts of attention with a cue exposure time of 33ms.
3. Rapid processing is a key feature of the dorsal stream computations that, according to Milner & Goodale (2006) enable visually guided actions to be performed. For example, it is clear that sports such as tennis or baseball require visual information to be translated very rapidly indeed into the motor activity responsible for racquet or bat control. Consistent with this, electrophysiological studies have shown firstly that M-cell channels of the dorsal stream conduct signals very rapidly, and secondly that visually responsive regions in parietal cortex, the target of the dorsal visual stream, respond with extremely brief latencies to the onset of visual stimuli. This has led authors such as Bullier (1990) to refer to these parietal regions as ‘the fast brain’. If attentional effects of landmark cues are mediated by rapid visual processing in the dorsal stream, then such effects should be apparent even when the delay between onset of the cue stimulus, and onset of the target stimulus is very brief. Clearly, cueing effects can only be observed if the information provided by the cue can be encoded with sufficient rapidity to affect target processing, and eye movement programming. Hence, we propose that the rapidity of cue encoding within the dorsal visual stream will give rise to reliable landmark cueing effects on eye movements, even when the temporal window between cue onset and onset of the target for an eye movement is extremely brief. In Experiments 1-5, in which effects of cues on covert

attention were studied, cue-target onset delays ranged from 150ms to 700ms. In an earlier study (Lambert *et al.*, 2000) we observed reliable effects of high contrast landmark cues on eye movements when the delay between cue and target onset was 100ms. In Experiment Six the delay between cue onset and target onset was reduced further to 66ms. It is perhaps worth noting here, that this delay is substantially briefer than cue-target onset delays that have been observed to elicit maximal orienting effects in studies of ‘endogenous orienting’ (Wright and Ward, 2008). This issue, and the relationship between landmark cueing and the notion of endogenous orienting is considered further in the General Discussion.

4. Effects of landmark cues on eye movements will be robust when cue information is presented to the periphery. Representation of the central and peripheral visual fields is relatively uniform in M-cell channels of the dorsal visual stream, while P-cell channel representation is strongly biased in favour of central visual regions (Merigan & Maunsell, 1993). Therefore, if attentional effects of landmark cues are driven by the M-cell inputs to the dorsal stream, then such effects will continue to be apparent when cue information is presented at a relatively peripheral visual location. In Experiment 6 the visual eccentricity of cue letters was 12.7°.
5. A final prediction was that effects of landmark cues on eye movements will be independent of conscious awareness of the cue stimuli. According to the framework of Milner and Goodale (2006) visual encoding in the dorsal stream proceeds independently of conscious awareness, and indeed is inaccessible to conscious awareness (Milner 2012). The aim of the manipulations described in 1-4 above (i.e. brief exposure time, low luminance contrast, peripheral presentation, and brief delay between cue and target onset) was to align properties of the cue stimulus with known physiological properties of the M-cell inputs to the dorsal stream. However, brief

exposure time and low contrast, together with presentation of the cues at a relatively peripheral visual location (12.7°), are also likely to impair conscious perception of the cues, by weakening ‘vision for perception’ representations generated within the ventral stream. An additional design feature of Experiment Six, intended to weaken further conscious access to perceptual representations of the cue stimuli, was that participants were not informed of the predictive relationship between cue and target stimuli, and indeed were not forewarned that peripheral targets would be accompanied by other briefly presented stimuli – the cues. If effects of landmark cues on eye movements are mediated by non-conscious processing within the dorsal stream, then one can predict such effects will be observed even for participants who remain unaware of the cues, or of their predictive relationship with target location.

In addition to evaluating effects of high and low luminance landmark cues on eye movements, Experiment 6 included a further task in which participants were required to discriminate consciously between the letter pairs that served as cues in the eye movement task. Properties of the P-cell inputs to the ventral visual stream and phenomenal awareness of objects in peripheral vision both suggest that reducing luminance contrast is likely to impair conscious discrimination. Therefore, while we expected to observe robust orienting under reduced luminance contrast in the eye movement task, in the discrimination task we predicted that performance would be impaired (slower and less accurate) when luminance contrast was reduced. In terms of the perspective developed by Milner and Goodale (2006), we propose that the eye movement task will recruit ‘vision for action’, while the discrimination task will rely on ‘vision for perception’. Accordingly, the terms ‘Vision for action (landmark) task’, and ‘Vision for perception (discrimination) task’ are used below when referring to these two experimental procedures.

METHOD

Participants: Thirty two adult volunteers (18 males) took part. All participants had normal or corrected to normal vision.

Apparatus: This was the same as for Experiment One. Before each experimental task participants completed a calibration procedure with the Tobii T120 eye tracker.

Vision for Action (Landmark) task

Display and stimuli: Letter cues, digit targets, and the central fixation cross were all shown in light grey against a dark grey background. A fixation cross ($0.29^\circ \times 0.29^\circ$; Luminance = 6.5 cd/m^2) was present in the centre of the screen at the beginning of every trial and during the inter-trial interval. Letter cues were the letters X and T, subtending $0.57^\circ \times 0.76^\circ$. The centre of each letter was 12.7° to the left or right of the screen centre, and 1.52° above the horizontal meridian. Cue letters were presented for 33ms against a dark grey background (Luminance = 0.58 cd/m^2), with either high contrast (Luminance = 6.5 cd/m^2), or low contrast (Luminance = 2.1 cd/m^2). Target stimuli were the digits '2' and '7', subtending $0.38^\circ \times 0.57^\circ$. The centre of each target was 12.7° to the left or right of screen centre, and was aligned with the horizontal meridian.

Procedure: Each trial began with presentation of a central fixation cross for 1,000ms, followed by a blank screen for 100ms, followed by re-presentation of the fixation cross for 1,000ms. The fixation screen was then replaced by a screen showing the two landmark cue

letters (X and T), presented for 33ms. Hence, the fixation cross ‘blinked’ for 100ms, one second prior to presentation of the cues. The aim of this was to ensure that participants were attending to the centre of the screen at the beginning of every trial. Offset of the cue letters was followed by a blank screen for 33ms, followed by presentation of a digit target, on the left or right of the screen. Participants were instructed to ensure that they were fixating centrally at the beginning of each trial, and to move their eyes to look at the target, as soon as it appeared. Participants were instructed to press the ‘Up-Arrow’ key if the digit was ‘7’, and the ‘Down Arrow’ key if the digit was ‘2’. The digit target remained on the screen until participants made a response, or until 4 seconds had elapsed. Offset of the target was followed by re-presentation of the central fixation cross, for an inter-trial interval that varied randomly between 1,000ms and 1,500ms.

On 80% of trials, the target appeared on the same side as a landmark letter. For 50% of participants ‘X’ served as the landmark letter; for the remaining participants, ‘T’ was the landmark letter. However, participants were not warned that target stimuli (digits) would be preceded by bilateral letter stimuli, and were not informed of the predictive relationship between cues and target location. They were simply instructed to move their eyes to look at targets on the left and right of the screen, in order to decide whether each digit was a ‘2’ or a ‘7’. The size and eccentricity of the two possible targets (‘2’ vs. ‘7’) were chosen so that an eye movement would be required in order to discriminate between them.

After completing this task all participants were given a brief questionnaire, similar to that employed previously by Lambert, Naikar, McLachlan and Aitken (1999). The six items in this questionnaire (see below) probed participants’ awareness of the presence of the cue letters (perceptual awareness), and awareness of the predictive relationship (contingency awareness) between the cue letters and target location.

1. While you were carrying out the experiment were you aware of any letter/s?

Please circle: Yes No

2. If yes, please state the letter/s

3. Were you aware of the relationship between the briefly presented letter/s and the location of the number target?

Please circle: Yes No

4. If yes, please describe the relationship.

5. Two pairs of statements concerning the experiment you have just performed are provided below. Your task here is to decide which of them is true. Please indicate which pair of statements you think is true by circling the appropriate letter.

A) The number usually appeared on the same side as the “X”, and on the opposite side to the “T”.

B) The number usually appeared on the same side as the “T”, and on the opposite side to the “X”.

6. Please indicate your confidence in the judgment you have just made by circling the appropriate letter.

I feel that my choice for question 5 was

A) A pure guess

B) Mainly guesswork

C) Possibly the correct choice

D) Probably the correct choice

E) Very likely the correct choice

F) Almost certainly the correct choice

Questions 1 and 2 were revealed first, followed by 3 and 4, and finally items 5 and 6 were revealed. The aim of this was to ensure that participants did not see the forced choice items, until they had finished responding to the earlier items.

Design: Before completing this task, participants were given 16 practice trials, in which the target always appeared on the same side as the landmark letter. Participants were then presented with three blocks of 80 experimental trials. Each block contained 64 'location valid' trials, in which the target appeared on the same side as the landmark letter, and 16 invalid trials, in which the target appeared on the side opposite the landmark letter. Each block contained an equal number of trials with high and low contrast cue letters. Trial validity and cue contrast varied pseudorandomly.

Vision for Perception (Discrimination) Task

Display and stimuli: These were identical with the vision for action task, except that a blank screen was presented in place of the screen containing the digit target.

Procedure: In this task, participants responded to the peripheral letter pair, rather than to a digit, and indicated the location of the landmark letter via a manual key-press response. Participants were instructed to press the right-arrow key if the landmark item, in the briefly presented letter pair, was on the right, and to press left-arrow if it was on the left. Participants were instructed to ensure that they were fixating centrally, before presentation of each letter pair.

Design: Following an initial block of 16 practice trials, participants performed a single block of 80 experimental trials. Letter contrast and the location of the landmark item varied pseudorandomly, with equal numbers of each trial type.

RESULTS

Vision for Action (Landmark) Task

As a result of technical difficulties with the eye-tracker, saccadic reaction time data were not available for nine of the original thirty two participants. The prediction that landmark cues would affect eye movement behaviour independently of conscious awareness was tested by dividing the remaining twenty three participants into two groups. Participants in the ‘Unaware Group’ fulfilled *both* of two criteria: Firstly, they provided a negative response to the first questionnaire item, which asked if they had been aware of seeing any letters while performing the eye movement task; and secondly, when asked to make a forced choice judgement as to whether the digit target usually appeared on the same side as the ‘X’ cue, or on the same side as the ‘T’ cue, participants indicated that their confidence in this judgement was “A pure guess”. Ten participants met these criteria. The ‘Aware Group’ comprised the remaining thirteen participants who failed to fulfil these criteria. That is, these participants either responded ‘yes’, when asked to indicate if they had seen any letters while performing the eye movement task; or when making a forced-choice judgement as to whether the target had usually appeared on the same side as the ‘X’ or on the same side as the ‘T’ they indicated a degree of confidence that was stronger than “A pure guess”.

Unaware Participants: Mean latencies of saccades initiated towards the target by unaware participants are illustrated in Figure 7. These data were entered into analysis of variance with two repeated measures factors: cue luminance contrast (high vs. low) and trial validity (valid vs. invalid). Participants initiated saccades more rapidly when the target appeared at the valid (Saccade RT = 282ms) compared to invalid (Saccade RT = 302ms) location, $F(1,9) = 34.14$, $p < .001$, $\eta^2_p = .79$. Notably, cue contrast had no effect on the magnitude of the advantage for

valid compared to invalid trials, $F(1,9) = 1.1$, n.s. (see Figure 7). No other main effects or interactions were reliable statistically.

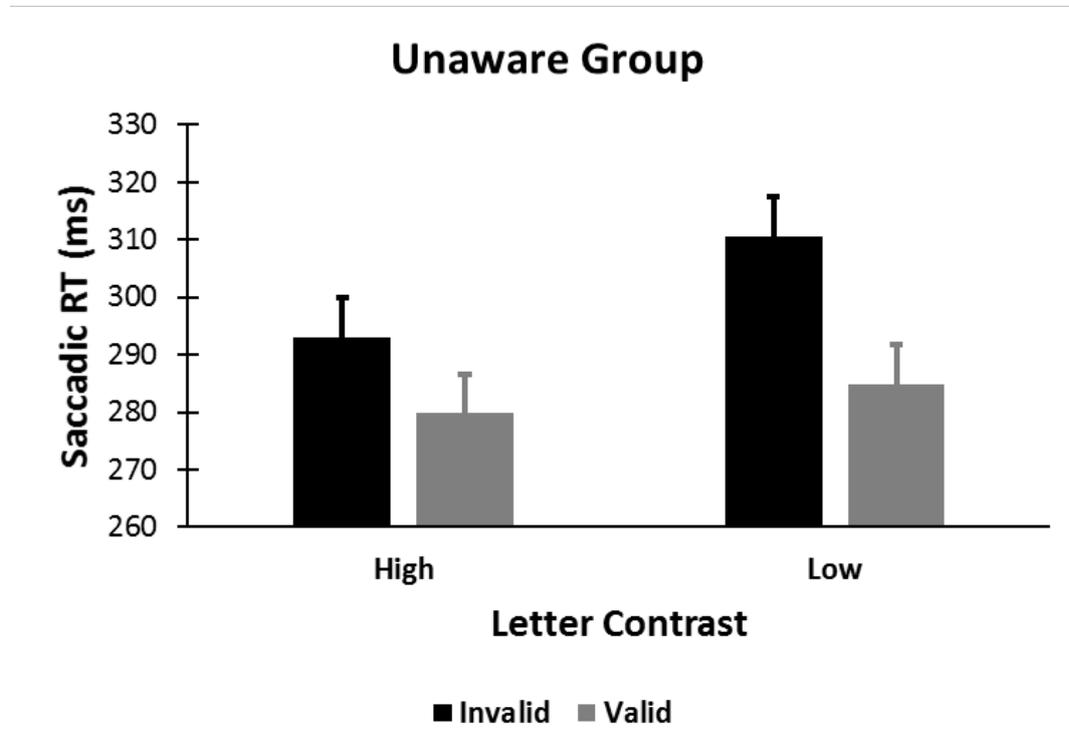


Figure 7. Mean saccadic latencies in Experiment 6, for participants who remained unaware of the presence of cue letters, or of their relationship with target location. Error bars represent the standard error of the difference in saccadic latency between valid and invalid trials.

Aware Participants: A sizeable minority of participants ($N=5$) in the 'Aware' group chose incorrectly, when asked to indicate whether the target usually appeared on the same side as the 'X' cue, or on the same side as the 'T' cue. Moreover, the average confidence with which these erroneous beliefs were expressed was substantial: mean confidence = 3.4, where confidence levels were scored from 1 ('A pure guess') to 5 ('Almost certainly correct'; see

Method). Accordingly, mean latencies of saccades initiated towards the target by participants in the 'Aware' Group were entered into a mixed model analysis of variance with cue contrast (high vs. low) and trial validity (valid vs. invalid) as repeated measures factors, and location belief (correct vs. incorrect) as an independent groups factor. The latter factor coded whether participants made a correct or incorrect choice, when judging whether the target usually appeared on the same side as the 'X' or 'T' cue. In contrast to results obtained from the Unaware Group, there was no overall advantage on valid compared to invalid trials in this analysis, $F < 1$. However, trial validity interacted with the independent groups factor, location belief, $F(1,11) = 16.67, p = .002, \eta^2_p = .60$. This interaction, illustrated in Figure 8, shows that participants who formed a correct belief about the likely location of the target with some confidence, tended to initiate eye movements towards the target more rapidly on valid (Saccade RT = 263ms) compared to invalid trials (279ms); and participants who believed confidently, but erroneously, that the target was more likely to appear at the invalid location tended to initiate eye movements more rapidly towards the invalid (Saccade RT = 293ms) compared to valid (Saccade RT = 305ms) location. No other main effects or interactions were significant.

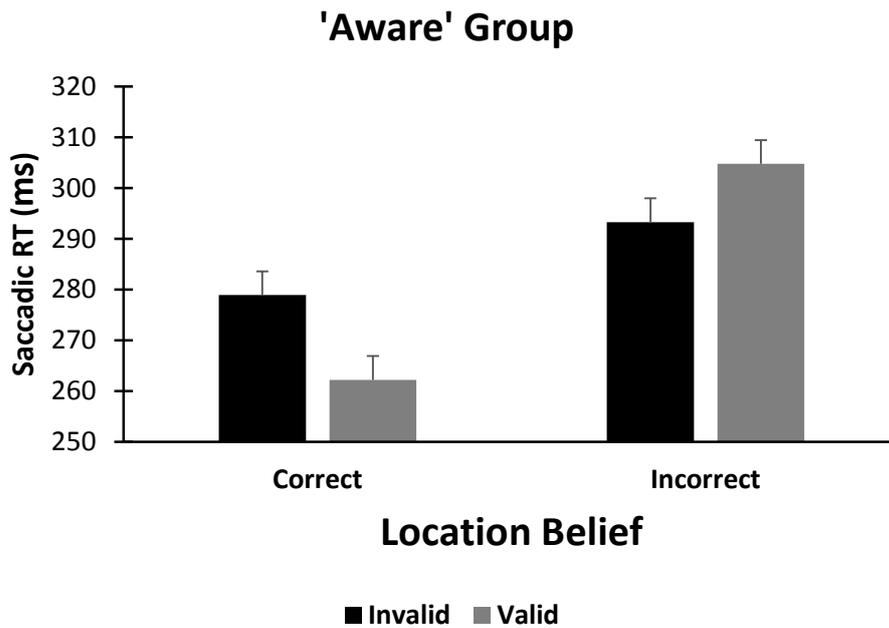


Figure 8. Mean saccadic latencies in Experiment 6, for participants in the ‘Aware’ Group.

Participants initiated saccades more rapidly when the target appeared at the location that was believed to be more likely, regardless of whether that belief was accurate or inaccurate. Error bars represent the standard error of the difference in saccadic latency between valid and invalid trials.

Vision for Perception (Discrimination) Task

Mean accuracy and mean response times in the vision for perception (discrimination) task are illustrated in Figure 9. As expected, when required to discriminate consciously between the peripheral letters that served as cues in the vision for action (landmark) task, clear effects of luminance contrast were seen. Participants responded more slowly on trials with low (Mean RT = 453ms) compared to high (Mean RT = 434ms), stimulus contrast, $t(31) = 2.99$, $p = .003$, one-tailed. Participants also responded less accurately on trials with low (96.3%) compared to high (97.7%) stimulus contrast, $t(31) = 2.43$, $p = .01$, one-tailed. Supplementary

analyses compared the Aware and Unaware Groups, assigned on the basis of performance in the Vision for Action task, with regard to discrimination performance in the Vision for Perception task. These analyses showed that the speed and accuracy advantage for high contrast trials in the Discrimination task did not vary as a function of awareness group (both $F < 1$). However, participants in the unaware group tended to respond more rapidly (Mean RT = 394ms) than aware participants (Mean RT = 505ms), $F(1,21) = 3.56$, $p = .07$, when discriminating peripheral letters.

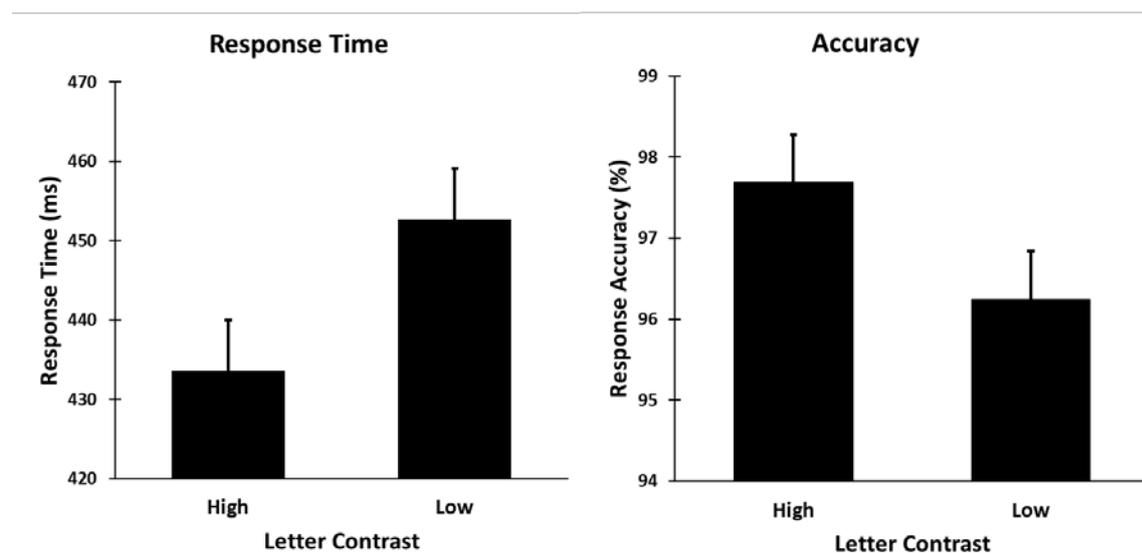


Figure 9. Mean response times and accuracy in the *Vision for Perception* task of Experiment Six. Error bars represent the standard error of the difference between low and very low contrast conditions.

DISCUSSION

The central prediction of Experiment Six was highly specific: that robust effects of landmark cues would be apparent when the cues were presented with very brief exposure time (33ms), with low luminance contrast, with a brief cue-target onset delay, at relatively peripheral visual locations, and for participants who were aware neither of the presence of cues, nor of their predictive relationship with target location. In agreement with this detailed prediction, participants who were unaware of the cues nevertheless initiated eye movements more rapidly on trials where the target appeared at a location marked as more likely, by the landmark cues. Although the absolute size of the effect of these cues on eye movement latency was relatively small (Invalid Saccade RT – Valid Saccade RT = 20ms), the effect for these unaware participants was remarkably consistent. Effect size calculations for the comparison between valid and invalid trials for the unaware group generated values corresponding to a large effect ($f^2_p = .79$; Cohen's $d = 1.95$).

Although the key prediction of Experiment Six was confirmed, findings from the 'Aware' group indicate that our proposal that landmark cueing effects are independent of conscious awareness needs to be qualified in an important way. On the one hand, it is clear that visual landmarks can affect attentional orienting in the *absence* of conscious awareness. A cueing effect was observed for participants who were unaware of the utility, or even the presence of peripheral cues (see also Lambert *et al.*, 1999; Lambert, 2003). On the other hand, findings from the 'Aware' group show that behaviour in this situation was not *independent* of conscious awareness: Rapid orienting in response to landmarks was influenced by consciously accessible beliefs concerning the utility of the cues. Participants who believed correctly that the target usually appeared at the location marked as more likely by the cues, initiated saccades more rapidly when the target appeared there; and participants who believed

(incorrectly) that the target usually appeared at the location marked as less likely, initiated saccades more rapidly when the target appeared at the invalid location. Therefore, orienting behaviour was influenced by participants' attentional set, as reflected in their beliefs about where targets were likely to appear. In a sense, this finding is perhaps not so surprising. As mentioned earlier, there is ample evidence that non-conscious processing in the dorsal stream plays a key role in the execution of reaching and grasping movements (Chen, Sperandio & Goodale, 2015). However, such movements are, of course, generally preceded by a conscious decision to perform the movement. Hence, reaching and grasping movements can be initiated (or interrupted) consciously, but once they have been programmed and initiated, on-line guidance of these actions is thought to rely on non-conscious, dorsal stream processing. In the same way, it appears that conscious beliefs about the utility of peripheral visual information can influence the onset of visual orienting in response to a new object of interest. As a consequence of our experimental conditions (brief presentation of low luminance peripheral stimuli), participants' awareness of the cue stimuli was relatively impoverished, and it appears that a substantial minority of the 'aware' participants formed incorrect beliefs, and adopted a sub-optimal attentional set concerning the likely location of the target. If cue stimuli gain access to consciousness on a relatively small number of trials, incorrect beliefs about target location may be developed if those occasions include a substantial number of invalid location trials.

When alerted to the presence of stimuli used as peripheral cues in the eye movement task, participants were able to judge the location of a landmark letter with high levels of accuracy (>96% - see Figure 9). Therefore, although 10/23 participants were unaware of the presence of peripheral letters when they performed the eye movement task, these stimuli were nevertheless well above threshold. To adopt the terminology suggested by Dehaene et al. (2006), the status of these stimuli during the eye movement task, for participants in the

unaware group can be described as preconscious. Preconscious stimuli, according to Dehaene et al. (2006) are those that potentially generate sufficient activation for conscious access, but fail to enter consciousness due to a lack of top-down attentional amplification.

GENERAL DISCUSSION

In addition to answering the question that motivated this project initially, results from Experiments 1-6 shed light on the neurocognitive mechanisms of attention, and in particular, they suggest that there may be a relatively simple relationship between two-process models of attention-shifting (Chica *et al.*, 2013; Corbetta & Shulman 2002; Posner, Snyder & Davidson, 1980) and dual-stream models of vision (Ungerleider & Mishkin, 1982; Milner & Goodale, 2006).

The question that prompted this work initially, was to discover why findings from some studies showed that attention shifting in response centrally presented precues was driven by visual-spatial (landmark) features of the cue, rather than by its symbolic designation as a cue for a target at a particular location (Lambert *et al.*, 2006; Shin *et al.*, 2011); while other studies have indicated the opposite - that attention shifting is driven by the symbolic identity of cues, independently of their visual-spatial features (Fischer *et al.*, 2003; Hommel *et al.*, 2001). Experiments 1-4 showed that at an empirical level the answer is straightforward. Firstly, when spatial cues were presented very briefly (for 67ms in Experiments 3 & 4) attentional effects were driven by landmark features of the cue stimulus, and the predictive association between these features and target location. (see also Lambert & Duddy, 2002; Lambert *et al.*, 2006; Shin *et al.*, 2011). Under these conditions, attentional effects were independent of the symbolic identity of the cue stimulus, as the signal for a target at a

particular location. Secondly, when spatial cues were presented for a longer period (300ms in Experiments 1 & 2, and 133ms in Experiment 4), attentional effects were independent of the visual-spatial features of the cue, and were driven instead by the symbolic identity of the cue, as the signal for a target at a particular location (see also Fischer *et al.*, 2003; Hommel *et al.*, 2001; Chica *et al.*, 2013, 2014).

As explained above, this dissociation between spatially driven and symbolically driven orienting under different stimulus conditions, is consistent with two theoretical proposals – namely, that attention shifting in response to visual-spatial properties of cues in the environment is driven by dorsal visual stream encoding, while attention shifting in response to the symbolic meaning of cues is driven by ventral visual stream encoding.

The dorsal visual stream and landmark cueing.

The transient responding properties of M-cell inputs to the dorsal visual stream led us to predict that landmark cueing effects would remain robust under conditions of brief cue exposure time, and this prediction was confirmed in Experiments 4 and 6. However, in a sense this finding merely adds to an already substantial body of evidence, indicating that landmark cueing effects rely on dorsal stream encoding of cue stimuli. Indeed, six previous findings provide converging support for this hypothesis:

1. Marrett *et al.* (2011) examined the ability of patient DF, studied extensively by Milner & Goodale (2006), to perform the landmark cueing task. DF suffered bilateral damage to the ventral stream, resulting in a dense visual agnosia. However, despite her agnosia, she remains able to perform a variety of visually guided actions. Milner & Goodale (2006) attribute these residual visual functions, termed ‘*vision for action*’, to the dorsal stream, which remains intact in patient DF. Marrett *et al.* (2011) found that DF was able to perform the landmark cueing task, and moreover, exhibited cueing

effects that were similar in magnitude to those of four neurologically intact controls. When asked to discriminate consciously between the stimuli used as landmark cues, DF performed extremely poorly, consistent with the bilateral lesions of her ventral stream, and consequent visual agnosia.

2. Electrophysiological studies of event-related potentials (ERPs) are also consistent with dorsal visual stream encoding of cue stimuli in the landmark task (Marrett *et al.*, 2011; Lambert & Wootton, 2016; Lambert, Wootton, Ryckman & Wilkie, 2014). Marrett *et al.* (2011) applied source localisation to the early phase of the P1 ERP component elicited by landmark stimuli, and found evidence of activation in a structure associated with the dorsal stream, the superior parietal lobule (SPL). When participants discriminated consciously between the stimuli used as landmark cues, source localisation applied to the same ERP component (early P1) revealed evidence of activation in two structures associated with the ventral stream (inferior temporal gyrus, ITG, and fusiform gyrus, FFG). This dissociation during the early P1 was replicated by Lambert & Wootton (2016), who also found that the earlier, C1 ERP component observed at parietal-occipital electrode sites, was larger when peripheral stimuli served as landmark cues, relative to a condition where participants discriminated consciously between the same stimuli. Moreover, application of source localisation to the C1 revealed evidence of widespread SPL activation in the landmark task, but not in the conscious discrimination task.
3. In addition to the feature of transient responding, M-cell inputs to the dorsal stream exhibit good luminance contrast sensitivity. That is, cells in this channel respond well to low-contrast visual stimuli (Bullier, 2001; Merigan & Maunsell, 1993; Shapley, Kaplan & Soodak, 1981). Therefore, effects mediated by this pathway will remain robust, under conditions of reduced contrast (Bullier, 2001). This prediction was

borne out in Experiments 5 and 6, and also in two earlier studies, where rapid covert orienting effects of similar magnitude were observed, regardless of whether the letters were presented with high or low contrast (Lambert & Shin, 2010; Shin & Lambert, 2012).

4. While, representation of the visual field is strongly biased, in favour of central visual regions in the ventral visual stream (Merigan & Maunsell, 1993), representation of the central and peripheral visual fields in the dorsal visual stream is relatively uniform (Brown, Halpert & Goodale, 2005; Colby, Gatass, Olson & Gross, 1988; Merigan & Maunsell, 1993). Consistent with dorsal stream encoding, Lambert & Duddy (2002, Experiment 1) found that the speed of onset and overall magnitude of landmark cueing effects were closely similar, regardless of whether the bilateral cue stimuli were presented centrally (0.35° from fixation) or peripherally (7.3° from fixation). Although a conscious discrimination task was not included in this study, there is little or no doubt that the ability to discriminate consciously between letter stimuli, mediated by the ventral stream, would be strongly affected by visual eccentricity, with slower and less accurate performance in the peripheral condition.
5. A striking property of the dorsal stream, M-cell derived pathway is that signal conduction speed is substantially quicker than in the P-cell channel, which forms part of the ventral stream. This feature appears to be responsible for the observation that cells in high-level structures of the dorsal stream respond very rapidly to visual stimulation, with latencies similar to those observed in V1, leading some authors to refer to these parietal regions as ‘the fast brain’ (Bullier, 2001). Consistent with mediation by M-cell derived fibres of the dorsal stream, Lambert & Duddy (2002) found that peripherally presented landmark cues influenced the orientation of attention with extremely brief delays between cue and target onset. Indeed, reliable

effects were seen even when peripheral landmark cues and targets were presented simultaneously (Lambert & Duddy, 2002, Experiments 3A and 4). In contrast, the attentional effects of visually similar identity cues followed a somewhat slower time-course (Lambert & Duddy, 2002, Experiment 3B).

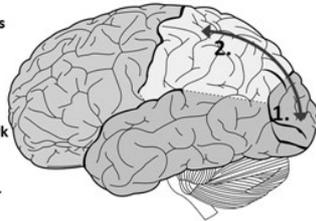
6. Milner (2012) reviewed evidence from neuropsychological and neuroimaging studies, concerning the relationship between conscious awareness and the dorsal visual stream, and concluded that processing in the dorsal visual stream is inaccessible to conscious awareness. Hence, if landmark cueing relies on dorsal stream processing, such effects should continue to be apparent in the absence of awareness. This prediction was confirmed in Experiment 6: participants who were unaware of the presence or predictive utility of peripheral landmark cues initiated eye movements more rapidly in response to information provided by the cues. Lambert *et al.*, (1999; Experiments 1 & 4), Lambert *et al.*, (2000) and Shin, Marrett & Lambert (2011) also found that shifting attention in response to landmark cues occurred independently of conscious awareness of the predictive relationship between cue stimuli and target location.

While critical readers will no doubt be able to identify weaknesses in each of the above, taken together, these six items of converging evidence, plus the seventh finding, from Experiments 3, 4, and 6 that landmark cueing effects are robust under brief exposure time, make a compelling case that landmark cueing effects are mediated by dorsal stream encoding of stimuli in the visual environment.

Figure 6

(a) LANDMARK CUEING - attention movements driven by dorsal stream encoding of visual-spatial features

1. Dorsal stream encoding of visual-spatial (landmark) features of environmental cues interacts with parietal attention circuits.
2. Attentional expectancies, established by predictive associations between landmark features and target locations, and represented in parietal attention circuits, leads to top-down facilitation of target processing at the cued location.



(b) IDENTITY CUEING - attention movements driven by symbolic encoding of information in the visual environment

1. Ventral stream encodes semantic-symbolic features of environmental cues.
2. The outcome of symbolic processing interacts with conscious goals, and recruits the fronto-parietal attention network.
3. Activity in the dorsal component of the fronto-parietal attention network generates top-down facilitation of target processing at the cued location.

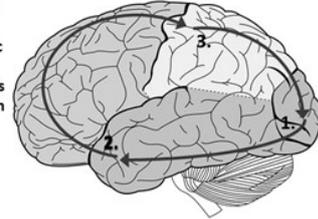


Figure 6. A model of the neurocognitive processes and pathways responsible for shifting attention in response to environmental cues. Dorsal stream-based visual orienting is represented in panel (a); ventral stream-based visual orienting is represented in panel (b).

A simple model of the attention shifting mechanism elicited by dorsal stream encoding of environmental cues is illustrated in Figure 6a. The target of the dorsal stream, parietal cortex, is of course, strongly associated with attentional functions, so it seems highly likely that dorsal stream encoding of environmental cues will interact with parietal attention circuits. We propose that spatial expectancies, represented in these parietal regions (Ungerleider & Mishkin, 1982), interact with the outcome of dorsal stream visual encoding, leading to top-down facilitation of target processing at the cued location (Bressler, Tang, Sylvester, Shulman & Corbetta, 2008; Lauritzen, D’Esposito, Heeger & Silver, 2009). Findings from Experiment 6 suggest that these expectancies may be established either non-consciously, by associative learning of the predictive links between landmark features of cue stimuli and target location, or via consciously held beliefs concerning the utility of particular stimuli.

The processing pathway depicted in Figure 6a is consistent not only with the classic investigations of Ungerleider & Mishkin (1982), establishing a link between the dorsal visual stream and landmark learning in monkeys, but also with the more recent dual-pathway model of vision developed by Milner & Goodale (2006). According to the latter model, the dorsal stream provides ‘*vision for action*’ – by performing the rapid computations needed for carrying out visually guided actions, such as reaching and grasping. The landmark cueing task can be said to require a specific kind of ‘*vision for action*’, where the visually guided action involved is a covert or overt movement of visual attention. According to the premotor theory of attention (de Haan, Morgan & Rorden, 2008; Rizzolatti *et al.*, 1987), covert shifts of attention are closely linked with a particularly important class of visually guided movements – movements of the eyes themselves. Thus, the pathway depicted in Figure 6a is consistent not only with Ungerleider and Mishkin’s (1982) proposal that a central function of the dorsal stream is to encode the spatial relationships between stimuli, but also with Milner & Goodale’s (2006) contention that a central function of the dorsal stream is to perform the visual computations needed for carrying out visually guided actions.

The ventral visual stream and symbolic cueing

Symbolic-semantic encoding is strongly associated with the ventral stream (Carlson *et al.*, 2014; Peelen & Caramazza, 2012) and appears to be outside the functional repertoire of the dorsal stream, which as we have seen specialises in encoding the visual-spatial features of environmental stimuli. In a sense, this overall characterisation of the different functions performed by the two cortical visual streams mandates the proposal that the ventral stream is the input route for attentional effects driven by symbolic encoding of cue stimuli – because the alternative hypothesis implies that the dorsal stream is capable of symbolic-semantic encoding, which seems unlikely, on the basis of current evidence (Carlson *et al.*, 2014;

Milner & Goodale, 2006). Nevertheless, in addition to this consideration, three further lines of evidence are consistent with the contention that identity cueing effects, driven by symbolic encoding, are mediated by the ventral stream. Firstly, Experiments 1-4 showed that, in contrast to landmark cueing effects, identity cueing effects are strongly dependent on cue exposure time. As seen above, this is consistent with mediation by the P-cell inputs to the ventral stream. Secondly, Experiment 5 showed that unlike landmark cueing, identity cueing effects collapsed when the luminance contrast of the cue stimuli was reduced. As explained earlier, this is consistent with ventral stream mediation of identity cueing, because the P-cell inputs to the ventral stream respond poorly to low contrast stimuli. Thirdly, Lambert & Duddy (2002; Experiment 2) found that, in contrast to landmark cueing effects, identity cueing effects were influenced by the visual eccentricity of cues, with stronger effects for centrally presented cues. This is consistent with ventral stream mediation, because representation of the visual field in the ventral stream is strongly biased, with better representation of central regions (Merigan & Maunsell, 1993).

A simple model of the attention shifting mechanism elicited by ventral stream encoding of environmental cues is illustrated in Figure 6b. An extensive series of neuroimaging studies, using fMRI methodology has shown that voluntary shifting of attention, in response to endogenous / symbolic cues is accompanied by activation of a network of frontal and parietal regions, known as the fronto-parietal attention network (Corbetta & Shulman, 2002, 2011; Kincade, Abrams, Astafiev, Shulman & Corbetta, 2005). The dorsal attention network (DAN), comprising regions of posterior parietal cortex and the frontal eye fields (Ptak & Schnider, 2010) is a major component of this overall system (Corbetta & Shulman, 2002, 2011). Figure 6b provides a simple representation of our proposal that the ventral stream is the input route driving activation of the fronto-parietal attention system, during endogenous / symbolic cueing. We propose that the outcome of ventral stream encoding of symbolic-

semantic properties of the cue interacts with consciously held goals and intentions, established via instructions given to participants and represented in frontal regions. This will be accompanied by activation of the dorsal attention network, and consequent top-down facilitation of target processing at the cued location (Bressler *et al.*, 2008; Kincade *et al.*, 2005; Lauritzen *et al.*, 2009).

A notable advantage of the model depicted in Figure 6a,b is that it explains the paradoxical observation that participants shift attention more slowly in response to an easily discriminable letter cue presented in central vision, than in response to visually similar peripheral letter cues, presented bilaterally at an eccentricity of 7° (Lambert & Duddy, 2002; Lambert *et al.*, 2006). Although we have yet to test this formally, it seems almost certain that if participants were asked to perform a conscious perceptual discrimination, which we assume will rely on ventral stream encoding, participants would respond more rapidly and accurately to stimuli presented in central vision, compared to a condition where the same stimuli are presented at an eccentricity of 7° – a pattern which is the precise reverse of that observed when the index of stimulus encoding is speed of attention shifting, rather than speed of conscious discrimination. The model presented in Figure 6 resolves this paradox in two ways. Firstly, the processing route recruited by symbolic identity cues (Figure 6b) is relatively indirect, compared with that recruited by landmark cues (Figure 6a); and secondly the processing route of the latter is mediated by the rapidly conducting M-cell inputs to the dorsal stream, whereas processing of symbolic-endogenous cues appears to be mediated by the P-cell inputs to the ventral stream, which conduct neural signals more slowly (Bullier, 2001).

In a closely related field, Wolfe and colleagues have recently outlined a two pathway model of visual search, which includes a rapid, non-selective processing route, and a slower selective processing route, together with semantic and non-semantic guidance of attention to

target locations. Wolfe, Vo, Evans & Greene (2011) conclude their paper by speculating about possible relationships between the two pathways proposed in their model and the dorsal and ventral visual streams. The visual search and spatial cueing paradigms have much in common (see Chun, 2000), so parallels between the model depicted in Figure 6 and that proposed by Wolfe *et al.* (2011) may be promising, in terms of achieving the goal of developing a general model, capable of explaining attentional behaviour across a range of task situations.

Does the distinction between landmark and identity cueing map directly onto the distinction between exogenous and endogenous attention?

The proposal that there is a direct correspondence between the identity cueing paradigm employed in Experiment 4, and other variants of the endogenous cueing paradigm (see Chica *et al.*, 2014) seems uncontroversial. In both cases, attention shifting appears to be driven by encoding the symbolic identity of the cue, as a signal indicating the probable target location.

The relationship between landmark cueing and the distinction between endogenous and exogenous attention is perhaps less straightforward. Exogenous orienting has generally been identified with attentional effects elicited by unilateral peripheral cues. In typical versions of the exogenous cueing paradigm, peripheral visual changes or stimulus onsets are employed as cues. In many studies using this paradigm, the location of the cue, is unrelated to the location of the target stimulus, and in this sense the cue is task-irrelevant (Chica, Martin-Arevalo, Botta & Lupiáñez, 2014; Posner & Cohen, 1984). Nevertheless, effects of peripheral cues on attention are assessed by comparing performance on trials where the location of the cue and target stimuli correspond, with trials where they do not. So, spatial correspondence between

cue and target is a feature common to both the unilateral cueing and landmark cueing procedures (Lambert & Duddy, 2002).

On the other hand, it might be argued that landmark cueing should be seen as a variant of endogenous cueing, because in both cases attention shifting is driven by encoding features of different cue stimuli, rather than the mere onset (or offset) of a peripheral cue. Thus, in the landmark cueing condition of Experiment 4, participants were presented with two kinds of cue (X-T or T-X), and appropriate attention shifting was contingent on encoding the distinction between them. However, findings from Experiments 4-6, together with an extensive series of earlier studies show that landmark cueing is distinct from identity (endogenous) cueing, and shares several key properties with exogenous orienting in response to unilateral peripheral cues. Firstly, the time-course of landmark cueing, like that of exogenous orienting in response to unilateral cues, can be extremely rapid (Experiment 6; Lambert & Duddy, 2002, Experiments 1,3A & 4; Marrett *et al.*, 2011). The time-course of identity cueing is somewhat slower, and resembles other variants of endogenous orienting (Lambert & Duddy, 2002, Experiments 2 & 3B). Secondly, landmark cueing effects, like exogenous orienting in response to unilateral cues, appears to be independent of conscious awareness: participants shift attention in response to landmark cues, regardless of whether they are aware or unaware of the predictive relationship between cues and targets (Experiment 6; Lambert, Norris, Naikar & Aitken, 1999, Experiments 1 & 4; Shin, Marrett & Lambert, 2011). Thirdly, landmark cueing effects, like exogenous orienting in response to unilateral cues, may be accompanied by inhibition of return effects (Lambert *et al.*, 1999, Experiments 1 & 4). Therefore, with respect to these three key features, landmark cueing tends to resemble exogenous orienting in response to peripheral cues, rather than endogenous orienting in response to symbolic cues. Moreover, whereas the key-task feature in studies of endogenous orienting is that participants must encode the *identity* of the cue stimulus, in both

landmark cueing and unilateral peripheral cueing, orienting is driven by the *location* of the cue stimulus, and the relationship between cue location and target location. These four considerations all suggest that the neural systems recruited during landmark cueing and exogenous orienting in response to peripheral onsets are likely to overlap to a substantial degree. It might even be argued that peripheral onsets or visual changes can be viewed as especially potent types of visual landmark cue (Lambert & Duddy, 2002; Shin *et al.*, 2011). Nevertheless, it is clear that further work will be required to establish the precise neurocognitive relationship between the attentional effects of bilateral landmark cues, and exogenous orienting in response to unilateral visual changes.

Conscious awareness and attention

The relationship between conscious awareness and selective attention has been an enduring source of fascination and controversy in this field (Graziano, 2013; Lamme, 2003; Kentridge, Heywood & Weiskrantz, 1999; Kentridge, Nijboer & Heywood, 2008; Webb & Graziano, 2015). Much debate has centred on the question of whether attending to something is a necessary or sufficient condition for becoming aware of that something. In a sense, the experiments described here approach the attention - consciousness relation from the opposite direction, by addressing the question of whether being aware of something is a necessary or sufficient condition for shifting attention in response to it. The answer is clear: being aware of a cue and its utility (in terms of predicting where an object of interest will appear), is neither a *necessary*, nor a *sufficient* condition for shifting attention in response to that cue.

Experiment 6, together with earlier evidence (Lambert *et al.*, 1999; Shin *et al.*, 2011) shows that participants who lacked awareness of spatially predictive cues nevertheless shifted attention appropriately in response to them. Therefore, conscious awareness of a cue, or its relation with target location is not a necessary precondition for shifting attention in response

to it. This conclusion is also consistent with a body of research investigating the *proportion validity effect*. It has been known for some time that attentional behaviour is sensitive to the predictive relationship between cue stimuli and target location: participants respond more rapidly to targets at locations indicated via cueing as more probable, and conversely respond more slowly targets appear at locations cued as less probable (Posner, 1980). Interestingly, it has been observed repeatedly that this behaviour is uncorrelated with participants' conscious awareness of the predictive link between cue stimuli and target location (Risko & Stolz, 2010; Lopez-Ramon *et al.*, 2011; Lanthier *et al.*, 2015).

Experiments 3 & 4, together with earlier evidence (Lambert *et al.*, 2006; Shin *et al.*, 2011) showed that when identity cues are presented at brief exposure times in central vision participants' *fail* to shift attention in response to them. Null findings are, of course, often uninformative and difficult to interpret. However, in this this instance, the null result may provide a key, and theoretically important datum. There is little doubt that in this situation the centrally presented cues were represented in perceptual awareness, especially since participants were informed that the cues were useful and were instructed to use them because they predicted the probable location of the next target. Hence, both perceptual awareness of the cue stimulus, and contingency awareness of its predictive value can be assumed. Despite both forms of awareness being present, participants failed conspicuously to shift attention in the relevant conditions of Experiments 3 & 4, and in two earlier studies that included similar conditions (Lambert *et al.*, 2006; Shin *et al.*, 2011). The brief exposure time, identity cueing condition of Experiment 4 (see Figure 5) is especially notable, because in this case the null effect was compared directly with effects of landmark cues presented at the same exposure time, and with effects of identity cues presented with a longer exposure time. Moreover, the inclusion of a relatively large number of participants (N=72) meant that the design was adequately powered, with respect to the task of detecting an attentional effect of briefly

exposed identity cues. Since none was observed, we conclude that awareness of a spatial cue and its predictive utility is not a *sufficient condition* for shifting attention in response to it.

The conclusion that awareness of a cue is neither a necessary nor a sufficient condition for shifting attention in response to it, warrants the further conclusion that (in some circumstances at least), conscious awareness of a cue plays no causal role in the attention shifting process elicited by that cue. Although at first blush this conclusion might seem surprising or counter-intuitive, it is, we propose, consistent with a conceptually coherent view of attention shifting mechanisms. A feature common to many theoretical perspectives is that the central function of attention is to strengthen certain representations, be they perceptions, thoughts or memories, at the expense of others (Desimone & Duncan, 1995; James, 1890; Petersen & Posner, 2012), enabling those representations to become conscious, perhaps by participating in a global neuronal workspace (Dehaene & Changeux, 2011). If the function of attention is to promote access to consciousness, a mechanism that required conscious access to stimuli in order to generate a shift of attention would seem doomed to fail, for obvious cart-before-horse reasons. Therefore, the proposal that conscious awareness has no causal role to play in the attention shifting process elicited by spatial cues is both supported by empirical evidence, and consistent with a theoretically coherent view of attention shifting mechanisms. As Michael Posner and colleagues noted several decades ago, the attention system appears to be functionally and anatomically distinct from other brain processing systems (Posner, 1978; Posner & Petersen 1990; Petersen & Posner, 2012). We propose that this separation extends to the level of visual input processing: Visual inputs that provoke a shift of attention to a new location may be represented in consciousness, perhaps because they fall within the current focus of attention, but the system responsible for generating conscious perceptual representations, and the system responsible for shifting attention appear to be functionally distinct from one another.

As explained earlier, the conclusion that visual encoding in the dorsal stream proceeds independently of conscious awareness is well supported (Milner & Goodale, 2006; Milner 2012; Chen, Sperandio & Goodale, 2015). Although visual encoding in the ventral stream is associated with conscious perception, there is also ample evidence that stimulus features, including complex, semantic attributes (Dehaene *et al.*, 2001; Lambert, Beard & Thompson, 1988), may be encoded by the ventral stream independently of conscious awareness. Moreover, it appears that proportion valid effects are uncorrelated with awareness of the cue-target relation, regardless of whether the cue stimuli are presented briefly and peripherally, and likely according to our interpretation to be encoded by the dorsal stream (Risko & Solz, 2010, Experiment 1; Lanthier *et al.*, 2015, Experiment 1), or centrally for a longer exposure duration, and likely according to our interpretation to be encoded by the ventral stream (Risko & Stolz, 2010, Experiment 2; Lanthier *et al.*, 2015, Experiment 2). Thus, the conclusion that conscious awareness of cues or cue-target relations plays no causal role in the attention shifting process that they elicit, may apply equally to landmark and identity cues, encoded by the dorsal and ventral streams, respectively.

Methodological implications

In addition to their theoretical value, the findings reported here carry an important methodological message concerning the need for careful control of stimulus parameters, in attentional cueing studies.

Visual-spatial features: Visual-spatial features of the stimuli employed as cues are crucially important. For example, in a frequently cited study, Kincade *et al.* (2005) investigated the neural correlates of attention shifting in response to exogenous and endogenous spatial cues, using an event-related fMRI design. However, in their endogenous orienting condition, the

cue stimulus comprised the transient brightening of two sides of a diamond-shape, forming an arrow-head cue pointing to the left or right. From the perspective presented here, this stimulus is clearly a landmark cue, and would be likely to recruit dorsal-stream mediated orienting, which as we have seen shares many features with exogenous orienting in response to peripheral onsets, and is quite distinct from symbolic (endogenous), ventral-stream mediated orienting. Clearly, this has serious implications, with respect to the theoretical interpretation of results reported by Kincade *et al.* (2005).

Cue exposure time: The current results indicate that cue exposure time is also a key stimulus parameter in studies of visual orienting. Experiments 1, 2 & 4 show that when cues were exposed for a relatively long period (300ms in Experiments 1 & 2; 133ms in Experiment 4), orienting effects were independent of cue visual-spatial (landmark) features, and were driven instead by its symbolic identity as a signal indicating the likely location of the target; and conversely, when cues were exposed briefly, (66ms or less), orienting effects were driven by landmark features, independently of symbolic identity (Experiments 3,4 & 6).

Cue contrast: Finally, the luminance contrast of cue stimuli appears to be an important factor. In Experiment 5, effects of identity cues collapsed when the luminance contrast of cue stimuli was low, but effects of landmark cues were robust under contrast reduction. Robust effects of low contrast, briefly presented peripheral landmark cues were also seen in Experiment 6.

In light of these findings we offer two recommendations concerning experimental method, which may be useful in future investigations of spatial cueing:

1. *To be sure of isolating endogenous orienting, driven by symbolic encoding of the cue stimulus, it is essential to use visually symmetric stimuli which are devoid of spatially predictive landmark features, and to use a relatively long cue exposure time (150ms or longer).*

2. *To be sure of isolating the contribution of exogenous orienting or landmark cueing, both of which may be mediated by dorsal stream encoding, it is necessary to use a brief cue exposure time (100ms or less). Presenting the cues under conditions of low luminance contrast may also be advisable.*

CONCLUSION

Conventionally, scientific reports tend to open by framing a set of hypotheses and predictions, which are revealed, as the paper progresses, to be uncannily accurate. The reality of scientific work is, of course very different, and is littered with failed ideas and predictions that turn out to be wrong. However, mistaken hypotheses and failed predictions rarely gain a mention in journal papers (see Chambers, Feredoes, Muthukumaraswamy, & Etchells, 2014). In the current report, the hypotheses that motivated Experiments 1 & 2, both of which turned out to be incorrect, have been described and included because of their important role in highlighting an ostensibly unpromising hypothesis, which eventually turned out to be correct (Experiments 3 & 4), and led to the development and testing of a useful new model (Experiments 4-6).

The model shown in Figure 6a,b represents two fairly straightforward theoretical proposals: that the dorsal stream is the input pathway for rapid orienting in response to visual landmark features, while the ventral stream is the input pathway for symbolically-driven, endogenous orienting. Both proposals are well supported by evidence, and are consistent with contemporary theoretical characterisations, firstly of attention shifting mechanisms, and secondly of the contrasting functions of the ventral and dorsal visual stream. Therefore, we propose that there is a simple one-to-one relationship between, on the one hand the distinction between rapid orienting in response to exogenous / landmark cues and slow

orienting in response to endogenous / symbolic cues, and on the other hand, the distinct functions performed by the dorsal and ventral visual streams. Although exogenous orienting elicited by unilateral peripheral cues and landmark cueing, examined in designs with bilateral cues, share several key features, leading us to suspect strong overlap in their underlying neurocognitive mechanisms, further work is needed to clarify the precise relationship between attention shifting in these two experimental paradigms. Further work will also be required to clarify the relationship between visual input pathways, and another important class of attention movements, those elicited by social stimuli.

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REFERENCES

- Bakeman, R. (2005). Recommended effect size statistics for repeated measures designs. *Behavior Research Methods*, 37, 379-384.
- Bressler, S.L., Tang, W., Sylvester, C.M., Shulman, G.L. & Corbetta, M. (2008). Top-down control of human visual cortex by frontal and parietal cortex in anticipatory visual spatial attention. *Journal of Neuroscience*, 28(40), 10056-10061.
- Brown, L.E., Halpert, B.A. & Goodale, M.A. (2005). Peripheral vision for perception and action. *Experimental Brain Research*, 165, 97-106.
- Bullier, J. (2001). Integrated model of visual processing. *Brain Research Reviews*, 36, 96-107.
- Carlson, T. A., Simmons, R. A., Kriegeskorte, N. & Slevc, L. R. (2014). The emergence of semantic meaning in the ventral temporal pathway. *Journal of Cognitive Neuroscience* 26, 120-131.
- Chambers, C.D., Feredoes, E., Muthukumaraswamy, S.D. & Etchells, P.J. (2014). Instead of “playing the game” it is time to change the rules: Registered Reports at AIMS Neuroscience and beyond (Editorial). *AIMS Neuroscience*, 1, 4-17.
- Chen, J., Sperandio, I. & Goodale, M.A. (2015). Differences in the Effects of Crowding on Size Perception and Grip Scaling in Densely Cluttered 3-D Scenes. *Psychological Science*, 26, 58–69.
- Chica, A.B., Bartolomeo, P. & Lupiáñez, J. (2013). Two cognitive and neural systems for endogenous and exogenous spatial attention. *Behavioural Brain Research* 237, 107–123.

- Chica, A.B., Martín-Arévalo, E., Botta, F. & Lupiáñez, J. (2014). The Spatial Orienting paradigm: How to design and interpret spatial attention experiments. *Neuroscience and Biobehavioral Reviews* 40, 35– 51.
- Chun, M.M. (2000). Contextual cueing of visual attention. *Trends in Cognitive Sciences*, 4, 170-178.
- Cohen, J. (1988). *Statistical power analysis for the behavioral sciences (2nd ed.)*. Hillsdale, NJ: Erlbaum.
- Colby, C.L., Gatass, R., Olson, C.R. & Gross, C.G. (1988). Topographical organization of cortical afferents to extrastriate area PO in the macaque: A dual tracer study. *The Journal of Comparative Neurology*, 269, 392-413.
- Corbetta M, Shulman GL. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3, 201–215.
- de Haan, B., Morgan, P.S. & Rorden, C. (2008). Covert orienting of attention and overt eye movements activate identical brain regions. *Brain Research*, 1204, 102-111.
- Dehaene, S. & Changeux, J-P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron*, 70, 200-227.
- Dehaene, S., Changeux, J.P., Naccache, L., Sackur, J., and Sergent, C. (2006). Conscious, preconscious, and subliminal processing: A testable taxonomy. *Trends in Cognitive Sciences*, 10, 204–211.
- Dehaene, S., Naccache, L., Cohen, L., Bihan, D.L., Mangin, J.F., Poline, J.B., and Rivière, D. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience*, 4, 752–758.

- Dennett, D.C. (2013). *Intuition Pumps and Other Tools for Thinking*. New York: W.W. Norton & Company.
- Desimone, R & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193-222.
- Findlay, J.M. & Gilchrist, I.D. (2003). *Active Vision: The psychology of looking and seeing*. New York: Oxford University Press.
- Fischer, M. H., Castel, A. D., Dodd, M. D., & Pratt, J. (2003). Perceiving numbers causes spatial shifts of attention. *Nature Neuroscience*, *6*, 555–556.
- Galfano, G., Rusconi, E. & Umiltà, C. (2006). Number magnitude orients attention, but not against one's will. *Psychonomic Bulletin & Review*, *13* (5), 869-874.
- Graziano, M.S.A. (2013). *Consciousness and the Social Brain*. Oxford: Oxford University Press.
- Hommel, B., Pratt, J., Colzato, L., & Godijn, R. (2001). Symbolic control of visual attention. *Psychological Science*, *12*, 360–365.
- Hubbard, E.M., Piazza, M., Pinel, P. & Dehaene, S. (2005). Interactions between number and space in parietal cortex. *Nature Reviews Neuroscience*, *6*, 435-448.
- Jiang, Y.V., Won, B-Y. & Swallow, K.M. (2014). First saccadic eye movement reveals persistent attentional guidance by implicit learning. *Journal of Experimental Psychology: Human Perception & Performance*, *40*, 1161-1173.
- Kentridge, R. W., Heywood, C. A., & Weiskrantz, L. (1999). Attention without awareness in blindsight. *Proceedings of the Royal Society of London, Series B*, *266*, 1805–1811.
- Kentridge, R.W., Nijboer, T.C.W. & Heywood, C.A. (2008). Attended but unseen: Visual attention is not sufficient for visual awareness. *Neuropsychologia*, *46*, 864–869.

- Klein, R.M. (2004). On the control of visual orienting. In M.I. Posner (Ed.), *Cognitive Neuroscience of Attention*, (pp.29-44). New York: The Guilford Press.
- Kronbichler, M., Klackl, J., Richlan, F., Schurz, M., Staffen, W., Ladurner, G. & Wimmer, H. (2008). On the Functional Neuroanatomy of Visual Word Processing: Effects of Case and Letter Deviance. *Journal of Cognitive Neuroscience* 21, 222–229.
- Lambert, A.J. (2003). Visual attention and conscious awareness. In L.Jimenez (Ed.), *Attention and Implicit Learning* (pp.253-276). John Benjamins Publishing: London.
- Lambert, A.J. Beard, C.T. & Thompson, R.J. (1988). Selective attention, visual laterality and perceiving the meaning of parafoveally presented words. *Quarterly Journal of Experimental Psychology*, 40A, 615-652.
- Lambert, A. J., & Duddy, M. (2002). Visual orienting with central and peripheral precues: Deconfounding the contributions of cue eccentricity, cue discrimination and spatial correspondence. *Visual Cognition*, 9, 303-336.
- Lambert, A. J., Naikar, N., McLachlan, K., & Aitken, V. (1999). A new component of visual orienting: Implicit effects of peripheral information and sub-threshold cues on covert attention. *Journal of Experimental Psychology: Human Perception and Performance*, 25, 321-340.
- Lambert, A.J., Norris, A., Naikar, N. & Aitken, V. (2000). Effects of informative peripheral cues on eye movements: Revisiting William James’ “derived attention”. *Visual Cognition*, 7, 545-569.
- Lambert, A. J., Roser, M., Wells, I., & Heffer, C. (2006). The spatial correspondence hypothesis and orienting in response to central and peripheral precues. *Visual Cognition*, 13, 65-88.

- Lambert, A.J. & Shin, M-J. (2010). The hare and the snail: Dissociating visual orienting from conscious perception. *Visual Cognition*, 18, 829-838.
- Lambert, A.J. & Wootton, A. (2016). The time-course of activation in the dorsal and ventral visual streams during landmark cueing and perceptual discrimination tasks. *Submitted for publication*.
- Lambert, A.J., Wootton, A., Ryckman, N. & Wilkie, J. (2014). *Role of the Dorsal Visual Stream in Shifting Attention in Response to Peripheral Visual Information*. Poster presented to the 12th International Cognitive Neuroscience Conference, Brisbane, Australia. July 2014.
- Lamme, V.A.F. (2003). Why visual attention and awareness are different. *Trends in Cognitive Sciences*, 7, 12-18.
- Lanthier, S.N., Wu, D.W., Chapman, C.S. & Kingstone, A. (2015). Resolving the controversy of the proportion validity effect: Volitional attention is not required, but may have an effect. *Attention, Perception & Psychophysics*, 77, 2611–2621.
- Lauritzen, T.Z., d’Esposito, M., Heeger, D.J. & Silver, M.A. (2009). Top-down flow of visual spatial attention signals from parietal to occipital cortex. *Journal of Vision*, 9(13):18, 1–14.
- Livingstone, M. & Hubel, D. (1988). Segregation of Form, Color, Movement, and Depth: Anatomy, Physiology, and Perception. *Science*, 240, No. 4853 (May 6, 1988), 740-749.
- López-Ramón, M. F., Chica, A. B., Bartolomeo, P., & Lupiáñez, J. (2011). Attentional orienting and awareness: Evidence from a discrimination task. *Consciousness and Cognition*, 20, 745–755. doi: 10.1016/j.concog.2010.10.024

- MacLean, G.H; Klein, R.M. & Hilchey, M.D. (2015). Does oculomotor readiness mediate exogenous capture of visual attention? *Journal of Experimental Psychology: Human Perception and Performance*, *41*, 1260-1270.
- Marrett, N.E., de-Wit, L.H. Roser, M.E., Kentridge R.W., Milner, A.D. & Lambert, A.J. (2011). Testing the dorsal stream attention hypothesis: Electrophysiological correlates and the effects of ventral stream damage, *Visual Cognition*, *19*, 1089-1121.
- Merigan, W. H., & Maunsell, J. H. R. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, *16*, 369-402.
- Milner, A.D. (2012). Is visual processing in the dorsal stream accessible to consciousness? *Proceedings of the Royal Society of London - Series B: Biological Sciences*. 279(1737), 2289-2298.
- Milner, A. D., & Goodale, M. A. (2006). *The Visual Brain in Action (2nd ed)*. Oxford, UK: Oxford University Press.
- Muller, H.J. & Rabbitt, P.M.A. (1989). Reflexive and voluntary orienting of visual attention: time-course of activation and resistance to interruption. *Journal of Experimental Psychology: Human Perception & Performance*, *15*, 315-330.
- Peelen, M.V. & Caramazza, A. (2012). Conceptual object representations in human anterior temporal cortex. *Journal of Neuroscience*, *32*, 15728-15736.
- Petersen, S.E. & Posner, M.I. (2012). The attention system of the human brain: 20 years after. *Annual Review of Neuroscience*, *35*, 73-89.
- Popper, K.R. (1959). *The Logic of Scientific Discovery*. London Hutchinson.
- Posner, M. I. (1978). *Chronometric Explorations of Mind*. Oxford: Lawrence Erlbaum.

- Posner, M.I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, 32, 3-25.
- Posner, M.I & Cohen, Y. (1984). Components of attention. In H. Bouma & D.G. Bouwhuis (Eds.), *Attention & Performance, Vol. 10*, (pp. 531-556). Hillsdale, NJ: Erlbaum.
- Posner, M.I., Petersen, S.E. 1990. The attention system of the human brain. *Annual Review of Neuroscience*, 13, 25–42.
- Posner, M.I., Snyder, C.R.R. & Davidson, B.J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology: General*, 109, 160-174.
- Pratt, J., Radulescu, P., Guo, R.M. & Hommel, B. (2010). Visuospatial Attention Is Guided by Both the Symbolic Value and the Spatial Proximity of Selected Arrows. *Journal of Experimental Psychology: Human Perception and Performance*, 36, 1321–1324.
- Ptak, R. & Schneider, A. (2010). The Dorsal Attention Network Mediates Orienting toward Behaviorally Relevant Stimuli in Spatial Neglect. *Journal of Neuroscience*, 30(38), 12557–12565.
- Risko, E., & Stolz, J. (2010). The proportion valid effect in covert orienting: Strategic control or implicit learning? *Consciousness and Cognition*, 19, 432-442.
- Ristic, J., Wright, A., Kingstone, A. (2006). The number line effect reflects top-down control. *Psychonomic Bulletin & Review*, 13 (5), 862-868.
- Rizzolatti, G., & Craighero, L. (1998). Spatial attention: Mechanisms and theories. *Advances in Psychological Science*, 2, 171–198.
- Rizzolatti, G., Riggio, L., Dascola, I., Umiltà, C., 1987. Reorienting attention across the horizontal and vertical meridians — evidence in favor of a premotor theory of attention. *Neuropsychologia* 25, 31–40.

- Robson, A.G. & Kulikowski, J.J. (2012). Objective assessment of chromatic and achromatic pattern adaptation reveals the temporal response properties of different visual pathways. *Visual Neuroscience*, *29*, 301–313.
- Seghier, M.L., Neufeld, N.H, Zeidman, P., Leff, A.P., Mechelli, A., Nagendran, A., Riddoch, J.M., Humphreys, G.W. & Price, C.J. (2012). Reading without the left ventral occipito-temporal cortex. *Neuropsychologia*, *50*, 3621–3635.
- Shapley, R., Kaplan, E. & Soodak, R. (1981). Spatial summation and contrast sensitivity of X and Y cells in the lateral geniculate nucleus of the macaque. *Nature* *292*, 543-545.
- Shin, M-J., & Lambert, A.J. (2012). Effects of varying target luminance and cue luminance on attentional effects of spatial cues. *Visual Cognition*, *20*, 1095-1109.
- Shin, M-J., Marrett, N. & Lambert, A.J. (2011). Visual orienting in response to attentional cues: Spatial correspondence is critical, conscious awareness is not. *Visual Cognition*, *19*, 730-761.
- Smith, D. T., Rorden, C., & Jackson, S. R. (2004). Exogenous orienting of attention depends upon the ability to execute eye movements. *Current Biology*, *14*, 792–795.
<http://dx.doi.org/10.1037/a0027794>
- Smith, D. T., Schenk, T., & Rorden, C. (2012). Saccade preparation is required for exogenous attention but not endogenous attention or IOR. *Journal of Experimental Psychology: Human Perception and Performance*, *38*, 1438–1447.
<http://dx.doi.org/10.1037/a0027794>
- Ungerleider, L.G. & Mishkin, M. (1982). Two cortical visual systems. In D.J. Engle, M.A. Goodale, & R.J. Mansfield (Eds.), *Analysis of Visual Behavior* (pp. 549-586). Cambridge, MA: MIT Press.

- Webb, T.W. & Graziano, M.S.A. (2015). The attention schema theory: A mechanistic account of subjective awareness. *Frontiers in Psychology*. Vol.6 Apr 2015, ArtID 500.
- Wolfe, J.M., Vo, M.L-H., Evans, K.K. & Greene, M.R. (2011). Visual search in scenes involves selective and nonselective pathways. *Trends in Cognitive Sciences* 15, 77-84.
- Wright, R.D. & Ward, L.M. (2008). *Orienting of Attention*. Oxford: Oxford University Press.

LIST OF FIGURE CAPTIONS

Figure 1. Mean response times in Experiment 1. Error bars represent the standard error of the difference in response times between valid and invalid trials.

Figure 2. Mean response times in Experiment 2. Error bars represent the standard error of the difference in response times between valid and invalid trials.

Figure 3. Mean response times in Experiment 3. Error bars represent the standard error of the difference in response times between valid and invalid trials.

Figure 4. Participants performed two cueing tasks in Experiment 4. The *Landmark Cueing* task is illustrated in the upper panel (a); the *Identity Cueing* task is illustrated in the lower panel (b).

Figure 5. Mean response times in Experiment 4. Error bars represent the standard error of the difference in response times between valid and invalid trials.

Figure 6. A model of the neurocognitive processes and pathways responsible for shifting attention in response to environmental cues. Dorsal stream-based visual orienting is represented in panel (a); ventral stream-based visual orienting is represented in panel (b).

Figure 1

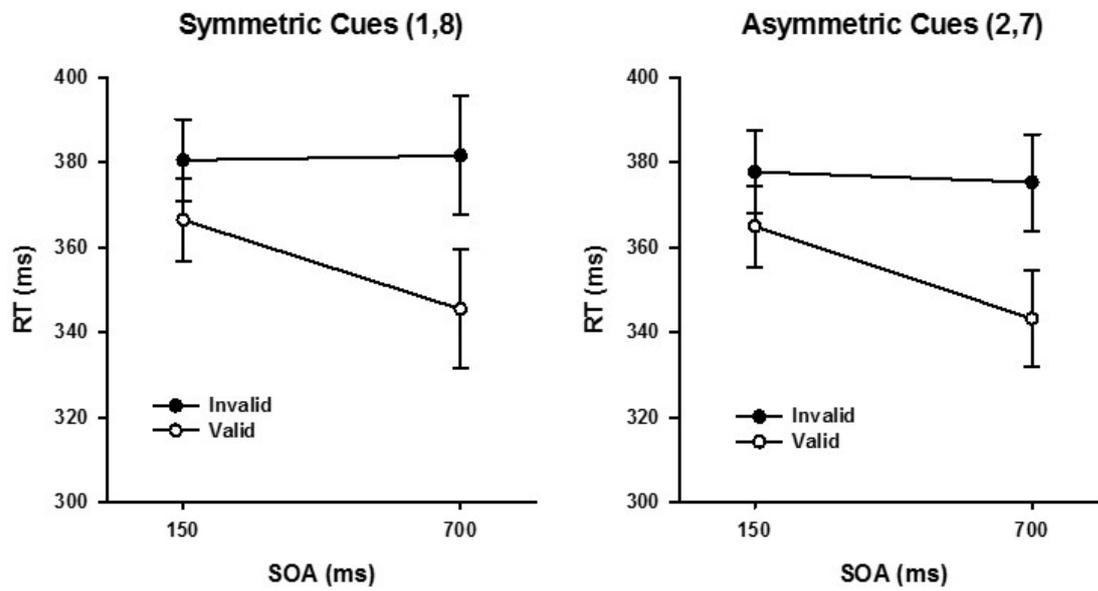


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Figure 2

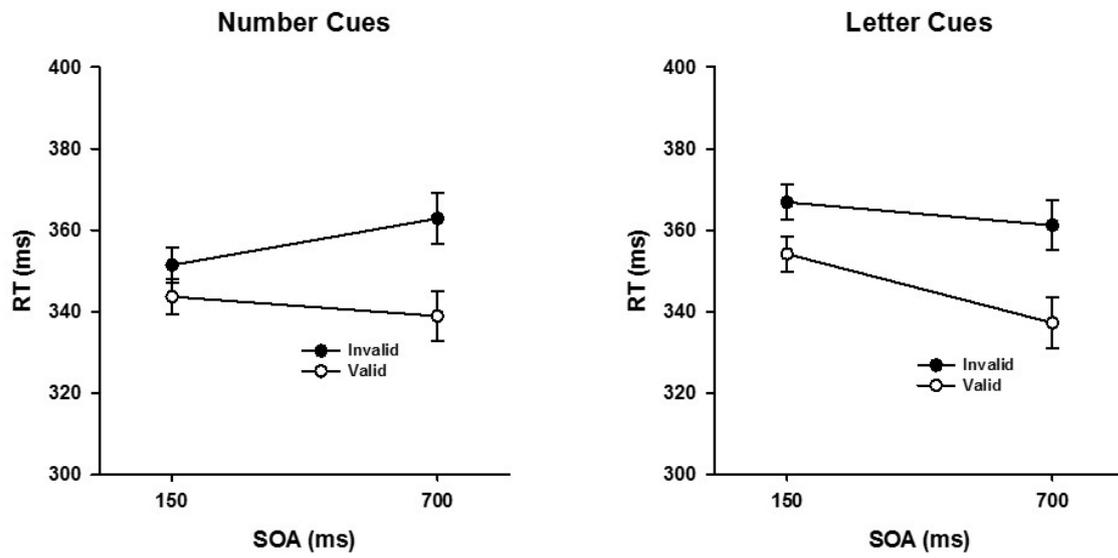


Figure 2. Mean response times in Experiment 2. Error bars represent the standard error of the difference in response times between valid and invalid trials.

Figure 3.

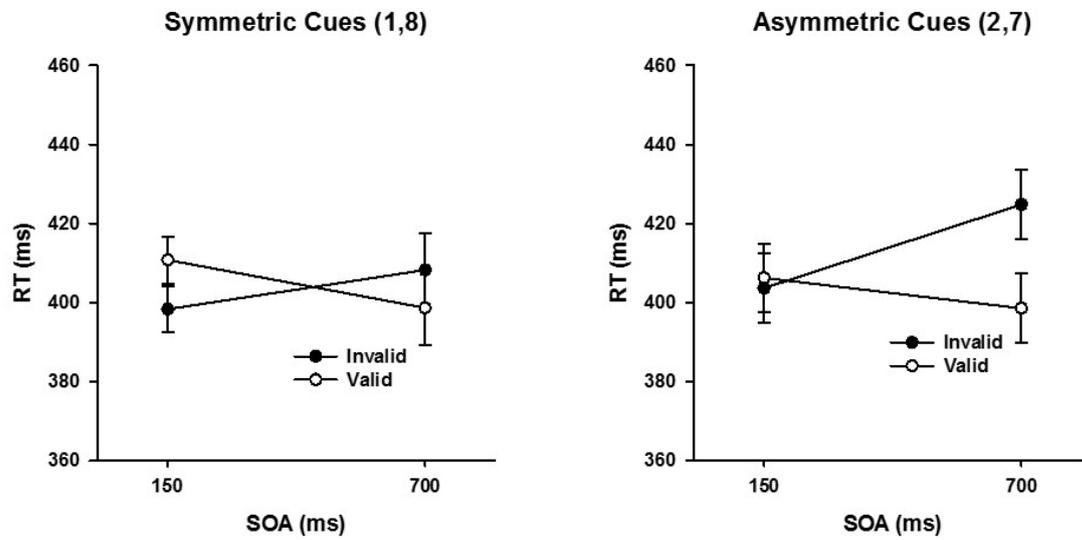


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Figure 4

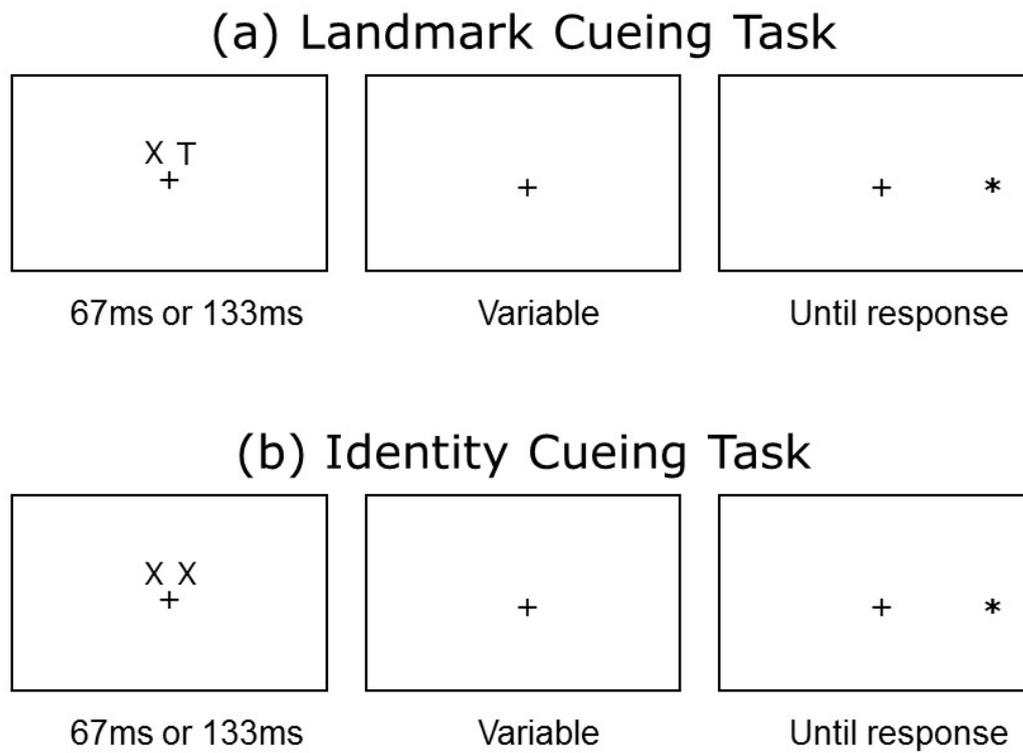


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Figure 5

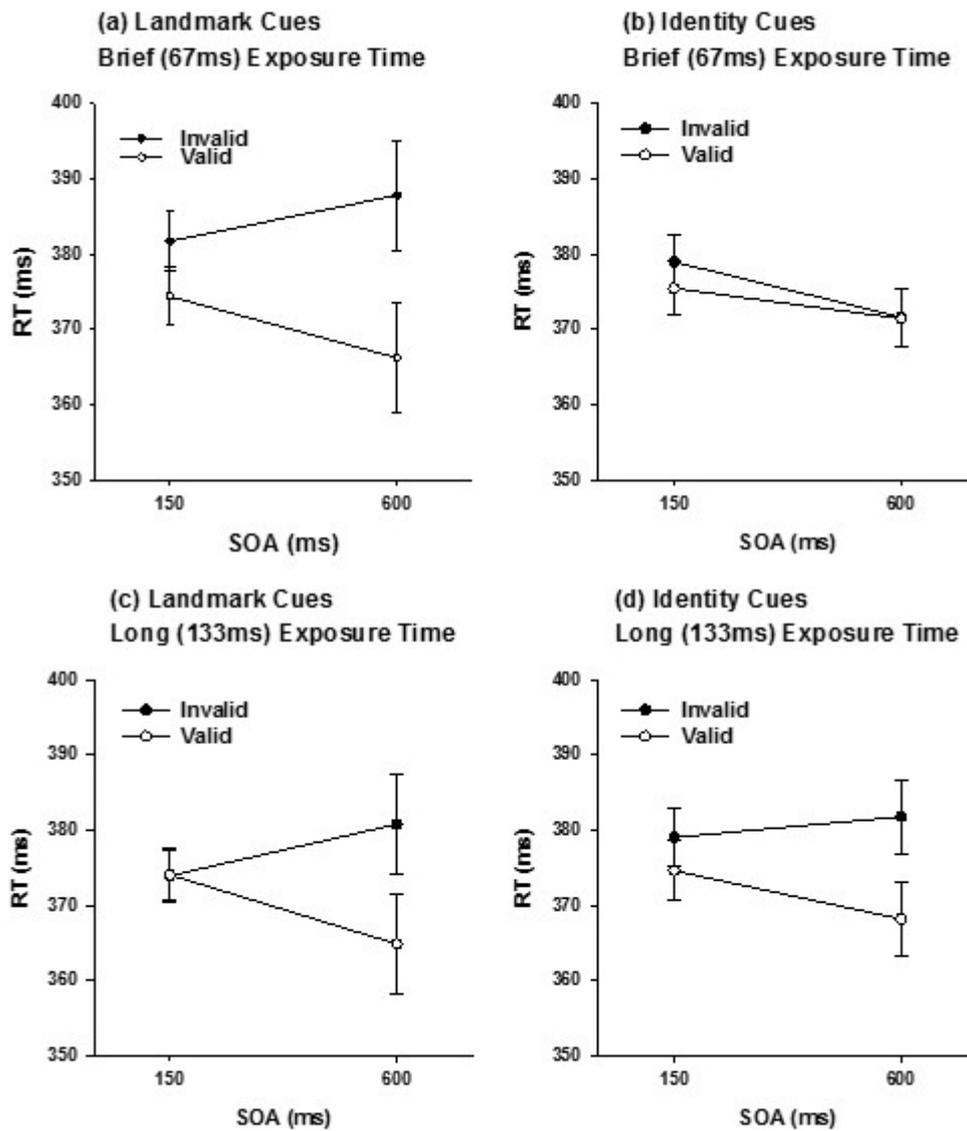
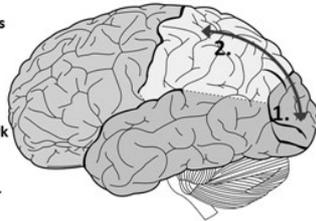


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Figure 6

(a) LANDMARK CUEING - attention movements driven by dorsal stream encoding of visual-spatial features

1. Dorsal stream encoding of visual-spatial (landmark) features of environmental cues interacts with parietal attention circuits.
2. Attentional expectancies, established by predictive associations between landmark features and target locations, and represented in parietal attention circuits, leads to top-down facilitation of target processing at the cued location.



(b) IDENTITY CUEING - attention movements driven by symbolic encoding of information in the visual environment

1. Ventral stream encodes semantic-symbolic features of environmental cues.
2. The outcome of symbolic processing interacts with conscious goals, and recruits the fronto-parietal attention network.
3. Activity in the dorsal component of the fronto-parietal attention network generates top-down facilitation of target processing at the cued location.

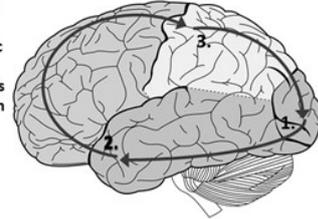


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