

"©American Psychological Association, [2017]. This paper is not the copy of record and may not exactly replicate the authoritative document published in the APA journal: Journal of Experimental Psychology: Human Perception & Performance. Please do not copy or cite without author's permission. The final article is available, upon publication, at: <http://dx.doi.org/10.1037/xhp0000474> "

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

Word count: 16,090

Anthony J. Lambert, Jaimie Wilkie, Andrea Greenwood, Nathan Ryckman, Evatte Sciberras-Lim, Laura-Jane Booker and Lenore Tahara-Eckl,

Research Centre for Cognitive Neuroscience and School of Psychology,

University of Auckland, New Zealand.

Running heading: Control of Attention

Corresponding author: Anthony J. Lambert, School of Psychology, University of Auckland,
Private Bag 92019, Auckland 1142, New Zealand.

Email: a.lambert@auckland.ac.nz.

Tel: +64 9 373 7599, ext. 88520

Mobile + 64 21 161 2980.

Fax: +64 9 373 7450

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 Experiment 1 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 2-6. 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

STATEMENT OF PUBLIC SIGNIFICANCE

Intriguingly, visual processing in the brain involves an *unconscious* pathway, as well as a pathway that delivers conscious visual experience. Although both pathways can be involved when visual attention shifts from one location to another, according to the theory described in this paper, an important function of the unconscious pathway is to guide rapid shifts of attention and eye movements. We describe six experiments that provided findings consistent with this theory. Moreover, this approach implies that conventional assessment methods, which involve asking individuals to report what can be seen *consciously*, provide an incomplete picture of visual functioning. Therefore, in addition to improving our theoretical understanding of vision and attention, we hope that this work will have practical value, by suggesting methods for assessing unconscious vision, by measuring eye movement behaviour.

[130 words]

A colleague once remarked to the first author, “There are only two kinds of people – there are those who think there are two kinds of people, and those who don’t”. In addition to being an amusing example of mental recursion, this remark highlights the popularity of simple binary categories in psychological theorising, both folk and systematic. In this paper we examine two theoretical dichotomies, which have been highly influential in studies of vision and attention respectively, and argue that the relationship between them may be surprisingly simple. Vision research has been influenced strongly by two-pathway theories (Milner & Goodale, 2006; Ungerleider & Mishkin, 1982) inspired by the anatomical division of cortical visual processing into two pathways, known as the dorsal and ventral visual streams. In the closely related field of visual attention, theorising has been heavily influenced by dual-mechanism models which distinguish between a rapid attention-shifting mechanism, known as exogenous or stimulus-driven attention, and a slower mechanism termed endogenous or goal-driven attention (Chica, Bartolomeo, & Lupiáñez, 2013; Corbetta & Shulman, 2002; Klein, 2004; Wright & Ward, 2008).

We describe six experiments, each of which produced results consistent with two relatively straightforward theoretical proposals:

1. Rapid, non-conscious shifts of attention are associated with visual encoding of landmark information by the dorsal visual stream.
2. A slower form of attention shifting, corresponding to endogenous orienting, is associated with encoding the symbolic-identity of visual cues by the ventral visual stream.

In this context, we use the term ‘landmark’ to refer to a visual feature that has a predictive *spatial relationship* with an object of interest; our proposals are illustrated in the model shown in Figure 1. As this figure shows, our central thesis is that a two-process view of

visual orienting can be mapped quite directly onto the cortical division of visual processing into parallel pathways, known as dorsal and ventral visual streams.

***** **Figure 1 about here** *****

Vision: In vision research, dual-pathway models, based on the anatomical division of cortical visual processing into distinct dorsal and ventral visual streams have attracted much interest. The latter refers to a network of visual processing areas linking primary visual cortex (V1) with inferotemporal cortex; the former comprises a network of visual areas linking V1 with posterior parietal cortex. Ungerleider & Mishkin (1982) described effects of visual stream lesions in rhesus monkeys, and found that 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. According to the theory developed on the basis of these findings, the ventral stream can be described as the ‘what pathway’, because it appears to be specialised for encoding the identity of visual objects, while the dorsal stream is characterised as the ‘where pathway’, because it appears to be specialised for encoding visual locations and spatial relationships.

In more recent decades, Ungerleider and Mishkin’s (1982) perspective has been to some extent superseded by the theory of Milner and Goodale (2006), which offers a rather different view of the functional distinction between the two 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 (2006), visual representations encoded by the dorsal stream play a critical role in

rapid, on-line control of visually guided actions, such as reaching and grasping. Moreover, Milner (2012) reviewed evidence in support of the proposal that dorsal stream visual processing that supports such movements is independent of, and inaccessible to, conscious awareness. In this paper we develop the idea that saccadic eye movements and rapid shifts of covert attention can be viewed within Milner and Goodale's framework as visually guided actions, largely under the control of the dorsal stream.

Attention: Research and theorising in the closely related field of visual attention, and more specifically concerning the dynamics of visual orienting – movements in the focus of attention – have been influenced strongly by findings obtained from spatial cueing tasks developed by Michael Posner, several decades ago (Posner, 1978; Posner & Cohen, 1984; Posner, Snyder & Davidson, 1980). In the 'central cueing' variant of this task, participants are presented with a stimulus (e.g. an arrow) in central vision that signals the location of a target object, presented shortly afterwards. On most trials, the target appears at the location indicated by the cue – these are referred to as valid trials – but, occasionally the target appears at an alternate location – these are referred to as invalid trials. In a second variant of the task, the cue stimulus is presented peripherally. Here, a valid trial is one where cue and target are presented at a similar location; and an invalid trial occurs when cue and target are presented at different locations. In both these cases, an improvement in accuracy or speed of responding when targets appear at the valid location, relative to invalid trials, is taken to indicate that participants have shifted attention in response to the cue (Wright & Ward, 2008). A critical difference between the two paradigms is that in the case of central cues, orienting appears to be driven by encoding the identity and meaning of the cue, as a signal that the target is likely to appear at a specific location (e.g. on the left or right of the screen). For this reason, cues of this general kind are sometimes described as 'symbolic cues' (Hommel *et al.*, 2001; Pratt, *et al.*, 2010). However, in the peripheral cueing task the likely location of the

target is marked directly by the cue. In this case, attention movements are driven not by the *identity* of the cue, but by its *location* with respect to the target.

The central and peripheral cueing procedures just described are associated theoretically with two related, but distinct attentional control mechanisms, known as endogenous and exogenous orienting respectively. Central cues are thought to elicit endogenous orienting, which has been described as a relatively slow process that is under voluntary control (Chica et al., 2013; Klein, 2004; Wright & Ward, 2008). Peripheral cues, in contrast are thought to elicit exogenous orienting, which appears to be rapid and non-conscious (Chica et al., 2013; Klein, 2004; Wright & Ward, 2008).

Broad parallels between the two theoretical frameworks just described are readily apparent. Ventral stream processing and encoding of central cues are both associated with conscious awareness, with (relatively) slow visual processing, and with encoding the identity and meaning of stimuli in central vision. Conversely, dorsal stream processing and encoding of peripheral cues are both associated with non-conscious processing, with (relatively) rapid encoding, and with processing of information about location and spatial relationships. Although these parallels are readily apparent to anyone familiar with introductory psychology, it is also true that they did not become fully apparent to *us* until we had completed the work described below. As will be seen, although our final theoretical destination was a simple model, the empirical route to this proposal was quite circuitous.

PREAMBLE: EXPERIMENTS 1A, 1B & 1C

Our first series of experiments addressed a troubling inconsistency in the attention literature concerning effects of central cues on attention (Lambert, Roser, Wells & Heffer 2006; Fischer, Castel, Dodd & Pratt, 2003). Lambert *et al.* (2006) tested the hypothesis that visual orienting in response to central cues may be influenced not only by the *meaning* of the cue as

a signal for target location, but also by its *visuospatial features*, and associations between those features and target location. To test this hypothesis, attentional effects of central cues that included a visual feature that corresponded spatially with target location, were compared with effects elicited by cues that were devoid of such features. In the former condition, the letter ‘d’ served as the cue for a left target, while ‘b’ was the cue for a right target. One can readily see that the leftward or rightward curving portion of each letter (d or b) corresponded spatially with the likely location of the target. In the terminology adopted here, these visual elements are ‘landmark features’, spatially associated with target location. Effects of these cues were compared with those elicited by laterally symmetric letters (X,T,v,o), which were devoid of landmark features that could be associated with left and right target locations. It was found that the presence or absence of landmark features did indeed influence visual orienting. Surprisingly, attentional effects of visually symmetric cues that lacked spatial landmarks were not merely reduced, compared to those elicited by cues containing landmarks - cues that lacked visual landmarks failed to influence attention at all, even when the delay between cue and target onset was relatively long, and participants had 400-500ms to prepare and execute a shift of attention. (see also Shin, Marrett & Lambert, 2011). In this situation attention-shifting appeared to be driven *exclusively* by the visual-spatial landmark features of the cue. As the authors noted, this appears to be an important result for two reasons. Firstly, exclusive dependence of orienting on *visual-spatial* features of central cues appeared inconsistent with the view that orienting in response to such cues is driven by encoding their *symbolic identity*, as the signal for a target at a specific location. Secondly, a large proportion of the many hundreds of central cueing studies (see Chica *et al.*, 2013,2014; Corbetta & Shulman, 2002; Klein, 2004; Wright & Ward, 2008) published since Posner’s seminal work (Posner, 1978) have employed stimuli such as arrows, or arrow-heads as central cues – stimuli which are, of course strongly asymmetric and that include obvious landmark features.

This raised the possibility that orienting effects observed in these studies could have been driven, not by encoding the symbolic identity of the cue, as implied by standard accounts of endogenous orienting, but by encoding its visual-spatial landmark features.

Although an interpretation of orienting in terms of encoding spatial landmark features was feasible for any study using central cues that were visually asymmetric, the literature on spatial cueing is extensive, and includes not only studies documenting visual orienting in response to asymmetric cues, such as arrow-like stimuli, but also a number of studies documenting reliable orienting effects in response to central cues that are visually symmetric. A striking example of work in the latter category, concerns attention shifts 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. This was interpreted as reflecting 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 subsequent explorations of number cueing effects (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 and those reported by our own group (Lambert *et al.*, 2006; Shin *et al.*, 2011) were mutually inconsistent.

The aim of Experiments 1A – 1C was to resolve this inconsistency, by systematically evaluating possible explanations for the differing results reported by Lambert *et al.* (2006) and Fischer *et al.* (2003). Experiment 1A assessed effects on attention of single digits, the stimuli used by Fischer *et al.* (2003). Critically, effects of cue symmetry, were evaluated by comparing effects of the visually asymmetric digits 2 and 7, which included landmark features associated with target location, with effects of the visually symmetric digits 8 and 1 (where ‘1’ was rendered as a single vertical line). This design enabled us to compare directly the influence of semantic value (high vs. low digits) and visuospatial features (symmetric vs. asymmetric features) on visual orienting in response to central digit cues. The outcome were unequivocal: orienting was driven exclusively by semantic value, with no effect of visuospatial features. These results were consistent with Fischer *et al.* (2003), but inconsistent with Lambert *et al.* (2006). Experiment 1B tested the hypothesis that the discrepancy between these two studies arose because digits were employed as cues in the former study, while letters served as cues in the latter case. We hypothesised that the well-documented close neurocognitive links between numerical and spatial processing (Hubbard, Piazza, Pinel & Dehaene, 2005) may render digits more effective than letters, as cues for spatial attention, leading to the observation of semantically driven effects by Fischer *et al.* (2003) and visuospatially driven effects by Lambert *et al.* (2006). Effects of visually symmetric number cues (1 vs. 8) and visually symmetric letter cues (I vs. X) were compared. If our hypothesis was correct, results from the latter condition should replicate Lambert *et al.* (2006), with symmetric letter cues failing to influence attention, and results from the former condition should replicate Fischer *et al.* (2003), with symmetric number cues eliciting reliable orienting. Once again, the results were unequivocal: symmetric cues affected attention reliably, regardless of cue category. This result forced us to consider a hypothesis that had seemed unlikely at the outset: that the discrepancy between the findings of Fischer *et al.*

(2003) and of Lambert et al. (2006) was driven by an ostensibly minor methodological difference between the two studies: the exposure duration of the cue stimuli. This was relatively long (300ms) in the study of Fischer et al. (2006), and quite brief (66ms) in the study of Lambert et al. (2006). Although this hypothesis was prompted by considerations that were purely empirical, as will be seen, the results turned out to be theoretically informative. In Experiment 1C, cue exposure duration was reduced to 66ms, and participants were presented with symmetric and asymmetric number cues, as in Experiment 1A. If the empirical discrepancy described above was driven by variation in cue exposure time, then findings from Experiment 1C should resemble those reported by Lambert et al. (2006). This hypothesis was confirmed: Participants shifted attention appropriately in response to visually asymmetric number cues (2 & 7), which included landmark features spatially associated with target location, but failed to shift attention in response to visually symmetric number cues (1 & 8) that were devoid of landmark features.

In summary, findings from our first series of experiments resolved the discrepancy between Lambert et al. (2006) and Fischer et al. (2003) in an unexpected way: When cues were presented briefly (for 66ms), orienting effects were driven by landmark features (visual features of the cue stimulus associated spatially with target location), and were unaffected by cue semantics – its meaning as a signal indicating the likely location of the target; but, when cues were presented for a longer period (300ms), orienting effects were driven by cue semantics, and were unaffected its visuospatial attributes. Although this finding emerged from the simple process of noting an empirical pattern, the association already noted between dorsal stream processing and encoding visual-spatial landmarks, and between ventral stream processing and encoding stimulus identity and symbolic-semantic features, led firstly to development of the model illustrated in Figure 1, and secondly to a series of predictions deduced from the model, which were tested in Experiments 2-6.

In response to editorial concerns regarding length, full descriptions of Experiments 1A-1C have been omitted from the main body of this paper. However, comprehensive details of these experiments are available to interested readers – see *Supplementary Materials*).

Why is cue exposure duration important?

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 1A-1C, 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 the location of an object of interest.

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 Experiments 1A-1C, together with our earlier findings (Lambert *et al.*, 2006; Shin *et al.*, 2011, Experiments 1 & 2) indicate that when cues are presented with a brief exposure time, visual orienting is insensitive to symbolic features of the cue. In the view of many authors symbolic attributes are encoded in the ventral stream, but are beyond the encoding repertoire of the dorsal stream (Peelen & Caramazza, 2012; Milner & Goodale, 2006). Thus, 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 learning the association between those features and target location (Experiment 1C; Lambert *et al.*, 2006; Shin *et al.*, 2011). A very different pattern was observed in Experiments 1A & 1B, 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. We propose that in this situation, visual orienting is driven by ventral stream encoding of the symbolic identity of the cue.

TESTING THE MODEL

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 Experiments 2-6 was to test this proposal, illustrated diagrammatically in Figure 1, by generating a series of predictions based on physiological characteristics of the dorsal and ventral visual streams.

Our general strategy was to study visual orienting performance in two task settings. In the *Landmark Cueing* task, illustrated in the upper panel of Figure 2, two different cue letters (X and T, or V and O) were presented bilaterally, and participants either made a simple detection response to a subsequent target that could appear on the left or right of the screen (Experiment 2,3,5,6), or moved their eyes in order to discriminate a target on the left or right (Experiment 4). Target stimuli were likely to appear on the same side as one of the cues (the visual landmark), but occasionally appeared at the alternate location. These constituted valid and invalid trials respectively. We hypothesised that under conditions that favour dorsal stream encoding, attention shifting in this situation will be driven by dorsal stream encoding of the visual landmark information available in the cue.

***** **Figure 2 about here** *****

In the *Identity Cueing* task, illustrated in the lower panel of Figure 2, the cue stimulus comprised two identical letters, and targets were more likely to appear on the right of the display following one letter pair (e.g. X X), and on the left following an alternate letter pair

(e.g. T T). Because these cues are perfectly symmetric and devoid of landmark features spatially associated with target location, visual orienting in this situation requires encoding the identity of the cue stimulus. We hypothesised that under conditions that favour ventral stream encoding, visual orienting in this situation will be driven by ventral stream encoding of the cue as a symbol, indicating the likely location of the target.

In normal circumstances, both cortical visual streams are, of course, active simultaneously and visual information is potentially available to either stream. However, the M-cell input to the dorsal visual stream and the P-cell fibres that provide the dominant input to the ventral stream differ in several key respects. In Experiments 2-6, the model depicted in Figure 1 was tested by probing the relationship between known attributes of the dorsal and ventral streams and performance of the *Landmark Cueing* and *Identity Cueing* tasks.

EXPERIMENT TWO

As we have already seen, M-cell channels, which provide input to the dorsal visual stream, respond well to briefly exposed stimuli, due to their transient response characteristics; whereas P-cell channels, the main input to the ventral visual stream, respond poorly to such stimuli, due to their sustained response characteristics. Hence, if orienting on the basis of landmark information relies on the dorsal stream then attentional effects of landmark cues will be robust when cue exposure time is reduced. Moreover, if orienting on the basis of cue identity relies on the ventral stream, attentional effects of identity cues should collapse in the manner observed by Lambert *et al.* (2006) and in Experiment 1C, when cue exposure time is reduced. These predictions, deduced from our model together with response properties of the M-cell and P-cell inputs to the dorsal and ventral visual streams, were tested in Experiment 1.

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 almost entirely 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, 2017; Lambert, Wootton, Wilkie & Ryckman, 2014; 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: 75 adult volunteers took part. Two participants made an excessive number of anticipations, and one made an excessive number of catch trial errors. Data from these participants were discarded, and three new participants were recruited, to ensure equal numbers (18) in each of the four counter-balancing conditions (see below).

Apparatus: The experiment was performed using a Dell Inspiron laptop 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. Each letter was 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, 'V' and 'O' were landmark cues. The letter used to cue target location was counterbalanced between participants, so that equal numbers of participants shifted 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 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).

In both *Landmark* and *Identity Cueing* blocks, 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. Cue letters were then presented for either 67ms or 133ms, with cue exposure time varying randomly from trial to trial. The target stimulus was presented either 150ms or 600ms after onset of the cue. Participants were told that the target would usually

occur in the location cued by the letters, but on some occasions it may not appear where expected. They were instructed to press the spacebar as soon as they detected the target, and to keep their eyes fixated on the central fixation cross throughout the experiment. 17% of trials were catch trials, where a cue was presented but there was no target stimulus.

Participants were instructed to refrain from responding on these trials.

Design: Each participant performed 10 landmark cueing practice trials, followed by 2 blocks of 96 landmark cueing experimental trials; and 10 identity cueing practice trials, followed by 2 blocks of 96 identity cueing experimental trials. Within each experimental block, there were 64 valid, 16 invalid, and 16 catch trials, with trial type varying randomly. The order of participating in the two cueing conditions was counter-balanced between participants.

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 3. 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 3 about here** *****

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, $F(1,71) = 6.09$, $p = .016$., $\eta^2_p = .08$. 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 3, panel a). Despite a relatively powerful experimental design, with 72 participants, there was no evidence that briefly exposed identity cues influenced attention: the main effect of trial validity, and interaction between validity and SOA failed to approach significance (both $F < 1$, see Figure 3b). 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 cue, response times on valid and invalid trials were essentially identical (Figure 3b).

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, and between cueing paradigm, trial validity and SOA were non-significant (both $F < 1$, see Figure 3c,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, should be independent of cue exposure time. Consistent with

this, effects of landmark cues were at least as large in the brief exposure time condition (Invalid RT (385ms) - Valid RT (370ms) = 15ms; see Figure 3a) compared to the long exposure time condition (Invalid RT (377ms) - Valid RT (369ms) = 8ms; see Figure 3c).

DISCUSSION

Results from Experiment 2 were clear. Reducing cue exposure time had a dramatic 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 very 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 earlier, this pattern is consistent with our model, together with the transient and sustained response characteristics of the M-channel and P-channel inputs to the dorsal and ventral streams, respectively.

EXPERIMENT THREE

In addition to differing with respect to their response properties (transient or sustained), the M-cell and P-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, and respond well to low-contrast visual stimuli (Bullier, 2001; Merigan & Maunsell, 1993; Shapley, Kaplan & Soodak, 1981). The P-cell inputs to the ventral stream, on the other hand, respond strongly to stimuli presented with high luminance contrast, but only weakly to low contrast stimuli (Merigan & Maunsell, 1993). If orienting on the basis of landmark information relies on the dorsal stream, while orienting on the basis of cue identity relies on the ventral stream, then attentional effects of landmark cues will be robust under

reduced luminance contrast, but attentional effects of identity cues will collapse or be reduced when cue luminance contrast is low. These predictions were tested in Experiment 3.

METHOD

Participants: 20 adult volunteers with normal or corrected-to-normal vision took part.

Apparatus and Stimuli: Stimuli were presented on a Samsung Syncmaster 24" monitor.

Participants wore a high-density EEG cap containing 128 electrodes. EEG data were collected, but are not reported here; these are described separately, as part of an investigation of effects of normal ageing on visual attention (Sciberras-Lim, 2016).

All stimuli were presented in dark grey against a grey background (Luminance: 12.91cd/m²).

A fixation cross (Weber contrast: 82%) subtending 0.5° by 0.5° was presented centrally. Cue letters were presented 12.4° from the screen centre and 4.2° above the horizontal meridian.

Each 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 were presented in low contrast (7.62 cd/m²;

Weber contrast: 41%). As in Experiment 2, for half the participants the letters 'O' and 'V'

served as landmark cues and the letters 'T' and 'X' served as identity cues. This was reversed

for the remaining participants. 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 & Design: This was similar to Experiment 2. The SOA between cue and target

onset was always 600ms. As in Experiment 2, at the beginning of each trial the fixation cross

'blinked', by disappearing for 100ms. Following this a random interval of between 500ms-

800ms elapsed before the presentation of the cues. For both the *Landmark Cueing* and

Identity Cueing tasks, participants began with a practice block of 10 trials, followed by 2

blocks of 80 experimental trials (48 valid trials, 16 invalid trials, and 16 catch trials).

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 4 about here** *****

Mean response times are illustrated in Figure 4. These data were entered into a three-way, repeated measures analysis of variance with cueing task (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 4. 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 4, right): participants responded more rapidly on valid compared to invalid trials, regardless of cue contrast (both $p < .025$). However, in the Identity Cueing condition, trial validity interacted with cue contrast ($F(1,15) = 7.16, p = .017, \eta^2_p = .32$; see Figure 4, left): 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

Results of Experiment 3 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. Attentional effects of high contrast and low contrast landmark cues were of similar magnitude (see also Lambert & Shin, 2010; Shin & Lambert, 2012). 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 somewhat quicker in the Identity Cueing relative to Landmark Cueing condition. This effect was not predicted, and it is worth noting that in Experiment 2 there was no evidence of a 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 2 and 3, 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 FOUR

Within the ventral stream, representation across the visual field is highly biased, with strong representation of signals from central vision, and relatively weak representation of the visual periphery (Merigan & Maunsell, 1993). Visual field representation in the dorsal stream, on the other hand, is more uniform, with relatively good representation of the visual periphery

(Brown, Halpert & Goodale, 2005; Colby, Gatass, Olson & Gross, 1988; Merigan & Maunsell, 1993). In addition, as noted earlier, visual processing in the dorsal stream is thought to occur rapidly and non-consciously and these attributes are thought to be functionally important, with respect to the rapid, on-line control by the dorsal stream of visually guided actions such as reaching, grasping or catching thrown objects (Milner & Goodale, 2006; Chen, Sperandio & Goodale, 2015). Moving the eyes themselves (i.e. overt shifts of attention) can be viewed, from the perspective outlined by Milner & Goodale (2006) as a specific kind of visually guided action – one that has the interesting property of having immediate feedback consequences for processing in both visual streams and for visual consciousness. Of course, in everyday language, proficiency in visually guided actions (e.g. in fast ball sports, such as baseball or tennis) is typically referred to as *hand-eye* coordination. Moreover, according to the premotor theory of attention (Rizzolatti, Riggio, Dascola & Umiltà (1987) eye movements and covert shifts of attention enjoy a close functional relationship (see also de Haan, Morgan & Rorden, 2008; Smith, Rorden & Jackson, 2004; Smith, Schenk & Rorden, 2012).

If, as our model implies, overt as well as covert orienting in response to landmark information is mediated by the dorsal visual stream, then robust effects of landmark cues on eye movements should mirror multiple properties of the dorsal stream, including those described in the previous paragraph, as well as those addressed in Experiments 2 and 3, The design of Experiment 4 was tailored to five properties of the dorsal stream, (transient responding, good contrast sensitivity, representation of the visual periphery, independence from conscious awareness, and speed of encoding), by incorporating five corresponding design features, namely: (i) brief cue presentation, (ii) inclusion of low contrast cues, (iii) peripheral visual presentation, (iv) reduced awareness - participants were not informed of the presence of cues, (v) use of a brief delay between cue onset and onset of the target for a

saccadic eye movement - participants were instructed to move their eyes to discriminate whether a peripherally presented digit was '2' or '7'.

Accordingly, in Experiment 4 high- and low-contrast cues were presented peripherally (12.7° eccentricity) for 33ms, with a very brief delay (66ms) between cue onset and onset of the eye movement target. The brevity of this delay means that predictive information carried by the cue must be encoded rapidly, for an effect on eye movements to be observed.

Participants were not informed that targets were preceded by peripheral letter cues, and consequently, were also not informed about the predictive link between cues and target location. If effects of landmark cues on eye movements are mediated by the dorsal stream, as proposed by our model, these effects should be independent of conscious awareness, and be observed for participants who remain unaware of the cues or their predictive utility.

In addition to evaluating effects of high- and low-contrast landmark cues on eye movements, Experiment 4 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: 32 adult volunteers with normal or corrected to normal vision took part.

Apparatus: The experiment was conducted using a Tobii T120 eye-tracker. Before each experimental task participants completed a calibration procedure.

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 central cross ($0.29^\circ \times 0.29^\circ$; Luminance = 6.5 cd/m^2) was present at the beginning of every trial and during the inter-trial interval. Letter cues were '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. Cues 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: This was similar to Experiment 2, aside from these features. Cue exposure duration was 33ms, and the SOA between cue onset and onset of the target digit was 66ms. 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, on the left or right of the screen, 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.

Participants were not warned that target stimuli (digits) were preceded by bilateral letter stimuli, and were not informed of the predictive relationship between letter 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 Appendix) 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.

Design: Each participant performed 16 practice trials, in which the target always appeared on the same side as the landmark letter, followed by 3 blocks of 80 experimental trials, comprising 64 valid and 16 invalid trials. 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* (Landmark Cueing) task, except that a blank screen was presented in place of the screen containing the target digit.

Procedure: 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, 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: Each participant performed 16 practice trials, followed by one 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 5. 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 5). No other main effects or interactions were reliable statistically.

***** **Figure 5 about here** *****

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 Appendix). 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 6, 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 6 about here** *****

Vision for Perception (Discrimination) Task

Mean accuracy and mean response times in the vision for perception (discrimination) task are illustrated in Figure 7. 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.

***** **Figure 7 about here** *****

DISCUSSION

The central prediction of Experiment 4 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 ($\eta^2_p = .79$; Cohen's $d = 1.95$).

Although the key prediction of Experiment 4 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.*, 1999,2000; 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.

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 7). 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.

EXPERIMENT FIVE

Although results obtained from Experiments 1-4 agree closely with predictions derived from our model (Figure 1), these findings are also amenable to an alternative, and arguably simpler

interpretation. Thus far, we have tested the model by manipulating stimulus dimensions in order present stimuli that are encoded well by the M-cell inputs to the dorsal visual stream, but less well by the P-cell inputs to the ventral stream. That is, we have presented cue stimuli with brief exposure times (Experiments 1C, 2 & 4), at relatively peripheral visual locations (Experiment 4), with low brightness contrast (Experiments 3 & 4), and with brief cue-target intervals (Experiment 4); and have demonstrated that landmark cueing effects are robust under all these conditions. While these findings are consistent with the model shown in Figure 1 and with known physiological properties of the dorsal visual stream, an alternative interpretation is also feasible. It is possible that the visual-spatial properties of landmark cue stimuli simply render them easier to encode than identity cues. Hence, the robustness of landmark cueing effects might have nothing to do with physiological properties of the M-cell inputs to the dorsal stream, but be simply due to the ease with which they are encoded perceptually. The aim of Experiment 5 was to pit this hypothesis against predictions derived from our model by manipulating: (i) a feature (namely, isoluminant colour) that is known to be encoded well by the ventral stream, but poorly or not at all by the dorsal visual stream; and (ii) a feature (luminance contrast) that, as we have argued in earlier sections, is encoded well by the dorsal stream, but less well by the ventral stream.

While the M-cell inputs to the dorsal stream respond well to changes in stimulus luminance, as we have noted (Bullier, 2001; Merigan & Maunsell, 1993; Shapley *et al.*, 1981), they display little or no response when a stimulus changes in chrominance (colour) with no change of luminance (Cavanagh, Adelson & Heard, 1992; Livingstone & Hubel, 1988; Lambert, Wells & Kean, 2003). Thus, the dorsal visual stream appears to be essentially ‘blind’ to stimuli that differ from the background in colour, but not luminance. On the other hand, the P-cell inputs to the ventral stream respond well to isoluminant chromatic borders (Cavanagh *et al.*, 1992; Livingstone & Hubel, 1988). Hence, stimuli rendered with an isoluminant

change of colour will be encoded well by the ventral stream, but poorly or not at all by the dorsal stream. As many readers will be aware, generating stimuli that differ from the background in colour, but not luminance is less than straightforward. Cavanagh,*et al.*, (1992) describe a multitude of technical difficulties which can cause subtle luminance artifacts, confounding attempts to generate stimuli of different colours that are reliably isoluminant. Fortunately, Cavanagh et al. (1992) describe a method, the *tritanopic* technique that circumvents these problems (see also Lambert, Wells & Kean, 2003). In Experiment 5, this tritanopic technique was used to present participants with isoluminant landmark cues.

According to the account just described, isoluminant stimuli are visible to the ventral stream, but essentially invisible to the dorsal stream. This leads to a straightforward prediction: if landmark cueing effects are mediated by the dorsal visual stream, these effects should collapse when cues are rendered as isoluminant, tritanopic stimuli. This prediction was tested in Experiment 5. As in Experiments 1C, 2 & 4 cues were presented with a brief exposure time (67ms), and participants were instructed to shift attention in response to spatially predictive landmarks. Landmark cues were presented in two alternative conditions. In the isoluminant condition, cues differed from the background in chrominance, but not luminance, using the tritanopic stimulus technique (see Cavanagh et al., 1992; Lambert et al., 2003). If the landmark cueing effects observed in Experiments 2-4 are driven by dorsal visual stream encoding, as we have proposed (see Figure 1), then these effects should collapse under isoluminance. A second condition, the luminance condition, acted as a control for the first. Here, cue letters differed from the background, in luminance but not chrominance. According to our model, cues in this condition should drive the luminance sensitive M-cell inputs to the dorsal stream, and elicit landmark cueing effects, as in Experiments 2-4. Hence, Experiment 5 compared attentional effects elicited by cues rendered with isoluminant chromatic borders, with those elicited by cues rendered with isochromatic luminance borders.

In addition to performing the landmark cueing task, participants also performed a cue discrimination task that was closely similar to the *Vision for Perception (Cue Discrimination)* task employed in Experiment 4. It was important to include this task in order to compare conscious perceptual encoding of the stimuli used as spatial cues in the isoluminant and luminance condition. As in Experiment 4, we assume that performance of this cue discrimination task reflects *vision for perception* – conscious visual encoding of cue stimuli by the ventral stream (Milner & Goodale, 2006). According to our experimental rationale, isoluminant cues should be ‘invisible’ to the dorsal stream, causing landmark cueing effects to collapse, but remain phenomenally visible via encoding within the chromatically sensitive pathways of the ventral stream, enabling accurate performance of the *Vision for Perception* task.

METHOD

Participants: Thirty six adult volunteers, with normal or corrected to normal vision took part.

Apparatus: This was the same as for Experiment 3.

Stimuli: In E-Prime colours can be rendered in RGB space with coordinates that vary from 0,0,0 (black) to 255,255,255 (white). All stimuli were presented against a yellow background with RGB coordinates 230,230,0 (Luminance = 157.6 cd/m²). RGB coordinates of cue stimuli in the luminance condition were 238,238,0 (Luminance = 172.8 cd/m²). RGB coordinates of cue stimuli in the isoluminant condition were 230,230,180 (Luminance = 163.6 cd/m²).

Although the physical luminance of letters in the isoluminant condition was slightly higher than the background, the additional energy in this condition was made up entirely of blue light, which will stimulate the S-cones. In this situation luminance channels will be driven strongly by activity of the L- and M-cones caused by the intense yellow background; and because the contribution of S-cones to luminance is relatively weak, the addition of blue light

to form a tritanopic stimulus will have little or no additional effect on luminance channels, which are already being stimulated strongly by the yellow background field (see Cavanagh et al., 1987, 1992; Lee & Stromeyer, 1989). Phenomenally, the cues appeared as greyish letters against a yellow background. Flicker tests confirmed that the phenomenal brightness of the tritanopic stimuli did not differ from that of the yellow background. Letters were presented 12.0° to the left or right of centre, and 0.4° above the horizontal meridian. RGB coordinates of the fixation and target stimuli were 255,255,255 (Luminance = 184.2 cd/m²). Thus, onset of the target in the *Landmark Cueing* task was signalled by a change of chrominance *and* a change of luminance. Targets were presented 12.0° to the left or right of centre, centred on the horizontal meridian.

Procedure - Landmark Cueing task: This was similar to the *Landmark Cueing, brief exposure time* condition of Experiment 4. Letter cues were presented for 67ms, and the interval between cue onset and target onset was 100ms. Participants were informed that on each trial a pair of letters (X and T) would appear briefly, on either side of central fixation, and that the target would usually appear on the same side as one of the letters. For half the participants the letter X was the landmark cue; while for the other half the letter T was the landmark cue.

Procedure - Vision for Perception (Cue Discrimination) task: This was similar to the *Vision for Perception* task of Experiment 4.

Design – Landmark Cueing task: This was similar to the *Landmark Cueing* condition of Experiment 2. Each participants performed 20 practice trials, followed by two blocks of 96 experimental trials. The type of cue that was presented (luminance or isoluminant) varied randomly from trial to trial.

Design – Vision for Perception (Cue Discrimination) task: This was similar to the *Vision for Perception (Cue Discrimination)* task of Experiment 4. Each participants performed 16

practice trials, followed by two blocks of 80 experimental trials. The type of stimulus that was presented (luminance or isoluminant) varied randomly from trial to trial.

RESULTS

One participant made an excessive number of errors (40.5%) when performing the Vision for Perception (Cue Discrimination) task, and appeared to be disengaged from task instructions; and one participant made an excessive number of catch trial errors (21.9%) when performing the Landmark Cueing task. These participants were excluded from further analysis.

Landmark Cueing Task

The average rate of catch trial errors (1.6%) and anticipations (0.8%) were acceptably low.

Results from the Landmark Cueing task are shown in Figure 8. As predicted, in the Luminance condition participants responded more rapidly on valid trials (mean RT = 408ms) compared to invalid trials (mean RT = 420ms), $t(33) = 2.60$, $p = .007$, one-tailed, $\eta_p^2 = .17$. Secondly, consistent with prediction, in the isoluminant condition, response times on valid (mean RT = 411ms) and invalid trials (mean RT = 410ms) did not differ, $t < 1$. Moreover, when these data were entered into a two-way analysis of variance, with cue type (luminance vs. isoluminant) and trial validity (valid vs. invalid) as repeated measures factors, the only statistically significant effect was the predicted interaction between cue type and trial validity, $F(1,33) = 4.96$, $p = .03$, $\eta_p^2 = .13$, showing that landmark cueing effects in the luminance and isoluminance conditions differed reliably.

***** **Figure 8 about here** *****

Vision for Perception (Cue Discrimination) Task

Results from this task, where participants attempted to discriminate between the two alternative arrangements of landmark cue letters, are summarised in Table 1. Although isoluminant letters failed to elicit landmark cueing effects in the attention task (see above),

participants were able to discriminate isoluminant letters in the context of the *Vision for Perception* task, with a high degree of accuracy. Indeed, cue discrimination performance was *better* in the isoluminant condition (mean accuracy = 97.0%) than in the luminance condition (95.8%), $t(33) = 2.49$, $p = .018$, two-tailed, $\eta^2_p = .16$.

Several participants noted that when performing this task there were some trials where they failed to notice that any stimulus at all had been presented. This was manifest in the data as trials with very long response times, and low accuracy. Accordingly, latency data from the *Vision for Perception (Cue Discrimination)* task were analysed in two ways. Firstly, we compared the luminance and isoluminant conditions with respect to the latency of correct responses, on trials where response latency was less than 2,000ms. On these trials responses were marginally quicker in the isoluminant condition (mean RT = 457ms) relative to the luminance condition (mean RT = 469ms), $t(33) = 1.69$, $p = .10$, two-tailed, $\eta^2_p = .08$.

Secondly, we compared the number of very long responses (defined as those with a latency greater than 2,000ms) in the luminance and isoluminant conditions. Thirty participants made at least one long response when performing the cue discrimination task, and the proportion of long responses made by these participants was higher in the luminance condition (mean = 7.4%) relative to the isoluminant condition (4.3%), $t(29) = 3.12$, $p = .004$, two-tailed, $\eta^2_p = .25$.

***** **TABLE 1 about here** *****

DISCUSSION

Results from Experiment 5 agreed with predictions derived from our model (Figure 1), and indicate that the robustness of landmark cueing effects in Experiments 1C-4 cannot simply be attributed to ‘ease of perceptual encoding’. These earlier experiments showed that landmark cueing effects were robust when four stimulus parameters (brief exposure time, low

luminance contrast, peripheral visual location, and brief cue-target delay) favoured encoding by the dorsal visual stream. Moreover, identity cueing effects collapsed under brief exposure time and low stimulus contrast. In Experiment 5 we applied the converse rationale: because the M-cell inputs to the dorsal stream show little or no response to isoluminant, chromatic borders, we predicted that landmark cueing effects would collapse under isoluminance. This prediction was confirmed. However, when the cues were rendered via an isochromatic luminance border, reliable landmark cueing effects were seen, consistent with our model, and with the sensitivity of the dorsal visual stream to luminance contrast borders.

The presence of landmark cueing effects in the luminance condition, and their absence in the isoluminant condition cannot be explained by simply arguing that in the former condition cues are more salient, and therefore encoded more effectively and easier to ‘see’ than cues in the latter condition. In fact, in the context of the *Vision for Perception (Cue Discrimination)* task, the reverse was true: stimuli in the luminance condition were discriminated *less* accurately, somewhat more slowly, and tended to be missed completely, more frequently than letters in the isoluminant condition. This finding is also consistent with our model. As in Experiment 4, it is assumed that discriminating consciously between the two alternative stimuli in this task is mediated by the ventral visual stream, and the inputs to this stream are, as we have noted, sensitive to isoluminant chromatic borders.

In summary, results from Experiment 5 showed firstly that, as predicted, *Landmark Cueing* effects were observed in the luminance condition, but collapsed under isoluminance; and secondly, in the *Vision for Perception (Cue Discrimination)* condition isoluminant letters were discriminated more accurately and more rapidly than letters in the luminance condition.

EXPERIMENT SIX

Experiment 5 showed that when cues were presented briefly (for 67ms), and with a brief delay between cue and target (100ms), landmark cueing effects collapsed under

isoluminance, in agreement with our model, and consistent with the known insensitivity of M-cell inputs to the dorsal visual stream to isoluminant chromatic borders. However, according to our model the ventral stream also participates in visual orienting, and is associated with endogenous shifts of attention, elicited via symbolic encoding of visual cues (see Figure 1, panel b). Therefore, a further prediction of our model is that isoluminant spatial cues *will* elicit visual orienting, under appropriate experimental conditions – those associated with endogenous orienting. Endogenous orienting is typically associated with relatively long delays between cue and target onset; and in Experiments 1A, 1B, and 2 we found that when cues were presented with relatively long exposure times, orienting effects were driven by the symbolic identity of cues, rather than by their landmark features. In Experiment 6, isoluminant cue letters were presented with a relatively long exposure time (150ms), and with a relatively long delay between cue and target onset (300ms), in both *Landmark Cueing* and *Identity Cueing* conditions. Under these conditions, our model predicts that ventral stream-mediated endogenous orienting effects will be apparent, in both the *Landmark* and *Identity* cueing conditions. That is, we predict results that parallel the pattern observed in the long exposure time condition of Experiment 2.

METHOD

Participants: 16 adult volunteers with normal or corrected to normal vision took part.

Apparatus & stimuli: This was the same as for the isoluminant condition of Experiment 5, with these differences. In the *Identity Cueing* condition participants were presented with two identical stimuli on each trial (X + X, or T + T, or V + V, or O + O); in the *Landmark Cueing* condition participants were presented with two different letters on each trial (X + T, or T + X, or V + O, or O + V), as in Experiment 2. In both conditions, cue stimuli were presented for 150ms, and the interval between cue onset and target onset was 300ms.

Procedure: Participants performed 2 blocks of 96 *Landmark Cueing* trials and 2 blocks of 96 *Identity Cueing* trials, with task order counter-balanced across participants. In the *Landmark Cueing* task participants were informed that the target would usually appear on the same side as one of the letters (X or T, V or O), counter-balanced across participants. In the *Identity Cueing* condition participants were informed that the target would usually appear on the left side of the screen following one pair of letters (X + X or T + T, V + V or O + O) counter-balanced across participants), and on the right following the other letter pair.

Design: Within each cueing condition, participants performed 10 practice trials, followed by two blocks of 96 (64 valid, 16 invalid, 16 catch) experimental trials.

RESULTS

Rates of anticipations (0.45%) and catch-trial errors (0.68%) in Experiment 6 were both acceptably low. Mean response times are shown in Figure 9. As predicted, participants responded more rapidly on valid compared to invalid trials in both the *Identity Cueing* task (mean valid RT = 349ms; mean invalid RT = 369ms), $t(15) = 2.12$, $p = .026$, one-tailed, $\eta^2_p = .23$, and in the *Landmark Cueing* task (mean valid RT = 356ms; mean invalid RT = 375ms), $t(15) = 1.91$, $p = .038$, one-tailed, $\eta^2_p = .20$. Moreover, when these data were entered into a two-way analysis of variance, with *Cueing Condition* (identity vs. landmark) and trial validity (valid vs. invalid) as repeated measures factors, the only significant effect was the predicted main effect of trial validity, $F(1,15) = 5.52$, $p = .033$, $\eta^2_p = .27$.

***** **Figure 9 about here** *****

DISCUSSION

When experimental conditions, namely relatively long cue exposure time (150ms) and relatively long cue-target interval (300ms), that were associated in Experiments 1A, 1B & 2, and in previous work (Chica *et al.*, 2013,2014; Klein, 2004) with endogenous / symbolic

orienting, isoluminant cue stimuli elicited reliable attentional orienting: participants responded more rapidly on valid compared to invalid trials, in both the *Landmark* and *Identity* cueing tasks. Thus, as in Experiments 1A & 1B and in the long exposure-time condition of Experiment 2, orienting effects were observed regardless of whether spatially predictive visual landmarks were present (*Landmark Cueing* condition) or absent (*Identity Cueing* condition). These findings are consistent with our model (Figure 1), and we propose that in both the *Landmark* and *Identity* cueing conditions of Experiment 6, visual orienting was driven by ventral stream encoding of the symbolic identity of the cues (as a signal predicting a left or right target), assigned via experimental instructions. That is, we propose that in both experimental conditions, cues were encoded using the ventral stream input pathway depicted in panel (b) of Figure 1.

GENERAL DISCUSSION

Results from Experiments 1-6 shed new 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; Klein, 2004; Posner, *et al.*, 1980) and dual-stream models of vision (Ungerleider & Mishkin, 1982; Milner & Goodale, 2006).

Our theoretical proposals are illustrated in Figure 1. Attention shifting associated with dorsal stream encoding of visual landmarks is illustrated in Figure 1a. The target of the dorsal stream, parietal cortex, is of course, strongly associated with attention, 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).

Attention shifting elicited by ventral stream encoding of environmental cues is modelled in Figure 1b. 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 & Schneider, 2010) is a major component of this overall system. Figure 1b 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 our model 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; see below – *The dorsal visual stream and landmark cueing*, Point 4). 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 1 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-identity cues appears to be mediated by the P-cell inputs to the ventral stream, which conduct neural signals more slowly (Bullier, 2001).

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 2, 4 and 5. Findings from the experiments reported here, together with earlier studies (Lambert & Duddy, 2002; Lambert & Shin, 2010; Lambert & Wootton, 2017; Lambert et al., 1999,2000,2006,2014; Marrett et al., 2011; Shin & Lambert 2012; Shin *et al.*, 2011) provide a substantial body of evidence, indicating that landmark cueing effects rely on dorsal stream encoding of cue stimuli. Indeed, this hypothesis is now supported by no fewer than eight sources of converging evidence:

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 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, 2017; Lambert, *et al.*, 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). These findings have now been replicated (Lambert & Wootton, 2017; Lambert *et al.*, 2014).
 3. 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 *et al.*, 1981). Therefore, effects mediated by this pathway will remain robust, under conditions of reduced contrast (Bullier, 2001). This prediction was borne out, with respect to landmark cueing effects, in Experiments 3 and 4, and also in two earlier studies, where rapid covert orienting effects of similar magnitude were observed, regardless of whether landmark cues 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, *et al.*, 2005; Colby *et al.*, 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 letters, 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). In the current study, robust landmark cueing effects were seen with very brief cue-target delays in Experiment 4 (cue-target delay = 67ms) and Experiment 5 (cue-target delay = 100ms).
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 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.

7. As noted earlier, 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 Experiment 3,4,6 & 7.
8. The sensitivity of the dorsal visual stream to isoluminant chromatic borders is thought to be poor or non-existent (Cavanagh, *et al.*, 1992; Livingstone & Hubel, 1988; Lambert, Wells & Kean, 2003), as outlined in the introduction to Experiment 5. This property of the dorsal visual stream led us to predict that landmark cueing effects would collapse under isoluminance, and this prediction was confirmed in Experiment 5.

While critical readers will be able to identify weaknesses in each of the above, when viewed together these eight items of converging evidence make a compelling case that landmark cueing effects are mediated by dorsal stream encoding of stimuli in the visual environment.

The ventral visual stream and symbolic cueing: Symbolic-semantic encoding is strongly associated with the ventral stream (Carlson, Simmons, Kriegeskorte & Sleva, 2014; Peelen & Caramazza, 2012) and appears to be outside the functional repertoire of the dorsal stream, which as we have seen specialises in encoding visual-spatial features. In a sense, this overall characterisation of the different functions performed by the two cortical visual streams mandates a ventral stream 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, four further lines of evidence are consistent with the contention that identity cueing effects, driven by symbolic encoding, are mediated by the ventral stream.

1. Experiments 1A-1C & 2 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.
2. Experiment 3 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.
3. 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).
4. While Experiment 5 showed that when cues were exposed very briefly, landmark cueing effects collapsed under isoluminance, Experiment 6 showed that isoluminant cues presented for a longer period, did affect attention. Since the ability of the dorsal visual stream to encode isoluminant stimuli is thought to be poor or non-existent (Cavanagh, Adelson & Heard, 1992; Livingstone & Hubel, 1988), it is reasonable to assume a ventral stream input route in this situation. As in Experiments 1A,1B, and the long exposure time condition of Experiment 2, orienting effects were seen in both the identity and landmark cueing conditions in Experiment 6. We propose that in all four of these experiments using

a long cue exposure time, identity and landmark cues were both encoded in terms of their symbolic properties, as a signal predicting a left or right target, by the ventral stream.

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 Experiments 2, 3 & 6 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, and in this sense the cue is task-irrelevant (Chica *et al.*, 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 conditions of Experiment 2-6, participants were presented with two kinds of cue (e.g. X-T or T-X), and appropriate attention shifting was contingent on encoding the distinction between them. However, findings from Experiments 2-5, 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 cues, can be extremely rapid (Experiments 4 & 5; Lambert & Duddy, 2002; Marrett *et al.*, 2011). The time-course of identity cueing is somewhat slower, and resembles other variants of endogenous orienting (Lambert & Duddy, 2002). 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 (Lambert, *et al.*, 1999,2000; Shin *et al.*, 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). 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 unilateral 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 experiments described here can be viewed as 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 predictive utility is neither a *necessary*, nor a *sufficient* condition for shifting attention in response to that cue. Experiment 4, together with earlier evidence (Lambert et al., 1999,2000; 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. (see also Risko & Stolz, 2010; Lanthier *et al.*, 2015).

Experiments 1C & 2, together with earlier evidence (Lambert et al., 2006; Shin et al., 2011) showed that when identity cues are presented centrally with brief exposure time, participants' *fail* to shift attention in response to them. Null findings are, of course, often uninformative and difficult to interpret. However, in this case the null result may provide a 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 target location. Hence, both perceptual awareness of the cue, and contingency awareness of its predictive value can be assumed. Despite this, participants failed conspicuously to shift attention in the relevant conditions of Experiments 1C & 2, and in two earlier studies that included similar conditions (Lambert et al., 2006; Shin et al., 2011). Therefore it appears 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 counter-intuitive, it is, we propose, consistent with a conceptually coherent view of attention shifting mechanisms. A feature common to many theories 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 attentional mechanisms. 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.

In a closely related field, Wolfe, Vo, Evans & Greene (2011) 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. Wolfe *et al.* (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 1 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. Our integrated model of vision and attention (Figure 1), also shares a number of features with recent work examining altered vision near the hands (Gozli, West and Pratt, 2012; Taylor, Gozli, Chan, Huffman & Pratt, 2015). An intriguing task for future investigation will be to explore possible

relationships between our model and the modulated visual pathways account of altered vision near the hands proposed by these authors (Gozli et al., 2012; Taylor et al., 2015).

METHODOLOGICAL IMPLICATIONS

In addition to their theoretical value, our findings have methodological implications, concerning the need for careful control of stimulus parameters, in attentional cueing research.

Visual-spatial features: Visual-spatial features of the stimuli employed as cues are crucially important. For example, 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 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. When cues were exposed for a relatively long period, 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.

Cue contrast: Finally, the luminance contrast of cue stimuli appears to be an important factor. Effects of identity cues collapsed when the luminance contrast of cue stimuli was low, but landmark cueing effects were robust under contrast reduction.

In light of these findings we offer two methodological recommendations:

- 1. To be sure of isolating endogenous orienting, driven by symbolic encoding of the cue, 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

The model shown in Figure 1 embodies two straightforward theoretical proposals: that the dorsal stream is the input pathway for rapid orienting in response to visual landmark features, and the ventral stream is the input pathway for symbolically-driven, endogenous orienting. Both proposals are well supported by evidence, and 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.

ACKNOWLEDGMENTS

This work was supported by the University of Auckland Research Committee and by the Marsden Fund of New Zealand (Project Number: 3711736). We thank Cameron Ellis Juan Lupiáñez, Ana Chica and Sam Askelund for helpful discussions. We thank Gabriela Vives for assistance with Experiment 6.

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.
- Cavanagh, P., Adelson, E., & Heard, P. (1992). Vision with equiluminant contrast: 2. A large scale technique and observations. *Perception, 21*, 219-226.
- Cavanagh, P. Anstis, S. M. & MacLeod, D. I. A. (1987). "Equiluminance: Spatial and temporal factors and the contribution of blue-sensitive cones" *Journal of the Optical Society of America A 4*, 1428-1438.
- 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.

- Desimone, R & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193-222.
- 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.
- Gozli, D. G., West, G. L., & Pratt, J. (2012). Hand position alters vision by biasing processing through different visual pathways. *Cognition*, 124(2), 244-250.
- 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.
- James, W. (1983). *The Principles of Psychology*. Cambridge, MA: Harvard University Press. (Original work published 1890).
- 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., & 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., Wells, I. & Kean, M. (2003). Do isoluminant color changes capture attention? *Perception and Psychophysics*, 65, 495-507.
- Lambert, A.J. & Wootton, A. (2017). The time-course of activation in the dorsal and ventral visual streams during landmark cueing and perceptual discrimination tasks. *Manuscript undergoing revision*.
- 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.

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.

Lee, J. & Stromeyer, C.F. III. (1989). Contribution of human short-wave cones to luminance and motion detection. *Journal of Physiology* 41, 3563-593.

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.

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.

- 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.
- 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., Snyder, C.R.R. & Davidson, B.J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology: General*, *109*, 160-174.
- Ptak, R. & Schnider, 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., 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>.
- Taylor, J. E. T., Gozli, D. G., Chan, D., Huffman, G., & Pratt, J. (2015). A touchy subject: advancing the modulated visual pathways account of altered vision near the hand. *Translational Neuroscience*, *6*, 1-7.

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.

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. 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 2. Predictions derived from our model (see text and Figure 1) were tested in Experiments 2-6 by exploring performance of *Landmark Cueing* (upper panel) and *Identity Cueing* tasks (lower panel), under varying stimulus and task conditions. In the *Landmark Cueing* task targets usually appeared at a location near to one of the letters – the landmark cue. In the *Identity Cueing* task targets usually appeared on the right following one pair of letters (e.g. X + X), and on the left following another letter pair (e.g. T + T).

Figure 3. Mean response times in Experiment 2. Error bars represent the standard error of the difference in response times between valid and invalid trials.

Figure 4. Mean response times in Experiment 3. Error bars represent the standard error of the difference in response times between valid and invalid trials.

Figure 5. Mean saccadic latencies in Experiment 4, 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.

Figure 6. Mean saccadic latencies in Experiment 4, 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.

Figure 7. Mean response times and accuracy in the *Vision for Perception* task of

Experiment 4. Error bars represent the standard error of the difference between high and low contrast conditions.

Figure 8. Mean response times in the *Landmark Cueing* task of Experiment 5. Error bars

represent the standard error of the difference in response times between valid and invalid trials.

Figure 9. Mean response times in the *Landmark* and *Identity Cueing* conditions of

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

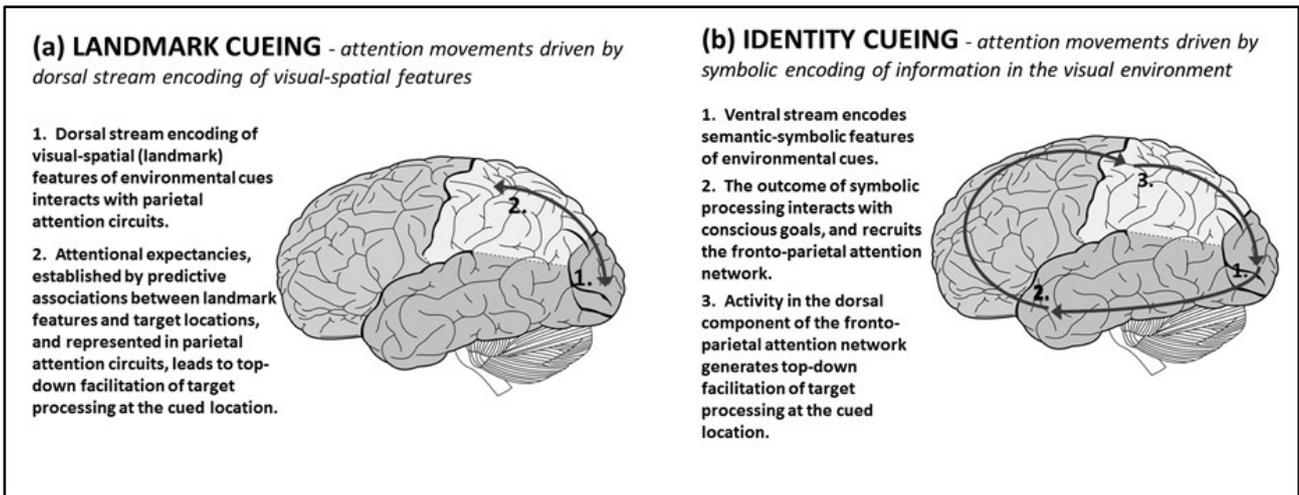


Figure 1. A model of the neurocognitive processes and pathways responsible for shifting attention in response to environmental cues. Dorsal stream-based visual orienting is represented in panel (a); ventral stream-based visual orienting is represented in panel (b).

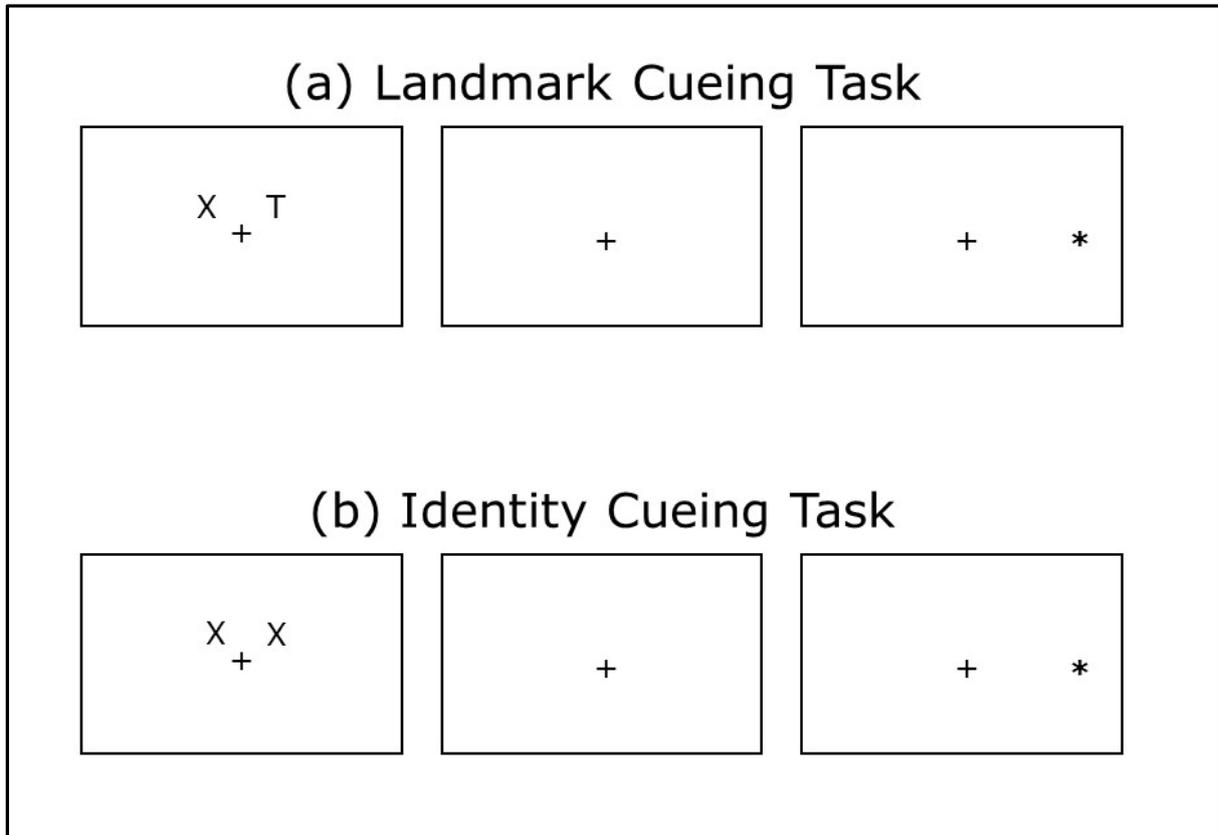


Figure 2. Predictions derived from our model (see text and Figure 1) were tested in Experiments 2-6 by exploring performance of *Landmark Cueing* (upper panel) and *Identity Cueing* tasks (lower panel), under varying stimulus and task conditions. In the *Landmark Cueing* task targets usually appeared at a location near to one of the letters – the landmark cue. In the *Identity Cueing* task targets usually appeared on the right following one pair of letters (e.g. X + X), and on the left following another letter pair (e.g. T + T).

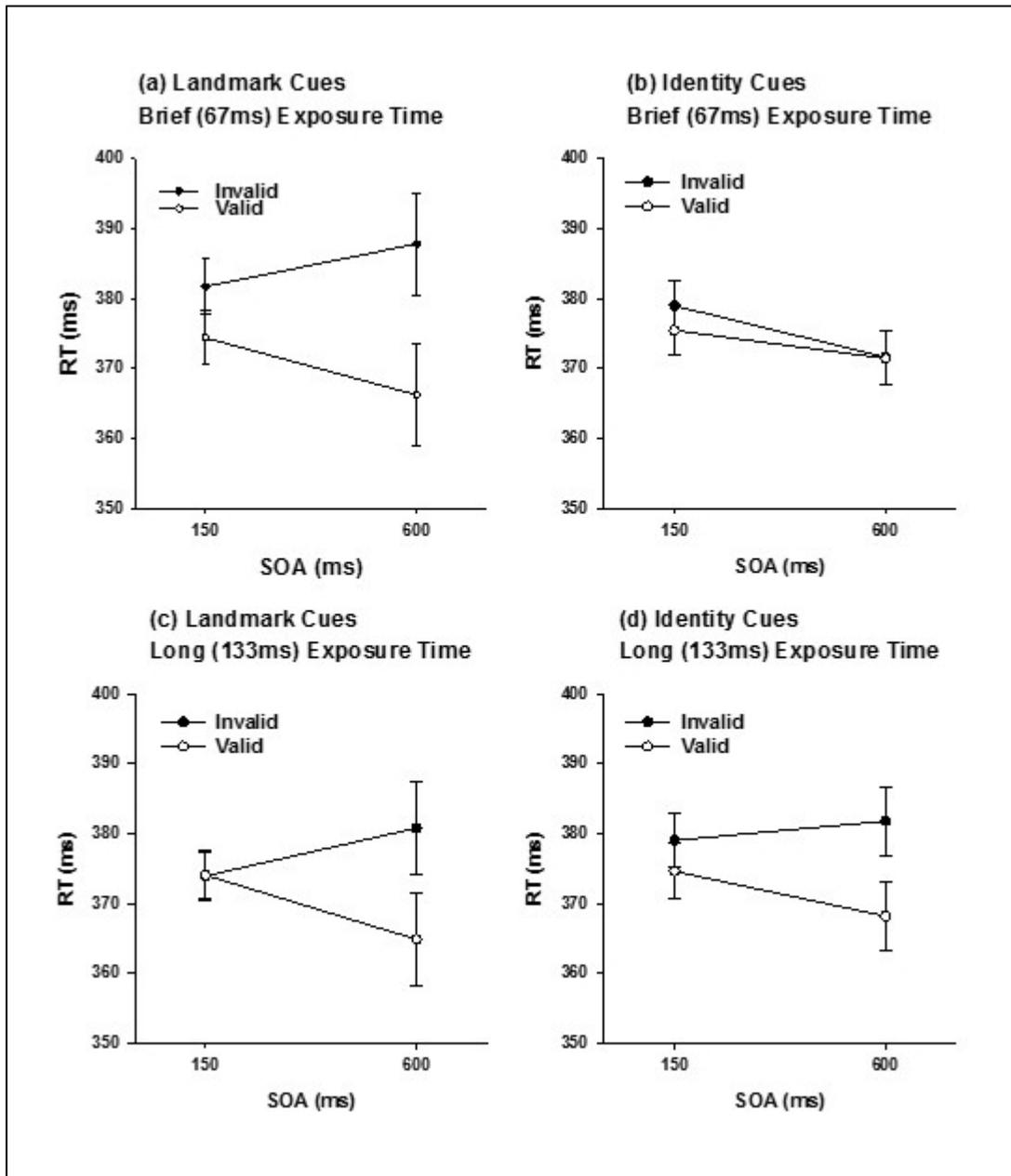


Figure 3. Mean response times in Experiment 2. Error bars represent the standard error of the difference in response times between valid and invalid trials.

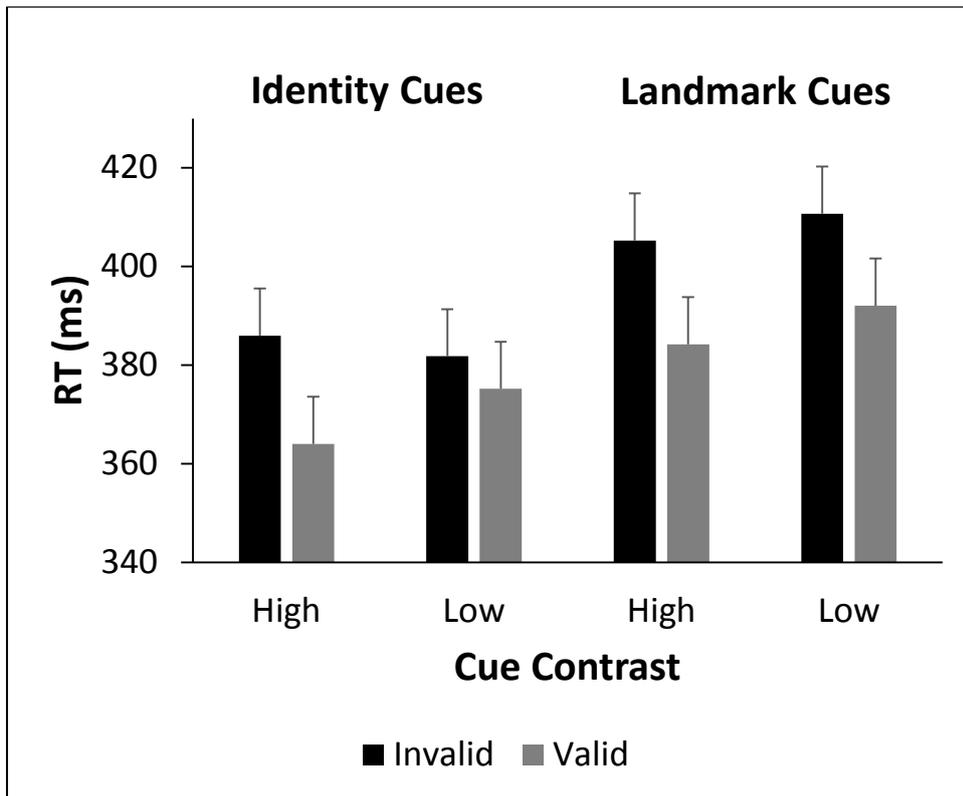


Figure 4. Mean response times in Experiment 3. Error bars represent the standard error of the difference in response times between valid and invalid trials.

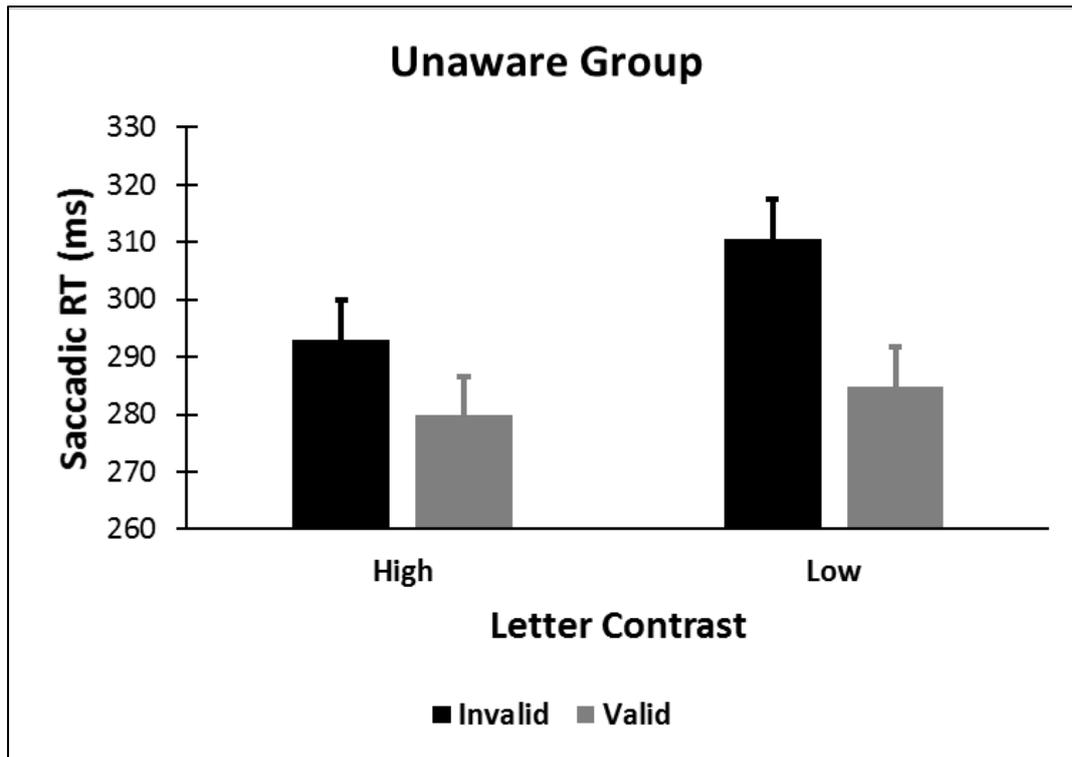


Figure 5. Mean saccadic latencies in Experiment 4, for participants who remained unaware of the presence of cue letters, or of their relationship with target location. Error bars represent the standard error of the difference in saccadic latency between valid and invalid trials.

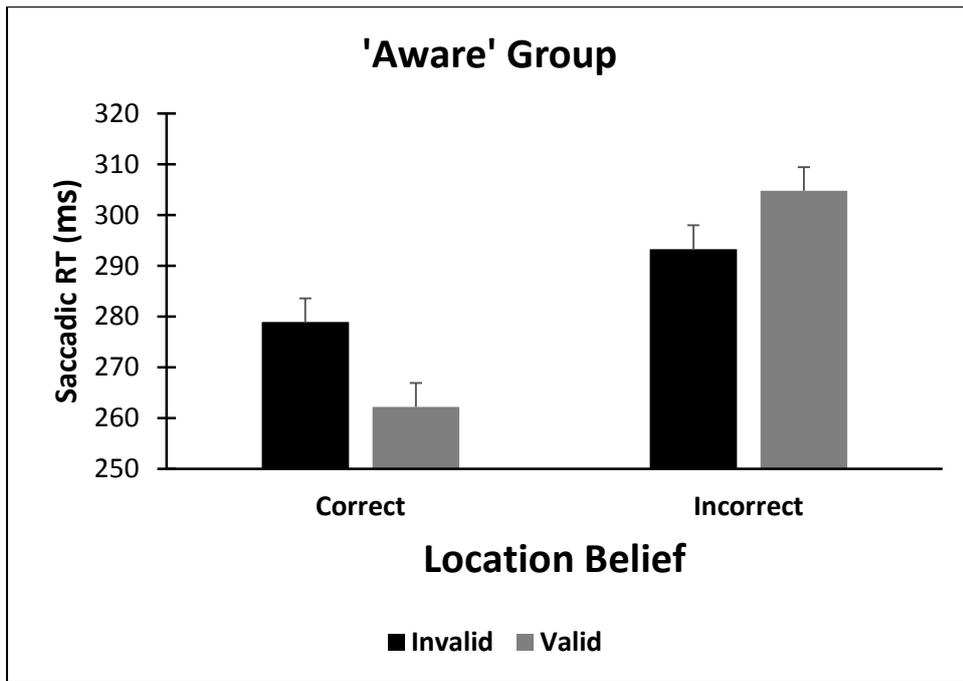


Figure 6. Mean saccadic latencies in Experiment 4, for participants in the ‘Aware’ Group.

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.

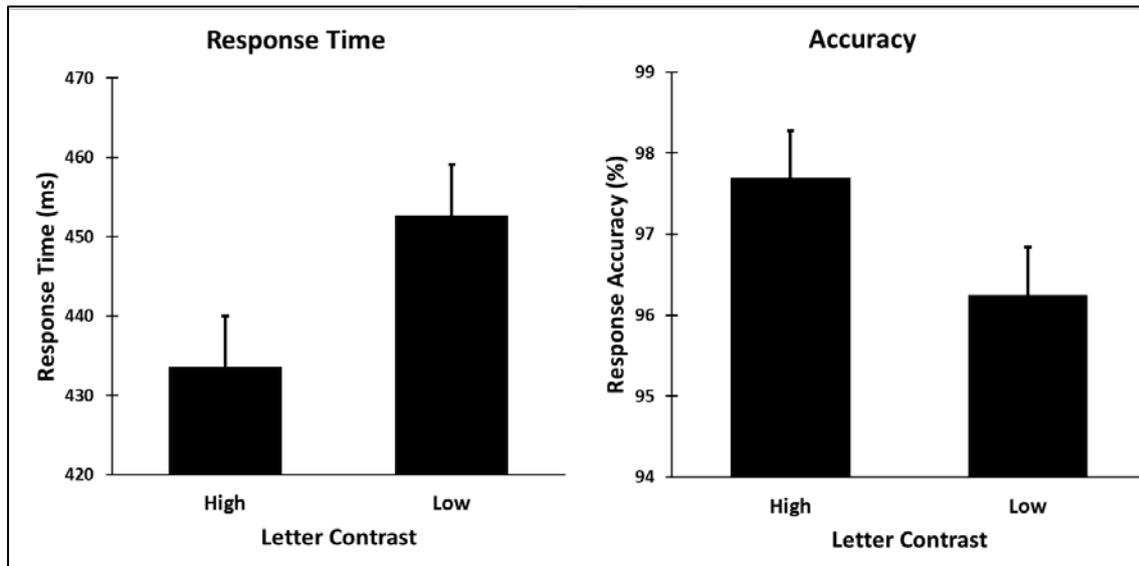


Figure 7. Mean response times and accuracy in the *Vision for Perception* task of Experiment 4. Error bars represent the standard error of the difference between high and low contrast conditions.

Landmark Cueing Task

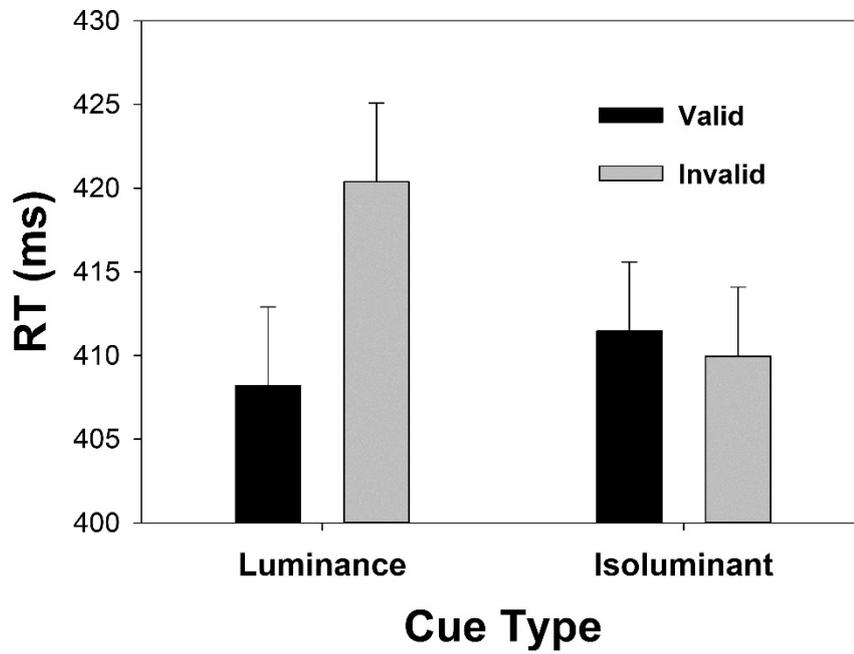


Figure 8. Mean response times in the *Landmark Cueing* task of Experiment 5. Error bars represent the standard error of the difference in response times between valid and invalid trials.

Effects of Isoluminant Cues

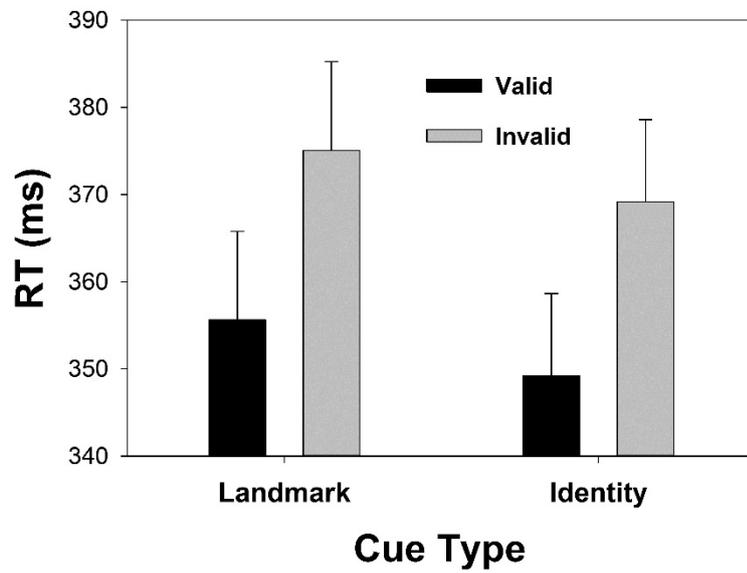


Figure 9. Mean response times in the *Landmark* and *Identity Cueing* conditions of Experiment 6. Error bars represent the standard error of the difference in response times between valid and invalid trials.

TABLE 1 Vision for Perception (Cue Discrimination) Task

| | Isoluminant | Luminance | <i>p (2-tailed)</i> |
|---|--------------------|------------------|---------------------|
| Percent Correct | 97.0% | 95.8% | .018 |
| Mean Correct RT (<2,000ms) | 457 ms | 469 ms | .10 |
| Long Responses (RT > 2,000ms) | 4.3% | 7.4% | .004 |

APPENDIX:

Post-Task Questionnaire (Experiment 4)

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.