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# Testing the dorsal stream attention hypothesis: Electrophysiological correlates and the effects of ventral stream damage

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Short title: Dorsal stream attention hypothesis

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**ABSTRACT**

The roles of dorsal and ventral processing streams in visual orienting and conscious perception were examined in two experiments. The first employed high density EEG with source localisation. The second comprised a neuropsychological case study. Visual orienting was assessed with an *attention procedure*, where peripheral letters cued participants towards a target location. In the *perception procedure* participants responded to the same letters by performing an explicit conscious discrimination. In Experiment 1, the peripheral letters elicited rapid dorsal-stream activation in the attention procedure, and this activation preceded top-down enhancement of target processing in occipital cortex. In the perception procedure early ventral-stream activation was seen. In addition, peripheral letters elicited an “early directing attention negativity” (EDAN) over parietal recording sites in the attention procedure, but not in the perception procedure. In Experiment 2, a patient with a bilateral ventral stream lesion but preserved dorsal stream function showed clear disruption to performance in the perception procedure, whilst exhibiting a normal visual orienting effect in the attention procedure. Taken together these findings (a) highlight the distinct roles of the dorsal and ventral streams in attention and perception, and (b) suggest how these streams might interact, via re-entrant effects of attention on perceptual processing.

**Keywords:** Attention, visual perception, visual orienting, dorsal stream, ventral stream.

## GENERAL INTRODUCTION

When faced with a complex visual scene, our brain somehow has to pick out those items that may be of interest or importance, in order to direct the focus of our selective attention to the best advantage. What visual pathway or pathways are used to achieve this?

Cortical visual processing arises from activity in two somewhat distinct neural pathways (Merigan & Maunsell, 1993). The potentially distinct functional specialisation of these two streams has however been a matter of debate. Ungerleider and Mishkin (1982) argued that the ventral pathway, leading from area V1 in occipital cortex to infero-temporal cortex was responsible for recognising what an object is, whereas the dorsal pathway, from V1 to parietal cortex, was responsible for localising where an object was. Milner and Goodale (1995, 2006) proposed a different interpretation, arguing that ‘what’ and ‘where’ processing was done in both streams but in the dorsal stream the information was used to guide actions, whereas in the ventral stream the information leads to our explicit perception of what and where an object is. Fang and He (2005) recently provided functional MRI data consistent with Milner and Goodale’s proposal that object selectivity is present in the dorsal visual stream. Furthermore Fang and He showed that this dorsal-stream object-selective activation was not differentially associated with conscious perception. Only in the ventral stream was the object-selective activation associated with conscious object perception. Thus, there is clear evidence in support of the idea that the contents of conscious visual perception are selectively associated with processing in the ventral stream.

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3 At the same time however, there is clear evidence that processing in the dorsal stream  
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5 plays a critical role in influencing what we become conscious of. A case in point is visual  
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7 extinction following parietal lesions, in which patients do not consciously perceive the  
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9 more contralesional of two visual stimuli when presented simultaneously. The typical  
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11 interpretation of this disorder is that it reflects an inability to orient attention towards one  
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13 side of space. Given the known dissociation between allocating attention and conscious  
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15 perception (Kentridge et al., 1999) it seems likely that parietal lesions do not influence  
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17 conscious perception directly, but do so via their role in allocating attention (Milner  
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19 1995). We (Lambert & Shin, 2010) have developed a shape-cue contingent spatial  
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21 priming paradigm that further highlights how perception can be dissociated from  
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23 attention. In this paradigm, contingencies between peripherally presented cue items and  
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25 target location can be rapidly learnt and exploited by the visual system in allocating  
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27 spatial attention, independently of having consciously perceived the contingent relations  
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29 between target location and cue items (Shin, Marrett & Lambert, 2011). Our previous  
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31 behavioural work has provided some indications that this shape cue-contingent priming  
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33 effect might be mediated by attentional systems in the dorsal stream (Lambert & Shin,  
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35 2010). Here we used high density EEG together with source localisation, in combination  
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37 with a single case neuropsychological study, to test the hypothesis that visual encoding  
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39 that triggers a shift of attention, in response to a peripheral object, is mediated via the  
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41 dorsal visual stream. We refer to this below as the dorsal stream attention hypothesis.  
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43 Furthermore we use the EEG data to explore how computations performed in both  
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45 streams could interact via a top-down enhancement of occipital sites from which both  
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47 streams receive their input.  
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In our previous paper, we reported an initial test of the dorsal stream attention hypothesis, which exploited known differences in luminance contrast sensitivity between the two visual pathways (Lambert & Shin, 2010). The dorsal stream is composed almost entirely of rapidly conducting fibres originating from magnocellular (M) layers of lateral geniculate nucleus (LGN), and neurophysiological studies have shown that M-cells respond well to low contrast stimuli (Merigan & Maunsell, 1993). In addition, Bullier (2001) has noted the very short response latencies of visually responsive neurons in parietal cortex, and refers to these dorsal stream areas as the ‘fast brain’. The ventral stream, on the other hand, receives input from both parvocellular (P) and magnocellular (M) layers of LGN. P cells exhibit lower contrast sensitivity, and conduct signals more slowly (Merigan and Maunsell, 1993). If attentional orienting in response to peripheral visual stimuli is mediated by encoding in M-system neurons in the dorsal stream, then such effects should be robust even under reduced luminance contrast. Consistent with this, Lambert & Shin (2010) observed a dramatic dissociation between effects of luminance contrast on visual orienting and on conscious perception of peripheral stimuli. In this paradigm, which is essentially an adaptation of the well known Posner spatial cueing task (Posner, 1980), participants are presented with bilateral spatial cues (e.g. the letters X and T), and are informed that a target object is likely to appear on the same side as one of the letters (see also Lambert & Duddy, 2002). Participants make a simple detection response to the target, and visual orienting in this situation is indexed by comparing response time on *valid trials*, where the target appears at the likely location, as indicated by the cue, with response time on *invalid trials*, where the target appears at the unlikely location. In agreement with the dorsal stream attention hypothesis, Lambert &

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3 Shin (2010) found that the magnitude of rapid visual orienting effects elicited by  
4 peripheral letter cues was unaffected by the luminance contrast of the cues. This was  
5 consistent with two characteristic properties of the dorsal stream – good contrast  
6 sensitivity (Merigan & Maunsell, 1993) and rapid signal conduction (Bullier, 2001).  
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8 Conscious perception of the peripheral letter stimuli was indexed by the speed and  
9 accuracy with which participants were able to indicate whether one of the letters (e.g. X)  
10 was on the left or right of the display. It was observed that conscious perception of low  
11 contrast peripheral letters was massively slower and less accurate than perception of high  
12 contrast peripheral letters. This was consistent both with perceptual phenomenology (the  
13 peripheral letters *appeared* faint and difficult to see), and with involvement of slower  
14 acting parvocellular (P) pathways, which contribute heavily to the ventral visual stream.  
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16 Whilst this finding was in agreement with the dorsal stream attention hypothesis, it  
17 nevertheless constitutes somewhat indirect evidence, being based on a pattern of  
18 behavioural performance predicted by properties of the dorsal stream – sensitivity to  
19 luminance contrast and speed of response. A further caveat is that while robustness under  
20 low contrast is certainly a prediction of the dorsal stream attention hypothesis, as we have  
21 noted the ventral stream includes neurons fed from both parvocellular *and* magnocellular  
22 layers on LGN. Thus, robustness under low contrast could in principle be mediated by  
23 the ventral stream, if the task under investigation were performed via the M component of  
24 that stream.  
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52 Here we tested the dorsal stream attention hypothesis more directly in two  
53 experiments. The first examined the electrophysiological correlates of visual encoding of  
54 peripheral visual objects, using high density EEG recording, together with source  
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3 localisation. The second tested this dorsal stream attention hypothesis by exploring visual  
4 task performance in patient DF, who has a bilateral lesion to the shape processing area  
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6 LO in her ventral stream, but preserved dorsal stream function.  
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## 10 11 12 13 14 15 16 **EXPERIMENT ONE** 17

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20 Figure 1 illustrates the two tasks used in the experiment. In both tasks, a pair of  
21 peripheral letters (X and T) was presented initially, for 67ms, on the left and right of a  
22 visual display. In the *attention procedure* (upper panel) participants made a speeded key-  
23 press response to a target object, having been informed that the target was likely to  
24 appear ( $p=.75$ ) on the same side as one of the letters. In this task, the letters acted as  
25 figural cues and triggered a shift of spatial attention towards the target location, but  
26 participants did not make an explicit response to them. In earlier work we found that  
27 participants are able to shift attention very rapidly indeed in this situation. Lambert &  
28 Duddy (2002) observed attentional benefits in response to peripheral letter cues, even  
29 when there was no delay between onset of the cues and onset of the target. That is,  
30 encoding of bilateral letter cues generated immediate top-down facilitation of a  
31 simultaneously presented target. In the current experiment the stimulus onset asynchrony  
32 (SOA) between onset of the cues and onset of the target was either zero (cues and targets  
33 presented simultaneously) or 700ms.  
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54 In the *perception procedure* (see Fig. 1, lower panel) the initially presented letters  
55 acted as a perceptual preview: 700ms after letter onset the same letters were presented  
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3 again, and participants indicated with a key-press whether a designated letter was on the  
4 left or right of the display. This feature ensured that the temporal structure of the  
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6 left or right of the display. This feature ensured that the temporal structure of the  
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8 perception procedure was identical with the long (700ms) SOA condition of the attention  
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10 procedure, and enabled us to compare directly the neural activation elicited by peripheral  
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12 letters in the context of the attention and perception procedures respectively.  
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17 \*\*\* **Figure 1 about here** \*\*\*  
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23 The dorsal stream attention hypothesis (Lambert & Shin, 2010), together with  
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25 findings from our earlier work (Lambert & Duddy, 2002) enabled several predictions to  
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27 be made regarding performance of these two tasks. These predictions were derived from  
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29 the proposal of Lambert & Shin (2010) that in the attention procedure “rapid dorsal  
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31 processing of cue information is followed by re-entrant feedback, leading to ventral  
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33 stream facilitation of target processing, manifest behaviourally as the cued trial  
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35 advantage” (p. 835). Thus, our first prediction was that in the attention procedure the  
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37 letter cues would generate immediate top-down facilitation of target processing (Lambert  
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39 & Duddy, 2002). This facilitation should be manifest both behaviourally, in shorter  
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41 response latencies when the target appears at the cued (valid) location in the zero SOA  
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43 condition; and electrophysiologically, in enhancement of the P1 event related potential  
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45 (ERP) evoked by the target stimulus over occipital recording sites. Previous work,  
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47 notably by Steven Hillyard’s group (Anllo-Vento, Schoenfeld, & Hillyard, 2004) has  
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49 shown that orienting attention to a visual location is associated with enhancement of the  
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51 P1 component over occipital cortex, consistent with top-down facilitation of target  
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3 processing at early sites in the visual pathway. Secondly, it was predicted that rapid  
4 visual orienting, elicited by peripheral letters in the context of the attention procedure  
5 would be accompanied by rapid neural activation of the dorsal stream, in response to the  
6 cue stimuli. Thirdly, it was predicted that neural activation elicited by peripheral letters in  
7 the context of the perception procedure would reveal activation in the ventral stream, and  
8 that this activation would have a slower time-course than that associated with the dorsal  
9 stream (see Bullier, 2001; Lambert & Shin, 2010).

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These predictions were tested by using high density EEG, together with a source localisation tool, sLORETA (Fuchs, Kastner, Wagner, Hawes, & Ebersole, 2002; Jurcak, Tsuzuki, & Dan, 2007; Pascual-Marqui, 2002). The high temporal resolution offered by this technique allowed us to examine the micro-timing of activations in response to cue and target stimuli. Although the spatial resolution of EEG is coarser than that of other techniques such as fMRI, it was sufficient for the purpose of discriminating between activation in the ventral and dorsal streams, which follow anatomically well separated routes to inferior temporal and superior parietal cortex respectively.

No previous studies have examined the electrophysiological correlates of visual orienting in response to bilateral peripheral letter cues, as employed in our earlier work (Lambert & Shin, 2010, Lambert & Duddy, 2002). However, several earlier studies have examined the electrophysiological correlates of visual orienting in response to centrally presented arrow-head stimuli (Harter, Miller, Price, LaLonde, & Keyes, 1989; Jongen, Smulders, & van der Heiden, 2007; Nobre, Sebestyen, & Miniussi, 2000; Praamstra & Kourtis, 2010; van Velzen & Eimer, 2003). This work has identified three ERP

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3 components elicited by presentation of cue stimuli, each of which is lateralised as a  
4 function of whether attention is being directed to the left or right. These components  
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6 comprise an early directing attention negativity (EDAN), which has been observed  
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8 between 200-400ms after cue onset, an anterior directing attention negativity (ADAN),  
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10 which has been observed at frontal and central sites between 300-500ms after cue onset,  
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12 and a late directing attention positivity (LDAP), which has been observed at posterior  
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14 sites at 500-700ms after cue onset. Because our earlier work has shown that bilateral  
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16 peripheral cues elicit very rapid visual orienting, leading to the prediction of attentional  
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18 enhancement even when cues and target are presented simultaneously, it is clear that ERP  
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20 components with latencies as long as 300-700ms post-cue (ADAN and LDAP) will have  
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22 little or no functional significance in this task situation. However, it is possible that the  
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24 earliest component, the EDAN, may be observed in response to peripheral letter cues.  
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33 The status of the EDAN has been controversial since van Velzen and Eimer (2003)  
34 presented evidence that this component was not related to attention shifting *per se*, but  
35 reflected visual selection of the relevant part of the arrow-head cue stimuli. Visual search  
36 studies have shown that visual selection is associated with a negative ERP component,  
37 the N2pc, which has a latency similar to the EDAN (Eimer, 1996; Luck & Hillyard,  
38 1994). Van Velzen & Eimer (2003) argued that earlier electrophysiological studies of  
39 spatial cueing had misidentified the N2pc, arising from visual selection of the cue  
40 stimulus, as a new component, the EDAN. However, in a more recent report Praamstra  
41 & Kourtis (2010) have argued that the EDAN and N2pc are indeed separate  
42 electrophysiological components. Although the EDAN and N2pc are both negative  
43 components with a similar onset latency, these authors present evidence that they have  
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3 distinct scalp distributions. While the distribution of the N2pc is known to be posterior  
4 and lateral (occipito-temporal), Praamstra & Kourtis (2010) showed that the distribution  
5 of the EDAN is parietal. This evidence led to a fourth and final prediction regarding  
6 performance in the current experiment: that presentation of bilateral letter cues will be  
7 associated with an early directing attention negativity (EDAN), observed over parietal  
8 electrode sites.  
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## 23 Method

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27 *Participants.* Thirteen young adults participated in the experiment.  
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31 *Procedure.* The procedure used for the *attention procedure* was similar to that employed  
32 previously (Lambert & Duddy, 2002; Lambert & Shin, 2010) and is illustrated in the  
33 upper panel of Figure 1. Stimuli were presented in black against a white background ,  
34 7.9° to the left or right of a central fixation cross. Visual angles subtended by the letter  
35 stimuli were 0.6° (height) by 0.5° (width). The target was a small asterisk subtending  
36 0.5°. Participants responded to a target on the right by pressing the ‘/’ key with their right  
37 hand, and responded to a target on the left by pressing the ‘z’ key with their left hand.  
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39 Half the participants were informed that the target would usually ( $p = .75$ ) appear on the  
40 same side as the letter ‘X’, while the other half were informed that the target would  
41 usually appear on the same side as the letter ‘T’. Participants performed 32 practice trials  
42 followed by six blocks of 80 experimental trials.  
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3 The procedure used for the *perception task* was similar to that employed previously  
4 (Lambert & Holmes, 2004; Lambert & Shin, 2010) and is illustrated in the lower panel of  
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6 Figure 1. Participants who oriented towards ‘X’ in the attention procedure were required  
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8 to indicate whether ‘X’ was on the left or right of the display, by pressing the ‘z’ or ‘/’  
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10 keys respectively. Participants who oriented towards ‘T’ in the attention procedure  
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12 indicated whether ‘T’ was on the left or right. Participants performed 20 practice trials  
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14 followed by two blocks of 80 experimental trials. The order of performing the attention  
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16 and perception procedures was counterbalanced across participants.  
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23 *EEG recording.* EEG data were collected using 128-channel Ag/AgCl electrode nets  
24 (Electrical Geodesics Inc., Eugene, Oregon) with a sampling rate of 1000Hz. An average  
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26 reference was used, and signals were band-pass filtered (0.1 – 40Hz) using a digital 3-  
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28 pole Butterworth bi-directional filter. Vertical and horizontal electrooculogram (VEOG  
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30 and HEOG) were recorded and subsequently employed for artifact rejection  
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39 *Statistical analysis.* Analysis of variance was used to compared response times and the  
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41 amplitude of the P1 evoked potential elicited by the target stimulus in the attention  
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43 procedure on trials when it appeared at the likely location, as indicated by the letter cues,  
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45 relative to trials where the target appeared at the unlikely location. These are referred to  
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47 below as valid and invalid trials respectively. Our sLORETA analyses were performed in  
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49 two stages. During the first stage, grand averaged ERP data were modelled with  
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51 sLORETA (see Figure 4, panels a-d). Following this, statistical non-parametric mapping  
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53 (Manly, 2007; Nichols & Holmes, 2001) was used to compare: (i) neural activation  
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55 elicited by the target on valid and invalid trials (see Figure 2c), (ii) neural activation  
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3 elicited by peripheral letters in the context of the perception procedure and in the context  
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5 of the attention procedure (long SOA condition; see Figures 5a, 5b), and (iii) neural  
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7 activation elicited by peripheral letters that signalled a target on the left and activation  
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9 elicited by cues for a right target (see Figures 6c, 6d). These analyses were performed  
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11 using the sLORETA software package (available from  
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13 <http://www.uzh.ch/keyinst/loreta.htm>), and were based on techniques described by  
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17 Nichols & Holmes (2001). Base-line correction and variance smoothing were applied in  
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19 these analyses.  
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## 27 **Results**

### 28 29 30 *Analyses of Target Processing*

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32 These analyses tested our first prediction, that peripheral letter cues would generate  
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34 immediate top-down facilitation of target processing. In the analyses, illustrated in  
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36 Figure 2, electrophysiological activity evoked by the target stimulus, and response times  
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38 to the target were compared between valid trials, where the target appeared at the likely  
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40 location, as indicated by the letters, and invalid trials, where the target appeared at the  
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42 less likely location. It was especially important to establish the presence of a reliable  
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44 difference between valid and invalid trials in the *zero SOA* condition in these analyses,  
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46 because this condition bears directly upon our prediction that peripheral letter cues will  
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48 elicit immediate top-down facilitation of target processing. Although several earlier  
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50 studies have examined the electrophysiological consequences of spatial cueing on target  
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52 processing, most of these studies have used centrally presented cues, and those studies  
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3 which have employed peripheral cues (Anllo-Vento, 1995; Doallo et al., 2004; He,  
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5 Humphreys, Fan, Chen, & Han, 2008; Hopfinger & Mangun, 2001) have all employed  
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7 longer cue-target SOAs. Because this is the first study to examine the  
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9 electrophysiological sequelae of presenting bilateral peripheral cues with a zero SOA  
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11 condition, it was important to discover whether the behavioural effects documented in our  
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13 earlier work (Lambert & Duddy, 2002) would be accompanied by electrophysiological  
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15 effects that resemble those reported in other studies of spatial cueing (Anllo-Vento et al.,  
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17 2004; Klein, 2004).

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24 Response times were faster on valid compared to invalid trials,  $F(1,12) = 15.45, p < .005$ ,  
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26 (see Fig. 2a,b). Although this effect varied as a function of cue-target SOA,  $F(1,12) =$   
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28  $9.36, p < .02$ , the valid trial advantage remained reliable when data from the zero SOA  
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30 condition were examined separately,  $t(12) = 2.74, p < .02$ . Valid trials were also  
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32 associated with an enhancement of the P1 component of the target evoked potential,  
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34 recorded over occipital electrodes O1 and O2 (see Figure 2a,b),  $F(1,12) = 8.19, p < .02$ .  
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36 This effect did not vary as a function of cue-target SOA, target visual field, or electrode  
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38 site (O1 vs. O2). In earlier studies, both these effects have been linked with focusing  
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40 covert attention on a target location (Anllo-Vento, Schoenfeld, & Hillyard, 2004; Klein,  
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42 2004).

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49 Response times were quicker overall in the 700ms SOA condition (475ms), compared to  
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51 the zero SOA condition (511ms),  $F(1,12) = 32.58, p < .001$ . In keeping with earlier  
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53 studies of spatial cueing (e.g. Lambert & Hockey, 1986) we interpret this as reflecting a  
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55 general warning signal effect (Niemi & Naataanen, 1981). That is, presentation of the  
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3 cue provides a general warning that a target is about to be presented, in addition to  
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5 providing spatially specific information about where the target is likely to appear.  
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11 We then used sLORETA together with statistical, non-parametric mapping (SnPM)  
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13 (Manly, 2007; Nichols & Holmes, 2001) to compare neural activation on valid and  
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15 invalid trials in the zero SOA condition. The results, illustrated in Figure 2c, confirmed  
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17 that the P1 enhancement effect shown in Figure 2a was accompanied by stronger activity  
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19 in the occipital lobe. Activation on valid and invalid trials was compared within a 20ms  
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21 time window (136ms-156ms), centred on the P1 peak. Valid trials were associated with  
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23 stronger occipital activation,  $t(12) = 4.18$ ,  $p < .01$ , particularly in the precuneus region.  
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28 Thus, our first prediction was confirmed. Peripheral letter cues produced immediate, top-  
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30 down attentional enhancement of a simultaneously presented target, and this  
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32 enhancement was apparent in both behavioural and electrophysiological measures. An  
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34 important corollary of this finding is that the time-course of the cue encoding processes  
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36 responsible for generating this attentional enhancement must be very rapid indeed (see  
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38 below).  
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45 \*\*\* Figure 2 about here \*\*\*  
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#### 51 Analyses of Letter Processing in the Attention and Perception Procedures

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55 Participants' mean response time to the bilateral letters in the Perception Procedure was  
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57 379ms. Our second and third predictions were tested by examining electrophysiological  
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3 activations evoked by the peripheral letter stimuli. These analyses focused on the long  
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5 SOA condition of the attention procedure, and on comparisons of this condition with the  
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7 perception procedure. In both these conditions peripheral letters were presented on their  
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9 own, 700ms prior to a display that required a response.  
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14 Figure 3 shows waveforms recorded from occipital electrodes (O1 & O2) and occipito-  
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16 parietal electrodes (PO7 & PO8) in response to peripheral letters in the long SOA  
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18 condition of the attention procedure and in the perception procedure. In addition, this  
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20 figure shows waveforms recorded from parietal (P3 & P4), central (C3 & C4) temporal  
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22 (T3 & T4), and posterior midline (Pz & POz) electrodes in the two tasks. As this figure  
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24 shows, the early morphology of waveforms observed in the two task contexts is closely  
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26 similar. The earliest identifiable feature is a positive going component in the occipital  
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28 waveforms, the P1, which commences at around 80ms and reaches a peak at about 145ms  
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30 in both the attention procedure and the perception procedure (see Figure 3, upper two  
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32 panels). Our analyses of the zero SOA condition of the attention procedure (see above)  
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34 had shown that top-down enhancement of target processing was apparent within 136-  
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36 156ms from cue onset. Therefore the cue encoding processes responsible for generating  
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38 this attentional enhancement must have occurred even earlier. This consideration led us to  
39  
40 depart from the normal practice of applying source analysis to the peak of an ERP  
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42 component under consideration, the P1 in this case, because its latency was clearly  
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44 subsequent to the process of interest – the cue encoding processes that generated  
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46 immediate enhancement of target processing in the zero SOA condition. Therefore,  
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48 source analysis was applied to an earlier epoch (80-110ms), which corresponded to the  
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50 onset of the earliest positive going component of the waveforms illustrated in Figure 3a,b.  
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\*\*\* Figure 3 about here \*\*\*

The upper panels of Figure 4 show average scalp topographies, together with the outcome of sLORETA analyses applied to the attention and perception procedures during this early time window (80-110ms from letter onset), corresponding to the onset of the P1 depicted in Figure 3). The lower panels of Figure 4 show average scalp topographies and the outcome of sLORETA analyses during a later time window (130ms-160ms from letter onset), which was centred on the peak of the P1 shown in Figure 3a,b. When the letters served as spatial cues in the attention procedure, early activation was apparent in the dorsal pathway, particularly in the right hemisphere (see Figure 4a). The sLORETA solution suggested maximal activation in the superior parietal lobule of the right hemisphere. Thus, our second prediction, that letter encoding in the context of the attention procedure, would elicit rapid dorsal stream activation was confirmed. In contrast, when the letters served as perceptual previews, in the perception procedure, sLORETA indicated early activation at a high level of the ventral pathway, in the inferior temporal gyrus (ITG; see Figure 4b). In the later epoch, corresponding with the peak of the P1 component of the potential evoked by the letter stimuli, sLORETA analysis indicated very similar patterns of activation in the *attention and perception procedures*. In both cases this was characterised by widespread occipital activation (see Figures 4c, 4d). It is notable that closely similar patterns of occipital activation observed at the peak of the P1 waveform in each task, had dramatically different precursors, involving high level dorsal and high level ventral activation in the *Attention and Perception Procedures* respectively.

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3 \*\*\* Figure 4 about here \*\*\*  
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8 Statistical non-parametric mapping was used to compare early activation elicited by  
9 letters in the context of the *Attention Procedure* with activation elicited by the same  
10 stimuli in the context of the *Perception Procedure*. Consistent with the visual impression  
11 gained from comparing Figure 4a with Figure 4b, this confirmed that early activation  
12 patterns elicited by peripheral letters in the two task contexts differed reliably. As  
13 Figure 5 shows, this difference had two principal sources. Firstly, letters elicited stronger  
14 early activation in the superior parietal lobule of the right hemisphere when they acted as  
15 spatial cues in the *Attention Procedure*,  $t(12) = 2.25, p < .05$ . The orange coloured voxels  
16 shown in Figure 5a indicate sites with greater activation in the *Attention Procedure*,  
17 compared to *Perception Procedure*. Secondly, letters elicited stronger early activation in  
18 the fusiform gyrus of the left hemisphere when they served as perceptual previews in the  
19 *Perception Procedure*,  $t(12) = 2.73, p < .02$ . (see Fig. 5b). The blue coloured voxels  
20 shown in Figure 5b indicate sites with greater activation in the *Perception Procedure*  
21 compared to the *Attention Procedure*.  
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43 \*\*\* Figure 5 about here \*\*\*  
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49 *Analyses of Lateralised ERP Components Elicited by Letter Cues in the Attention*  
50 *Procedure*  
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55 Our fourth prediction was that an early directing attention negativity (EDAN) would be  
56 observed between 200-400ms after cue onset at parietal electrode sites (Jongen *et al.*,  
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3 2007; Praamstra & Kourtis, 2010). This prediction was tested by comparing ERP  
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5 waveforms at parietal electrodes elicited by cues indicating contralateral and ipsilateral  
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7 targets. Figure 6a shows the ERP waveforms elicited by these contra-cues and ipsi-cues<sup>i</sup>,  
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9 plotted separately for a group of four left parietal electrodes (electrodes 42, 47, 52 (P3)  
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11 and 54), and a homologous group of right parietal electrodes (electrodes 86, 92 (P4), 93  
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13 and 98; see Praamstra & Kourtis, 2010). The presence of an EDAN is shown in this  
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15 figure by greater negativity in the ERP waveforms for contra-cues. A tendency of this  
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17 kind is first apparent at both left parietal and right parietal electrode sites from about  
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19 225ms to 275ms post cue onset (see Figure 6a). To explore the scalp topography of this  
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21 effect, the average response from 225-275ms post-cue onset to cues indicating a right  
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23 target was subtracted from the average response to cues indicating a left target during the  
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25 same period. This left cue –right cue subtraction returns positive values over the left  
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27 hemisphere (greater negativity in response to right cues) and negative values over the  
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29 right hemisphere (greater negativity in response to left cues), in the presence of an  
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31 attention related negativity. Figure 6b shows the scalp topography of this difference  
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33 signal. Consistent with the presence of an EDAN, the left hemisphere displays a region  
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35 where the subtraction returned positive values, while the right hemisphere shows a  
36  
37 negative region. While both regions include parietal recording sites in agreement with  
38  
39 prediction, some asymmetry is apparent in the distribution. The positive region over the  
40  
41 left hemisphere appeared to have a parietal-central distribution, while the negative region  
42  
43 over the right hemisphere appeared to have a parietal-temporal distribution. To establish  
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45 the statistical reliability of the attention related negativities apparent over different  
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47 cortical regions, three further analyses were undertaken, each of which employed the  
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3 double subtraction technique used by Kiss, van Velzen, & Eimer (2008). In this  
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5 technique the difference between the left and right cue conditions for a set of left  
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7 hemisphere electrodes is subtracted from the difference between the left cue and right cue  
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9 conditions for homologous electrodes over the right hemisphere. This double subtraction  
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11 quantifies the degree of attention related negativity across both hemispheres. A one  
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13 sample  $t$  test can then be used to evaluate the double subtraction values against the null  
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15 hypothesis of no difference between left and right cue conditions over left and right  
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17 hemisphere recording sites. This procedure was followed for the parietal group of  
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19 electrodes listed earlier, for a group of central electrodes (left hemisphere electrodes: 29,  
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21 30, 36 (C3), 37; right hemisphere electrodes: 87, 104 (C4), 105, 111) and for a group of  
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23 temporal electrodes (left hemisphere electrodes: 40, 41, 45 (T3), 46; right hemisphere  
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25 electrodes: 102, 103, 108 (T4), 109). These analyses suggested that enhanced negativity  
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27 contralateral to the direction of cued attention was reliably present over parietal ( $t(12) =$   
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29 2.43,  $p < .05$ ) and central ( $t(12) = 2.67$ ,  $p = .02$ ) electrode sites, but not over temporal sites  
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31 ( $t(12) = 1.84$ , n.s.).  
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40 In addition, statistical non-parametric mapping and sLORETA was used to compare  
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42 activation elicited by letter cues that signalled a left target, with activation elicited by  
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44 letter cues signalling a right target, during the epoch that spanned 225ms – 275ms post  
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46 cue-onset. Consistent with the analyses described in the previous paragraph, this contrast  
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48 highlighted a right parietal area (inferior parietal lobule), that exhibited stronger activity  
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50 following cues that signalled a contralateral (i.e. left) target,  $t(12) = 6.69$ ,  $p < .01$ , see  
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52 Figure 6c. However, there was no reliable evidence of increased, or reduced, activity in  
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54 any left hemisphere regions, following a cue that signalled a right (contralateral) target.  
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3 The contrast between left cues and right cues revealed a further right hemisphere area,  
4 characterised by *reduced* activity following a cue for a left (contralateral) target (i.e.  
5 relatively stronger activity following a cue for a right (ipsilateral) target),  $t(12) = 11.0$ ,  $p$   
6  $< .01$ . This region was located in the middle frontal gyrus – see Fig. 6d.  
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14 A directly analogous set of analyses was then performed to test for the presence of a  
15 lateralised negative component in response to bilateral letters presented (as perceptual  
16 previews) in the context of the *Perception Procedure*. In this case lateralisation was  
17 assessed with respect to whether a target letter appeared on the left or right of the display.  
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19 No lateralised negativity was apparent in the *Perception Procedure* for any of the three  
20 electrode groups ( $t < 1$  in all cases).  
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30 Visual inspection of Figure 6a suggests the presence of a second phase of attention  
31 related negativity beginning at about 325ms and ending at about 375ms post cue onset.  
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33 However, this tendency was not reliable statistically for any of the three electrode groups.  
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39 \*\*\* **Figure 6 about here** \*\*\*  
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## 43 **Discussion**

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45 Results from Experiment 1 speak to two main issues. Firstly, the results provide direct  
46 support for the dorsal stream hypothesis – that the visual processing that triggers an  
47 attention movement relies on dorsal stream encoding. This hypothesis predicts that dorsal  
48 stream structures should be activated when participants encode peripheral objects that  
49 serve as cues for an attention movement. The activations illustrated in Figures 4a and 5a  
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3 show that this prediction was confirmed<sup>ii</sup>. Secondly, the results show that the  
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5 electrophysiological correlates of bilateral letter cues resemble those described in earlier  
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7 studies of spatial cueing (see Anllo-Vento et al., 2004).  
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15 *Relation of the current study with earlier work on spatial cueing of attention*  
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17 Although the behavioural effects of presenting bilateral letter cues to participants in a  
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19 spatial attention procedure are now well documented (Lambert, 2003; Lambert & Duddy,  
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21 2002; Lambert & Holmes, 2004; Lambert, Norris, Naikar, & Aitken, 2000; Lambert,  
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23 Roser, Wells, & Heffer, 2006; Lambert & Shin, 2010; Shin, Marrett & Lambert, 2011)  
24  
25 this is the first study to probe the electrophysiological sequelae of bilateral peripheral  
26  
27 cues. Results from the experiment show that in two important respects, the  
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29 electrophysiological correlates of bilateral peripheral cues show close correspondence  
30  
31 with effects reported in earlier studies of spatial cueing using both central and  
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33 peripherally presented cues (Anllo-Vento et al., 2004; Doallo et al., 2004; He et al., 2008;  
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35 Praamstra & Kourtis, 2010). Firstly, bilateral cues generated an enhancement of the P1  
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37 component of the ERP elicited by the target stimulus. Interestingly, this effect occurred  
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39 even when there was no delay between onset of the cue letters and onset of the target  
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41 stimulus, indicating that the time-course of the cue encoding that generated this  
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43 attentional enhancement was extremely rapid. Indeed, this time-course appears to be  
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45 more rapid than that observed in studies that have employed centrally presented arrows as  
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47 cues – even though the latter are presented in high acuity central vision, rather than  
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49 peripherally. One would expect that cue discrimination would be performed more rapidly  
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51 in central vision than in parafoveal or peripheral vision. At first sight, this might seem  
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3 paradoxical, but as we have argued elsewhere (Lambert & Duddy, 2002; Lambert et al.,  
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5 2006; Shin, Marrett & Lambert, 2011), the critical factor determining the speed and  
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7 strength of visual orienting effects in spatial cueing studies of attention is not the visual  
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9 location of the cue stimuli (central vs. peripheral), nor the requirement to discriminate  
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11 between cue stimuli (peripheral changes or onsets vs. discrimination of left-right arrows),  
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13 but the presence of *spatial correspondence* between a cue stimulus and a target object.  
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15 The current experiment embodied this feature because the location of the target asterisk  
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17 usually corresponded with the location of one of the peripheral letter cues (Lambert et al.,  
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19 2006). Therefore, in light of our earlier work, rapid orienting was expected, and was  
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21 observed, both behaviourally and electrophysiologically: In the zero SOA condition  
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23 response times were quicker on valid than invalid trials, and an enhancement of the P1  
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25 component of the target ERP was observed on valid trials.  
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33 A second correspondence with earlier studies of spatial cueing is that the ERP  
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35 waveform observed in response to the cue letters included an EDAN (early directing  
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37 attention negativity) component. As indicated earlier, the status of the EDAN and  
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39 whether it is distinct from the N2pc component has been a topic of some controversy  
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41 (Praamstra & Kourtis, 2010; van Velzen & Eimer, 2003). The current results provide  
42  
43 support for the contention of Praamstra & Kourtis (2010) that the EDAN and N2pc are  
44  
45 indeed separate components. Consistent with data reported by Praamstra & Kourtis  
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47 (2010), a statistically reliable EDAN was observed over parietal and central recording  
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49 sites which are clearly distinct from the lateral occipital sites associated with the N2pc  
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51 (see Praamstra & Kourtis, 2010 for analysis of N2pc scalp topography). Furthermore the  
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53 N2pc has been observed in studies, where participants make an explicit perceptual  
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3 response to a target object that is selected and discriminated from one or more non-targets  
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5 (Eimer, 1996). If the N2pc and the EDAN are indeed one and the same component, one  
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7 would expect that this component would also be observed in the *Perception Procedure*,  
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9 because in this task participants must select and respond to one of the peripheral letters  
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11 while ignoring the other. Our observation that an EDAN was observed in response to  
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13 letters in the *Attention Procedure*, but not in the *Perception Procedure* supports the view  
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15 that a central-parietal EDAN, associated with movements of attention is distinct from the  
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17 lateral-occipital N2pc, associated with selecting and responding explicitly to objects in  
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19 multi-element displays.  
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26 On the other hand, our EDAN findings contrast with results reported by McDonald  
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28 and Green (2008), who also used sLORETA to estimate the source of activity evoked by  
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30 a spatial cue. In this study, sLORETA indicated that the source of activity 250-300ms  
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32 post cue-onset, evoked by centrally presented cues comprising a colour change, was in  
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34 occipital cortex. The most salient difference between the Green and McDonald (2008)  
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36 study and the present experiment appears to lie with the nature of the cue stimuli. In  
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38 McDonald and Green (2008) these comprised a change in the colour of lateralised boxes,  
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40 that were present on the display at relatively central locations from the beginning of the  
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42 trial; in the current study the cues were peripheral onset stimuli – the bilateral letters. At  
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44 this stage, it is unclear which of these candidate factors – central vs. peripheral cue  
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46 location, onset vs. no onset cues; colour encoding vs. shape/letter encoding – is  
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48 responsible for the contrast between our findings and those of McDonald and Green  
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50 (2008).  
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3 While the EDAN observed in the present study was correlated with whether  
4 participants oriented attention to left or right, the functional significance of this ERP  
5 component with respect to attention shifting is unclear. It is clear from our analysis of  
6 performance in the zero SOA condition of the *Attention Procedure* that movements of  
7 covert attention in this setting were achieved rapidly, with a latency well below the  
8 quarter of a second or so which elapsed between cue onset and the EDAN (see Fig. 6).  
9 Thus it appears that the EDAN, though correlated with the orientation of attention, is not  
10 reflecting directly the critical cue encoding process that generated covert orienting in this  
11 setting. A similar point applies *a fortiori* to components with even longer latencies, the  
12 ADAN and LDAP, which have been observed in some spatial cueing studies (Jongen et  
13 al., 2007).  
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## 33 EXPERIMENT TWO

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37 The results of Experiment 1 are consistent with the central prediction that EEG activity  
38 during the attention procedure would be primarily associated with a rapidly emerging  
39 signal in the dorsal stream, whereas the Perception Procedure would be associated with  
40 signals in the ventral stream. Experiment 2 seeks to test the causal implications of these  
41 EEG correlates by exploring performance on these tasks in a patient (DF) who has a  
42 bilateral lesion to her ventral stream that severely impairs form perception. If the  
43 differences seen in the dorsal and ventral streams in Experiment 1 truly reflect the  
44 differential *causal* involvement of these streams in each of these tasks, then one should  
45 expect the Perception Procedure but not the Attention Procedure to be disrupted in this  
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3 patient. Indeed given this patient's profound visual form agnosia, her perceptual  
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5 performance is highly likely to be disrupted. The critical question therefore is whether  
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7 her preserved dorsal stream function will be sufficient to generate the shape contingent  
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9 cuing effect in the Attention Procedure, despite a predicted poor performance on the  
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11 perception task.  
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## 14 15 16 17 **Method**

### 18 19 Participants

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21 DF was aged 56 at the time of testing. Her clinical background has been described in  
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23 detail elsewhere (Milner & Goodale, 2006; Milner et al. 1991) including combined  
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25 anatomical and functional MRI scans of her brain by James et al. (2003). DF has severe  
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27 difficulties in discriminating simple geometric shapes (so-called 'visual form agnosia'),  
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29 including individual alphanumeric stimuli. This perceptual deficit is directly attributable  
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31 to her bilateral lesion of area LO, the ventral stream area responsible for basic form  
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33 perception (James et al., 2003; Malach, 1995).  
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38 In addition, four control healthy control participants were recruited from the  
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40 Leuven Experimental Psychology department (2 female, 2 male, mean age 23).  
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### 45 46 Procedure

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48 All experimental procedures were identical to the behavioural tasks used in Experiment 1,  
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50 except for the details listed below. The target was a square subtending 2° degrees of  
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52 visual angle, and targets and letters (height 1.3°, width 1.2°) were presented at 9° degrees  
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54 either side of fixation. The SOA between cue onset and target onset was always 150ms.  
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3 The background of the display was black. Participants responded with the 'W' key to  
4 targets on the left and the 'N' key to targets on the right. DF completed two 10 trial  
5 blocks as practice runs, then two 40 trial, and then sixteen 80 trial experimental blocks of  
6 the Attention Procedure with the 'T' as the prime. All 4 control participants completed a  
7 practice block followed by twenty blocks of 80 trials; two of the control participants were  
8 primed using the 'T' and two with the 'X'. The prime was valid on 80% of trials. The  
9 Perception Procedure was adapted such that participants were presented with an X and a  
10 T 9° either side of fixation for 67ms. Participants had to identify on which side a  
11 particular letter was presented. DF and all control participants completed one block of  
12 this Perception Procedure after the Attention Procedure.  
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### 29 Results analysis

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31 All results are based on accurate responses longer than 100ms, but within 1000ms of the  
32 target onset. Mean response times are calculated only for correct responses. Statistical  
33 comparisons between the performance of patient DF and the performance of controls  
34 were carried out using specifically designed tools by Crawford and Garthwaite (2002,  
35 2007) to analyse single case studies in comparison to small control samples.  
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### 46 **Results**

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48 A *t*-test on the reaction times to valid vs invalid trials revealed a significant cueing effect  
49 for DF and all four control participants (see Figure 7) in the Attention Procedure. Indeed  
50 most critically the cueing effect manifest in DF's reaction times does not differ from that  
51 seen in controls ( $p=0.87$ ).  
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\*\*\* Figure 7 about here \*\*\*

DF's performance in the Perceptual Procedure was however significantly disrupted, in that she correctly identified the side on which a letter was presented on only 66% of trials (chance 50%) compared to a mean accuracy of 95.6% for controls. This difference in accuracy on the perceptual task was highly significant ( $p < 0.001$ ). It should be noted that DF was adamant that she could not see any letters during the Attention Procedure, let alone discriminate on which side of the screen there was an 'X' or a 'T'. She was also adamant that she was entirely guessing during the Perception Procedure. Given that the Perception Procedure was completed immediately after the Attention Procedure, and given that DF was asked to spot the letter 'T' which had been used as a prime for the previous hour and a half of testing, it is quite possible that her above-chance (66% correct) response rate reflected the fact that her own orienting response was biasing her judgements, rather than that she was perceptually discriminating the two letters.

In the Attention Procedure, the four control participants also showed a similar trend in their accuracy data (valid 94%, invalid 89.7%) to that seen in their reaction times, a trend that was also apparent in DF (valid 90.6%, invalid 88.8%). Although this trend was not significant in the control sample ( $p = 0.13$ ) the trend shown by DF does not differ from that shown by the control sample ( $p = 0.28$ ). These trends towards a priming effect on accuracy as well as RTs indicate that the RT results indicated genuine priming, and not merely a speed-accuracy trade-off.

## Discussion

Despite a profound disruption to DF's ability to see the letter shape primes as a result of the damage to shape processing areas in her ventral stream, she showed a normal cue-contingent priming effect based on these letter shapes. This finding is clearly consistent with the hypothesis that the priming effect is mediated by the dorsal rather than the ventral stream, a matter that will be discussed further in the General Discussion.

We have previously explored DF's sensitivity to different attentional effects (de-Wit, Kentridge and Milner, 2009) in which we found that DF was sensitive to basic spatial cuing effects (Posner 1980) but not object-based attention effects (Scholl 2001). The current results extend these findings by demonstrating that DF's spatial attention can be guided by shape based cue-target contingencies. We argued on the basis of our previous results with DF (and other neuroimaging research by Martinez et al. 2006) that the object representations required to guide object based attention effects (Scholl, 2001) are developed within the ventral stream. The use of shape cues in the current experiment however should not lead one to confuse the effect observed here with an object-based attention effect, in which attention is preferentially allocated within a selected object. Instead this cueing effect reflects an allocation of spatial attention based on a shape-target contingency, rather than a preferential allocation of attention within a particular object. In other words, the surviving shape processing mechanisms in DF's dorsal stream are

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3 sufficient to guide her attention in response to shape cueing, but not sufficient to provide  
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5 the representations necessary to enable object-based attention effects to be seen.  
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## 11 12 13 14 **GENERAL DISCUSSION** 15 16 17

18 The results from both experiments are consistent with predictions based on our  
19 hypothesis that the priming seen in our peripheral shape-cue contingent paradigm derives  
20 from computations performed in the dorsal visual stream.  
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27 In everyday experience the processes of shifting attention in response to a peripheral  
28 object and consciously perceiving that object are so intimately entwined that it is difficult  
29 to 'see' the distinction (see Posner (1980) for discussion). The tasks described here  
30 provide a way of dissociating these processes in order to examine their distinct  
31 neurocognitive bases. Experiment 1 has provided evidence that when a peripheral object  
32 influenced visual attention, without necessarily entering conscious awareness, rapid  
33 activation of the dorsal visual stream was observed. Source localisation identified the  
34 superior parietal lobule (SPL) as the principal source of this activation. This region  
35 shows good correspondence with earlier PET (Corbetta, Miezin, Shulman, & Petersen,  
36 1993) and fMRI (Gitelman et al., 1999; Szczepanski et al., 2010) studies which have  
37 suggested that superior parietal cortex plays an important role in the control of spatial  
38 attention. Vandenberghe & Gillebert (2009) review a variety of fMRI studies, and  
39 conclude that the SPL is implicated as playing a specific role in spatial shifts of attention.  
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3 Moreover, in a recent fMRI study of spatial cueing, Szczepanski *et al.* (2010) identified a  
4 particular region in the right, but not left, SPL that carried spatial attention-related  
5 activations. This result is consistent with the lateralisation observed in our sLORETA  
6 analysis. As Figures 4a and 5a show, this analysis indicated that the right superior parietal  
7 lobule was more active in the *Attention Procedure* compared to the *Perception*  
8 *Procedure*. Furthermore, it is exactly these dorsal stream resources that remain preserved  
9 in patient DF, for whom a normal attentional cueing effect was revealed in Experiment 2.  
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21 In contrast, when a peripheral object required a conscious perceptual response,  
22 rapid activation of the ventral visual stream was observed in our healthy subjects. Source  
23 analysis with sLORETA indicated that the fusiform gyrus of the left hemisphere showed  
24 stronger early activation in the *Perception Procedure* relative to the *Attention Procedure*.  
25 This fusiform region is adjacent to the damaged region in DF's brain (area LO) which has  
26 caused her inability to distinguish simple shapes. It may therefore be that the activations  
27 seen during the perceptual task in our healthy subjects arise in and around this same area  
28 LO. Thus, the sites identified by sLORETA, when comparing activations in the *Attention*  
29 and *Perception Procedures*, correspond well with those identified in earlier research on  
30 the neural correlates of spatial attention and perceptual identification of simple shape  
31 stimuli respectively. In full agreement with this, we found in Experiment 2 that patient  
32 DF's bilateral lesion to shape processing areas within the ventral stream led to a serious  
33 disruption to performance in the *Perception Procedure*, whereas her functionally intact  
34 dorsal stream supported entirely spared performance in the attention task.  
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4 The electrophysiological and neurological dissociations reported here are consistent  
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6 with the behavioural dissociation described in our earlier study (Lambert & Shin, 2010),  
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8 in which reducing luminance contrast massively impaired conscious perception of  
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10 peripheral letters, but had no effect on rapid orienting in response to the same stimuli,  
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12 when they acted as cues in the *Attention Procedure*. Indeed, six lines of converging  
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14 evidence can now be marshalled in support of the dorsal stream attention hypothesis:  
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16 (a) As we have noted, the attentional effects of peripheral letter cues are robust under low  
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18 contrast, consistent with the physiological properties of the M-cell inputs to the dorsal  
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20 visual pathway (Lambert & Shin, 2010); (b) Experiment 1 provided evidence of rapid  
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22 dorsal activation, when bilateral letters served as spatial attentional cues;  
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25 (c) Experiment 2 showed that patient DF, in whom the ventral stream is damaged while  
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27 the dorsal stream remains intact, is able to orient in response to bilateral letter cues in the  
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29 Attention Procedure, but performs very poorly when asked to discriminate these stimuli  
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31 in the Perception Procedure; (d) consistent with temporal properties of dorsal visual  
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33 processing (Bullier, 2001; Milner & Goodale, 2006), peripheral letter cues affect target  
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35 processing, even when cue and target stimuli are presented with brief SOAs or  
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37 simultaneously (Experiment 1, zero SOA condition ; Lambert & Duddy, 2002);  
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40 (e) consistent with evidence that dorsal visual processing is largely unconscious (Milner  
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42 & Goodale, 2006), Lambert, Naikar, McLachlan & Aitken (1999) and Shin, Marrett &  
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44 Lambert (2011) found that peripheral cue stimuli, including letter cues of the kind used in  
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46 the current study, can influence attention independently of conscious awareness (see also  
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48 Risko & Stolz, 2010, Peterson & Gibson, 2011); (f) Lambert & Duddy (2002) compared  
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50 effects of bilateral letter cues presented centrally (immediately to left and right of a  
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3 central cross) and  $7.3^\circ$  from fixation. The time-course and magnitude of visual orienting  
4 effects were unaffected by whether the letter cues were presented centrally or  
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6 peripherally. Although participants did not perform a perceptual control task, one would  
7  
8 certainly expect that conscious discrimination of letters at  $7.3^\circ$  eccentricity would be  
9  
10 impaired relative to discrimination of the same letters in central vision. The observation  
11  
12 that visual orienting in response to letters is unaffected by whether they are presented  
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14 centrally or at  $7.3^\circ$  eccentricity is consistent with the dorsal stream attention hypothesis  
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16 because anatomical studies have shown that representation of peripheral visual locations  
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18 is stronger in the dorsal than the ventral stream (Merigan & Maunsell, 1993). Taken  
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20 together, these six empirical findings provide substantial and converging support for the  
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22 hypothesis that visual encoding which triggers a shift of attention arises from processing  
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24 in the dorsal visual stream.  
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33 In both the attention and perception procedures, rapid, high level activation – at  
34 superior parietal and inferior occipito-temporal sites respectively – was followed by  
35 strong activation at ‘earlier’ sites in the visual pathway, in occipital cortex. In contrast to  
36 the anatomical separation apparent in the early activations, the location of later  
37 activations, associated with the peak of the P1 evoked by the letter stimuli, was closely  
38 similar in the Attention and Perception Procedures (see Figure 4 c,d). The fine-grained  
39 timing of this pattern is consistent with the hypothesis that visual processing in each task  
40 involved a rapid, initial burst of feed-forward activity, followed by re-entrant feedback  
41 which modulated ‘lower level’ visual computations performed in occipital cortex  
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43 (Martinez et al., 1999). This proposal is consistent with previous evidence that  
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3 attentional enhancement can arise from temporally late top-down modulation of activity  
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5 at anatomically early sites in the visual pathway (see Olson, Chun, & Allison, 2001).  
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10 This view of perception and attention implies a startling temporal paradox, in which  
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12 high level processing in either visual pathway can precede and influence ostensibly  
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14 'lower' level processing. This raises the question of how high level processing can be  
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16 completed with sufficient speed to affect processing at an 'earlier' stage. According to  
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18 Bullier's (2001) 'integrated model of visual processing', rapid first-pass computations  
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20 performed in the dorsal stream are followed by re-entrant feedback which modulates  
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22 processing in the 'earlier' areas V1 and V2. According to this model, visual areas V1 and  
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24 V2 can be viewed as 'active blackboards', which integrate sensory, feed-forward signals  
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26 with re-entrant, feed-back signals. This 'active blackboard' interpretation is consistent  
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28 with a host of fMRI results highlighting that higher level perceptual interpretations are  
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30 evident in the signals recorded from early areas (Murray et al. 2006, Williams et al. 2008,  
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32 Harrison and Tong (2009). Bullier's (2001) model therefore suggests a promising  
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34 hypothesis for resolving one aspect of the seeming temporal paradox in our data.  
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36 According to this hypothesis, the initial burst of feed-forward processing elicited by  
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38 letters when they act as spatial cues is carried by rapid onset M-system neurons in the  
39  
40 dorsal visual pathway. Re-entrant feedback from 'fast brain' computations in the parietal  
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42 lobe are then fed back to occipital areas in time to affect target processing within the  
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44 ventral system, which leads eventually to a conscious perceptual response to the target  
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Although, as we have noted above, the temporal scenario implied by our findings appears surprising and paradoxical, it is nevertheless consistent with data gained from electrophysiological studies, regarding the speed of visual processing (see Tovee, 1994). It is important to remember here that for the letter cues to be effective in the attention procedure, it is not necessary to process them *as letters*. The cues are drawn from a stimulus set comprising just two items (X or T), and these stimuli differ at a very basic perceptual level: the former comprises two oblique lines, while the latter comprises one vertical and one horizontal line. It is known that simple attributes, such as line orientation are extracted early in visual processing, at V1. Three observations are pertinent here. Firstly, Tovee (1994) notes that cells with transient responses, which provide the major input for the dorsal stream respond with an average latency of 28ms. Secondly, by recording from successive areas in the visual processing stream, it has been estimated that it takes about 10-15ms for signals to be transmitted from one area (e.g. V1) to a succeeding area (e.g. V2; see Tovee, 1994). Thirdly, by recording from a large number of cells simultaneously, it is possible to estimate how long it takes for the visual signal associated with one stimulus to be discriminated from the visual signal associated with another stimulus. Although the very simple stimulus discrimination (X vs. T) used in this study has not, to our knowledge, been examined in this fashion, more complex stimuli, including faces have been studied in this way. In reviewing this work, Tovee (1994) suggests that most of the information encoded in a spike train is available with 20ms – 50ms from the onset of that spike train (see also Tovee & Rolls, 1995; Rolls & Tovee, 1994). Our interpretation of Experiment 1 implies that cue discrimination can be achieved very rapidly, within 80-110ms from stimulus onset. Though rapid, this temporal

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3 scenario is entirely consistent with data gained from electrophysiological studies, which  
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5 have examined the time course of visual processing directly, using single cell and  
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8 multiple cell recording techniques.  
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12 Our prediction that the *Perception Procedure* would generate stronger ventral activation  
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14 than the *Attention Procedure* was confirmed, but our prediction that this activation would  
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16 follow a slower time-course than that associated with dorsal (*Attention Procedure*)  
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18 activation was disconfirmed. It is noteworthy that dorsal-ventral differentiation between  
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20 evoked activity in the two task contexts involved not only early dorsal activation in the  
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22 *Attention Procedure*, as predicted, but also early ventral activation in the *Perception*  
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24 *Procedure*. We predicted that the latter would have a somewhat slower time-course than  
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26 the dorsal ‘fast brain’ activation associated with the *Attention Procedure* (Bullier, 2001).  
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28 As noted earlier, peripheral letters presented in the context of the *Perception Procedure*,  
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30 served as perceptual previews – participants released a conscious perceptual response to  
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32 the letters, when they were presented again, 700ms after onset of the preview display.  
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37 This design feature ensured that the two tasks shared an identical temporal structure, but  
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39 it also meant that the preview display acted as an identity cue, which predicted the nature  
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41 and location of the letters on the succeeding display with perfect fidelity. One possible  
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43 interpretation of early ventral activation in the *Perception Procedure* (see Figure 4b) is to  
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45 propose that while encoding of spatial primes is mediated, as we have shown, by rapid  
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47 dorsal activation, encoding of identity primes is mediated via rapid ventral activation,  
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49 perhaps mediated by the rapidly conducting M component of the ventral stream. Further  
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51 neuroimaging studies which compare directly the neural correlates of spatial and identity  
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53 priming will be required to test these hypotheses.  
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3 While our interpretation of the performance in the *Perception Procedure* has emphasised  
4 that participants make a direct conscious response to the letters, it is also germane to note  
5 that the incorporation of a delay in the *Perception Procedure* means that it can also be  
6 characterised as a working memory task. To the extent that one identifies working  
7 memory representations with representations that are maintained in conscious awareness,  
8 the *Perception Procedure* can be described as a working memory task. However, it is  
9 worth remembering that in both the *Attention Procedure* and the *Perception Procedure*,  
10 participants make a directional response that is determined by the nature of the peripheral  
11 cue items.  
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28 Our results with patient DF suggest strongly that visual letter shapes can be coded  
29 within the dorsal stream independently of the ventral stream. Our data suggest further  
30 that this coded information can impact directly upon attentional structures within the  
31 dorsal stream, the most prominent of which is the lateral intraparietal (LIP) complex.  
32 There is in fact good evidence not only for shape coding within dorsal stream areas  
33 dedicated for guiding hand and other bodily movements (James et al., 2002; Durand et al,  
34 2007), but also within the LIP itself (Janssen et al 2008; Sereno & Amador, 2006; Lehky  
35 & Sereno, 2007). It has been proposed that this kind of coding within the LIP complex  
36 may be useful in everyday life in constructing salience maps of complex visual scenes for  
37 the guidance of attention within those scenes (Arcizet et al., 2011). Thus, our results may  
38 also have implications for understanding the neurocognitive processes that are recruited  
39 in visual search tasks, and in particular with regard to the role of interactions between  
40 dorsal and ventral stream processing during visual search (see Vidyasagar, 1999).  
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### Summary & Conclusions

Both the ventral and dorsal streams were responsive to peripheral shapes, consistent with the idea that 'object' or 'what' processing is a feature of both streams. However the response to these shapes in each stream was selective for the task performed by the participant. We found that areas in the ventral stream were primarily responsive to the perceptual discrimination of our letter shapes, and indeed the ventral stream lesion in patient DF was associated with a profound disruption of the recognition of those shapes. In contrast, areas in the dorsal stream were primarily responsive to the use of these letter shapes as attentional cues, and indeed the preservation of these dorsal areas in patient DF was associated with a normal shape contingent cuing effect. These results are consistent with Milner and Goodale's (1995, 2006) contention that shape information is used by both streams, but for very different purposes.

The General Introduction outlined an apparent paradox between the ventral stream's role in conscious shape perception, and the profound influence that dorsal stream lesions have on conscious perception in extinction and neglect. The current results might help to resolve this paradox by demonstrating that the dorsal stream is able to rapidly compute perceptual contingencies that can be used to guide processing resources via a rapid feedback to occipital areas, thus highlighting how the unconscious learning of shape cue contingencies and the allocation of processing resources on the basis of those contingencies can have a clear influence on conscious perception. These results therefore not only highlight an important functional specialisation between the two streams in their role in perception and attention, but also highlight how these two streams might interact

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**Footnotes**

<sup>i</sup> It is important to remember here that the cue stimuli themselves were always bilateral. Contra-cues and ipsi-cues were cues that indicated a contralateral and ipsilateral target respectively.

ii Although the activations illustrated in Figures 5a and 6a confirm the prediction of the dorsal stream attention hypothesis, it is possible that activity in the tecto-pulvinar visual pathway could also have contributed to activation of these structures. With EEG techniques of the kind used here it is not possible to evaluate the relative contribution of the dorsal cortical visual pathway and the tecto-pulvinar pathway to the parietal activations illustrated in Figures 5a and 6a. However, evidence from an fMRI study that is currently underway is likely to shed light on this issue.

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## FIGURE CAPTIONS

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8 **Figure 1. Experimental tasks.** The upper and lower panels illustrate the sequence of  
9 events in each experimental task. In the *Attention Procedure* participants responded to  
10 the asterisk, and the peripheral letters acted as spatial cues: That is, participants oriented  
11 attention towards the likely target location in response to the letters. In the *Perception*  
12 *Procedure* participants made a conscious response to the letters themselves (see main text  
13 and Methods for further details).  
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24 **Figure 2. Effects of letter cues on target processing.** The upper panels (a, b) show that  
25 response times were quicker and perceptual processing was enhanced on valid compared  
26 to invalid trials. Response times were quicker ( $p < .005$ ) and the P1 evoked potential  
27 recorded over occipital electrodes O1 and O2 was enhanced ( $p < .02$ ) on valid compared  
28 to invalid trials. Each panel displays the average waveform recorded from electrodes O1  
29 & O2 for valid and invalid trials. The lower panel (c) shows the outcome of statistical  
30 non-parametric mapping analysis of the zero SOA condition. Activation on valid and  
31 invalid trials was compared within a 20ms time window (136ms-156ms), centred on the  
32 P1 peak. Valid trials were associated with stronger occipital activation ( $p < .01$ ),  
33 particularly in the precuneus region.  
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51 **Figure 3. Occipital, temporal, parietal, central and posterior midline waveforms in**  
52 **response to letter cues in the *Attention* and *Perception Procedures*.** The average  
53 responses recorded from occipital (O1 & O2; panel a), occipito-parietal (PO7 & PO8;  
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3 panel b), parietal (P3 & P4; panel c), temporal (T3 & T4; panel d), central (C3 & C4;  
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5 panel e), and posterior midline (Pz and POz; panel f) electrodes, in response to peripheral  
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7 letters presented in the context of the *Attention Procedure* (SOA 700ms condition) and  
8  
9 the *Perception Procedure* are shown.  
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15 **Figure 4. Neural activation in the Attention and Perception Procedures.** sLORETA  
16  
17 revealed a striking dissociation between the cortical sources of early activation evoked by  
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19 peripheral letters in the two experimental tasks. During the early epoch (80-110ms after  
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21 letter onset) activity in the *Attention Procedure* was observed at sites corresponding to the  
22  
23 dorsal visual pathway, with maximal activation in the superior parietal lobule (SPL;  
24  
25 panel a). During the same epoch, activity in the *Perception Procedure* was observed at  
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27 sites corresponding to the ventral pathway, with maximal activation in the inferior  
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29 temporal gyrus (ITG; panel b). During the later epoch (130-160ms after letter onset)  
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31 evoked activity in the two task contexts appeared indistinguishable, and was  
32  
33 characterised by widespread occipital activity, particularly in the precuneus region  
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35 (panels c, d). The rightmost frame of each panel shows the average scalp topography for  
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37 the early (panels a & b) and late (panels c & d) temporal epochs in each task context.  
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46 **Figure 5. Comparison of early activation in the Attention and Perception**  
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48 **Procedures.** Early activation evoked by letters in the context of the two experimental  
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50 tasks was compared. Orange coloured voxels indicate sites with greater activation in the  
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52 *Attention Procedure*, compared to Perception Procedure; blue voxels indicate sites with  
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54 greater activation in the *Perception Procedure*. Panel (a) shows that stronger activation  
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3 was observed in the *Attention Procedure* at parietal and superior parietal sites ( $p<.05$ ).  
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5 Panel (b) shows that stronger activation was observed in the *Perception Procedure* at  
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7 sites in the inferior temporal lobe ( $p<.02$ ).  
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12 **Figure 6. Early directing attention negativity (EDAN) in response to cue letters.**

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14 Panel a shows the average waveforms at four left parietal and four right parietal  
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16 electrodes (see text for further details of each electrode group) that were elicited in  
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18 response to cue letters indicating ipsilateral and contralateral targets. A statistically  
19  
20 reliable EDAN was observed between 225-275ms post cue onset (see *Results*). Panel b  
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22 shows the average scalp topography recorded during this temporal epoch. Panel c shows  
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24 the parietal area of the right hemisphere (inferior parietal lobule) that was identified by  
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26 statistical non-parametric mapping (see *Results*) as being more active in response to the  
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28 cue for a left target. Panel d shows the right frontal area (middle frontal gyrus) that was  
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30 identified by statistical non-parametric mapping as being less active in response to the  
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32 cue for a left target (i.e. more active in response to the cue for a right target; see *Results*).  
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44 **Figure 7. Reaction times to valid and invalidly cued targets for Patient DF and four**  
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46 **control subjects.** The asterisks indicate a significant t-test ( $p<0.05$ ) comparing the  
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48 individual reaction times for valid and invalid trials for each participant. DF and every  
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50 control participant showed a significant cuing effect. Furthermore using Crawford and  
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52 Garthwaite's (2007) statistic we found that the size of the cuing effect in DF does not  
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54 differ from that shown by controls. For further details of Crawford and Garthwaite's  
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3 approach to comparing single case studies to small control samples see  
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5 <http://www.abdn.ac.uk/~psy086/dept/SingleCaseMethodology.htm>.  
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21 <sup>i</sup> It is important to remember here that the cue stimuli themselves were always bilateral. Contra-cues and  
22 ipsi-cues were cues that indicated a contralateral and ipsilateral target respectively.  
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27 <sup>ii</sup> Although the activations illustrated in Figures 5a and 6a confirm the prediction of the dorsal stream  
28 attention hypothesis, it is possible that activity in the tecto-pulvinar visual pathway could also have  
29 contributed to activation of these structures. With eeg techniques of the kind used here it is not possible to  
30 evaluate the relative contribution of the dorsal cortical visual pathway and the tecto-pulvinar pathway to the  
31 parietal activations illustrated in Figures 5a and 6a. However, evidence from an fMRI study that is  
32 currently underway is likely to shed light on this issue.  
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(Lambert Fig. 1)

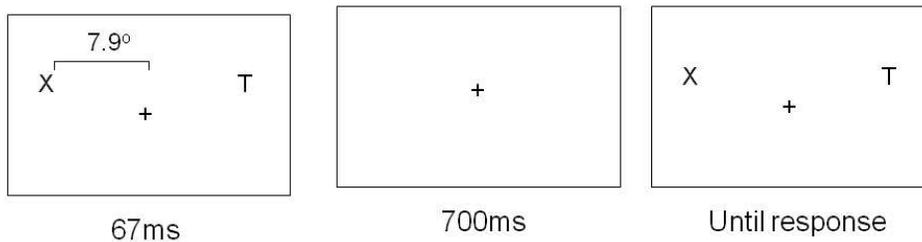
**(a) Attention Task****(b) Perception Task**

Figure 1. Experimental tasks. The upper and lower panels illustrate the sequence of events in each experimental task. In the Attention Procedure participants responded to the asterisk, and the peripheral letters acted as spatial cues: That is, participants oriented attention towards the likely target location in response to the letters. In the Perception Procedure participants made a conscious response to the letters themselves (see main text and Methods for further details).  
254x190mm (96 x 96 DPI)

(Lambert Fig. 2)

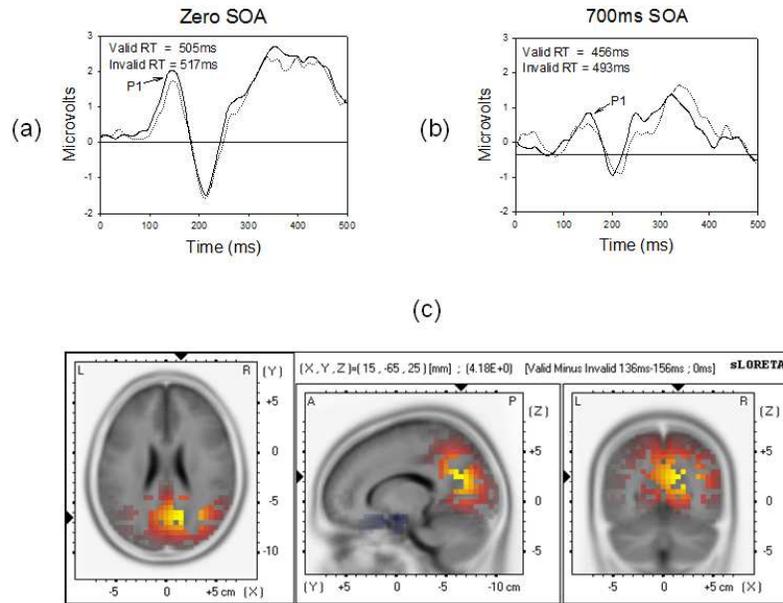


Figure 2. Effects of letter cues on target processing. The upper panels (a, b) show that perceptual processing of the target was enhanced by spatial cueing. Response times were quicker ( $p < .005$ ) and the P1 evoked potential recorded over occipital electrodes O1 and O2 was enhanced ( $p < .02$ ) on valid compared to invalid trials. Each panel displays the average waveform recorded from electrodes O1 & O2 for valid and invalid trials. The lower panel (c) shows the outcome of statistical non-parametric mapping analysis of the zero SOA condition. Activation on valid and invalid trials was compared within a 20ms time window (136ms-156ms), centred on the P1 peak. Valid trials were associated with stronger occipital activation ( $p < .01$ ), particularly in the precuneus region.

254x190mm (96 x 96 DPI)

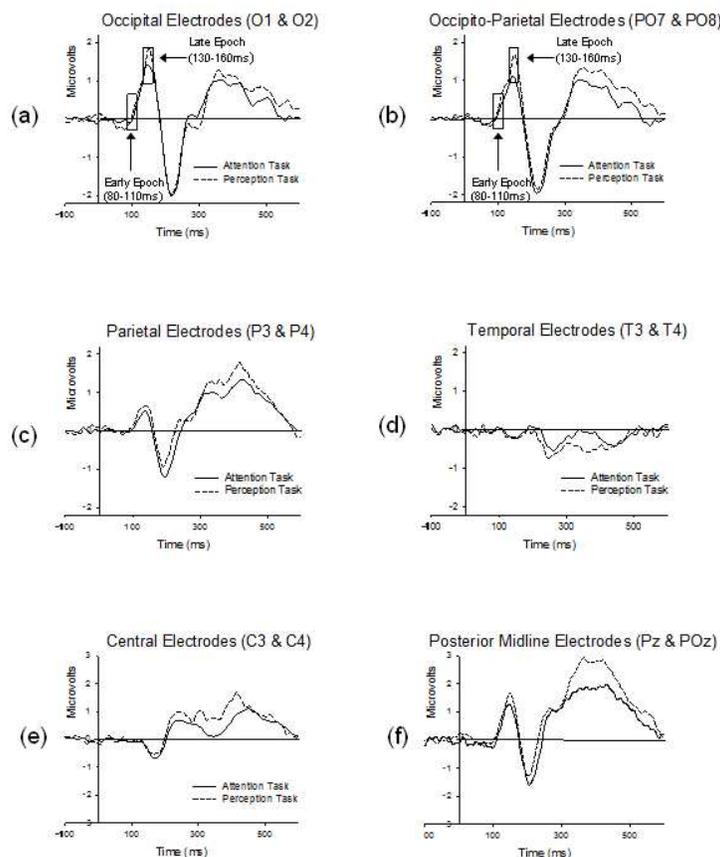


Figure 3. Occipital, temporal, parietal, central and posterior midline waveforms in response to letter cues in the Attention and Perception Procedures. The average responses recorded from occipital (O1 & O2; panel a), occipito-parietal (PO7 & PO8; panel b), parietal (P3 & P4; panel c), temporal (T3 & T4; panel d), central (C3 & C4; panel e), and posterior midline (Pz and POz; panel f) electrodes, in response to peripheral letters presented in the context of the Attention Procedure (SOA 700ms condition) and the Perception Procedure are shown.

190x254mm (96 x 96 DPI)

(Lambert Fig. 4)

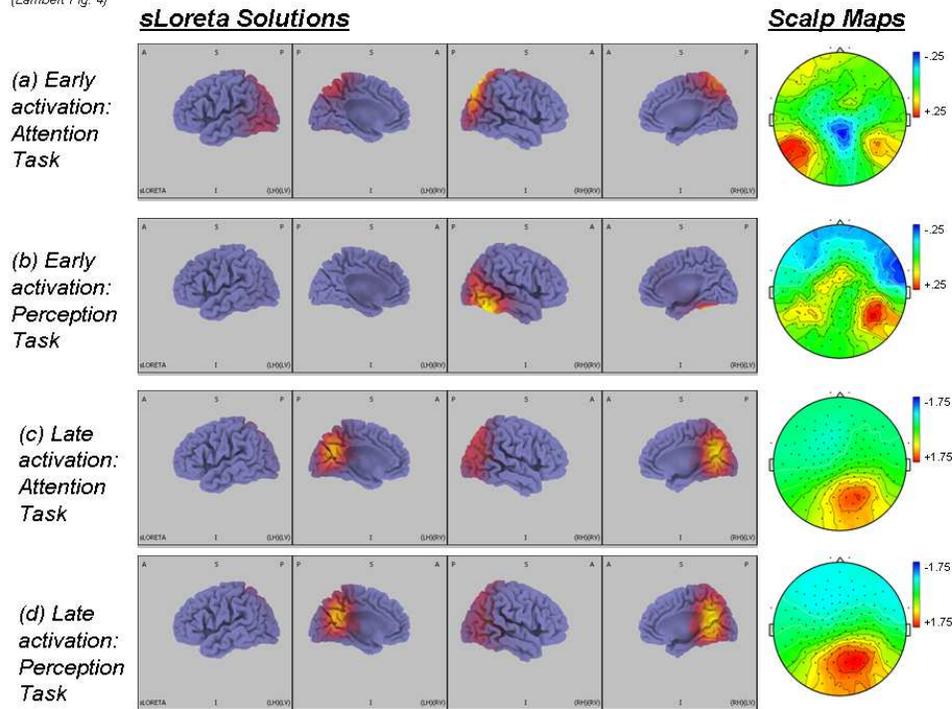


Figure 4. Neural activation in the Attention and Perception Procedures. sLORETA revealed a striking dissociation between the cortical sources of early activation evoked by peripheral letters in the two experimental tasks. During the early epoch (80-110ms after letter onset) activity in the Attention Procedure was observed at sites corresponding to the dorsal visual pathway, with maximal activation in the superior parietal lobule (SPL; panel a). During the same epoch, activity in the Perception Procedure was observed at sites corresponding to the ventral pathway, with maximal activation in the inferior temporal gyrus (ITG; panel b). During the later epoch (130-160ms after letter onset) evoked activity in the two task contexts appeared indistinguishable, and was characterised by widespread occipital activity, particularly in the precuneus region (panels c, d). The rightmost frame of each panel shows the average scalp topography for the early (panels a & b) and late (panels c & d) temporal epochs in each task context.

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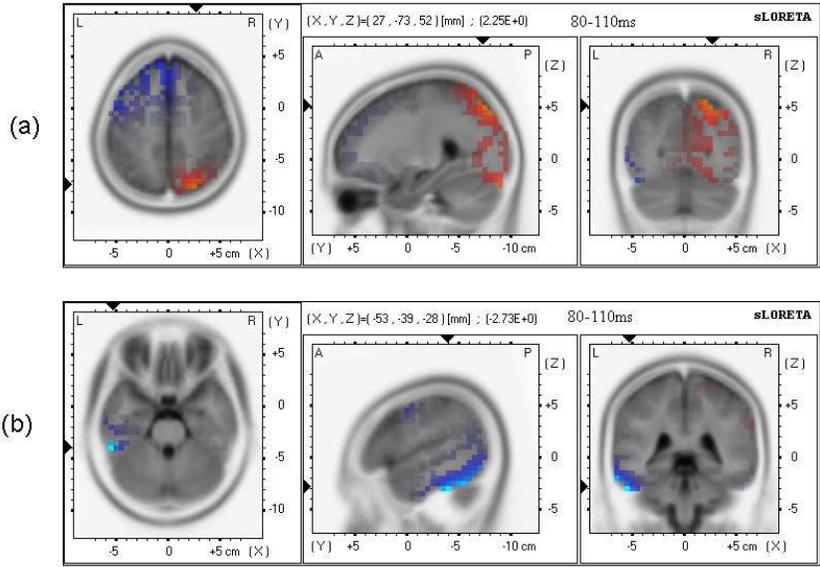


Figure 5. Comparison of early activation in the Attention and Perception Procedures. Early activation evoked by letters in the context of the two experimental tasks was compared. Orange coloured voxels indicate sites with greater activation in the Attention Procedure, compared to Perception Procedure; blue voxels indicate sites with greater activation in the Perception Procedure. Panel (a) shows that stronger activation was observed in the Attention Procedure at parietal and superior parietal sites ( $p < .05$ ). Panel (b) shows that stronger activation was observed in the Perception Procedure at sites in the inferior temporal lobe ( $p < .02$ ).  
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(Lambert Fig. 6)

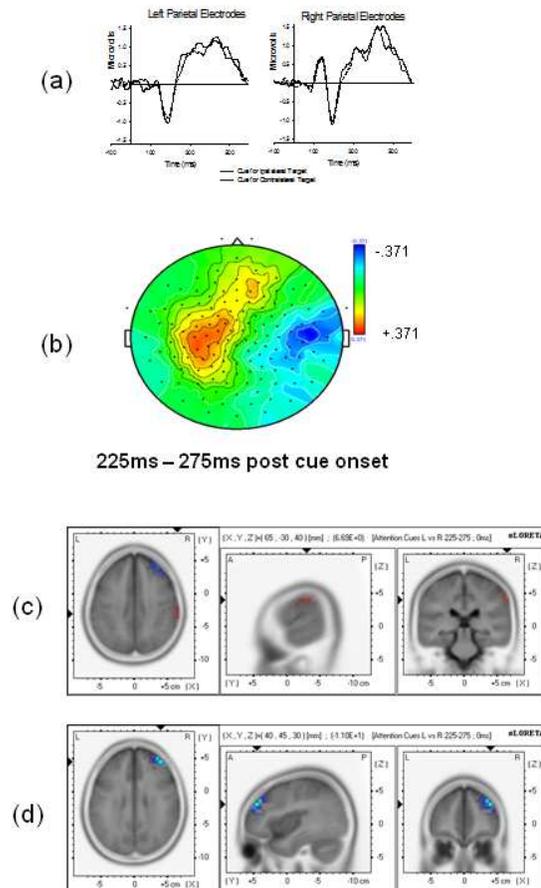


Figure 6. Early directing attention negativity (EDAN) in response to cue letters. Panel a shows the average waveforms at four left parietal and four right parietal electrodes (see text for further details of each electrode group) that were elicited in response to cue letters indicating ipsilateral and contralateral targets. A statistically reliable EDAN was observed between 225-275ms post cue onset (see Results). Panel b shows the average scalp topography recorded during this temporal epoch. Panel c shows the parietal area of the right hemisphere (inferior parietal lobule) that was identified by statistical non-parametric mapping (see Results) as being more active in response to the cue for a left target. Panel d shows the right frontal area (middle frontal gyrus) that was identified by statistical non-parametric mapping as being less active in response to the cue for a left target (i.e. more active in response to the cue for a right target; see Results).

190x254mm (96 x 96 DPI)

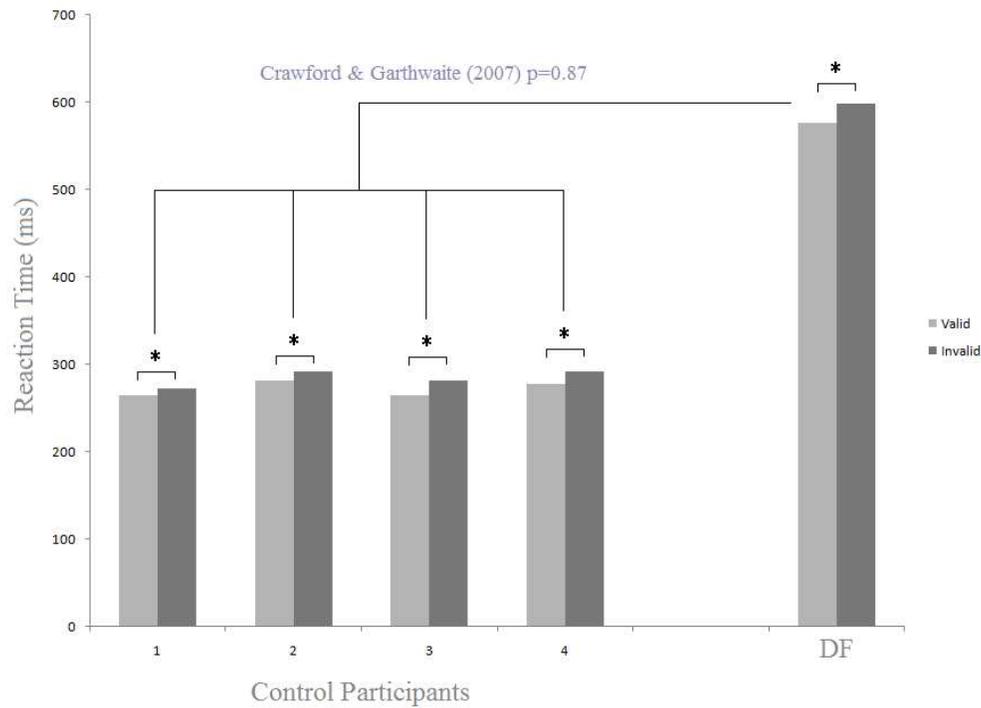


Figure 7. Reaction times to valid and invalidly cued targets for Patient DF and four control subjects. The asterisks indicate a significant t-test ( $p < 0.05$ ) comparing the individual reaction times for valid and invalid trials for each participant. DF and every control participant showed a significant cueing effect. Furthermore using Crawford and Garthwaite's (2007) statistic we found that the size of the cueing effect in DF does not differ from that shown by controls. For further details of Crawford and Garthwaite's approach to comparing single case studies to small control samples see <http://www.abdn.ac.uk/~psy086/dept/SingleCaseMethodology.htm>.  
232x168mm (96 x 96 DPI)