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Reflexive attention in touch: An investigation of event related potentials and behavioural responses

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ARTICLE INFO

ABSTRACT

Exogenous attention has been extensively studied in vision but little is known about its behavioural and neural correlates in touch. To investigate this, non-informative tactile cues were followed after 800 ms by tactile targets and participants either detected targets or discriminated their location. Responses were slowed for targets at cued compared to uncued locations (i.e. inhibition of return (IOR)) only in the detection task. Concurrently recorded ERPs showed enhanced negativity for targets at uncued compared to cued locations at the N80 component and this modulation overlapped with the P100 component but only for the detection task indicating IOR may, if anything, be linked to attentional modulations at the P100. Further, cue-target interval analysis showed an enhanced anterior negativity contralateral to the cue side in both tasks, analogous to the anterior directed attention negativity (ADAN) previously only reported during endogenous orienting.

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1. Introduction

Automatic, or exogenous attention, is when our attention is driven by external stimuli, such as a flash of light or a tap on our shoulder. The most commonly used method to investigate exogenous attention is a cue-target paradigm (e.g. Posner, 1978) where a non-informative exogenous cue is presented at a peripheral location followed by a target at either the same or a different location. Within the visual modality, if the target is presented less than approximately 250 ms after the cue and at the same location as the cue then facilitation of target detection is usually reported. Thus, participants are faster and more accurate at responding to stimuli presented at the same location (valid cue trial) compared to when cue and target presented at different locations (invalid cue trial). However, if the stimulus onset asynchrony (SOA) is larger than approximately 250 ms then slowing of response times and reduced accuracy for validly compared to invalidly cued targets is usually observed. This behavioural effect is known as inhibition of return (IOR) (Klein, 2000; Posner and Cohen, 1984).

Behaviourally IOR has been demonstrated within the visual (for review see Klein, 2000), auditory (Schmidt, 1996; Tassinari and Berlucchi, 1995), tactile modality (Cohen et al., 2005; Lloyd et al., 1999; Poliakoff et al., 2002; Röder et al., 2000, 2002), and between all modality pairings (Ferris and Sarter, 2008; Roggeveen et al., 2005; Spence et al., 2000a,b). Within the tactile modality

IOR has been demonstrated for SOAs between cue and target of 100 ms (Lloyd et al., 1999) to 6 s (Cohen et al., 2005) and contrary to the visual modality no early facilitation period for simple target detection has been shown. In addition to simple detection, discrimination of targets has been used as means to investigate exogenous attention. Discrimination tasks require a more in-depths processing of stimuli which reduce possible response biases influencing results (cf. Spence and McGlone, 2001). The few studies investigating discrimination of tactile targets (Chambers et al., 2007; Miles et al., 2008; Santangelo and Spence, 2007; Spence and McGlone, 2001; Brown et al., 2010) have demonstrated facilitation of responses to validly compared to invalid cued targets for short SOAs (up to 400 ms) between cue and target, no difference for an SOA of 550 ms, and IOR for a 1000 ms SOA (e.g. Miles et al., 2008; Brown et al., 2010). Taken together, exogenous studies of tactile attention have consistently demonstrated IOR in detection tasks. In discrimination tasks validly cued targets are facilitated when short SOA is used whilst IOR occurs at a cue-target interval of 1000 ms.

Event related potentials (ERPs) have been an important measure in understanding the neural basis of attention effects on different information processing stages. Within vision, electrophysiological studies have investigated the time course and neural correlates of IOR. The main component which has been linked to IOR in vision has been the P1, with a reduced amplitude for valid compared to invalid trials at around 100 ms after target onset (McDonald et al., 1999; Prime and Ward, 2004, 2006; Wascher and Tipper, 2004; Tian and Yao, 2008; Chica and Lupianez, 2009). Further, Luck et al. (2000) suggested that the P1 amplitude difference between valid and invalid trials is usually directly linked to behavioural

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performance. Thus, the reasoning is that slower reaction times for valid trials (IOR) may be linked to a suppression of the valid P1 amplitude as compared to the invalid P1 component. However, other studies have demonstrated a reduction in amplitude on valid trials without a behavioural IOR effect (Hopfinger and Mangun, 1998; Doallo et al., 2004) or a significant IOR effect but no P1 modulation (Prime and Ward, 2006). Nonetheless, Prime and Ward (2006) conclude that the P1 and IOR are likely to be associated as the majority of studies have demonstrated a P1 reduction and further, no study to date has shown a P1 enhancement of validly cued trials in a visual exogenous attention task. Importantly, to our knowledge no previous study has investigated the neural correlate of exogenous attention and IOR in touch.

A fundamental difference of touch compared to vision and audition is that touch is predominantly a proximal sense (Gibson, 1966). Likewise, recent research suggests that the neural mechanisms underlying tactile spatial endogenous attention differ in comparison to the other senses (Forster and Eimer, 2005; Forster and Gillmeister, 2010). The behavioural pattern of IOR also differs between vision and touch. In touch a facilitation period of validly cued targets is only present in discrimination tasks. In vision there is also such a facilitation period in detection tasks. Therefore, it is conceivable that the neural correlate of IOR may differ in touch from what is known from the visual modality.

The present study was designed to investigate for the first time the correlates of exogenous attention, and more specifically IOR, in touch. To achieve this participants performed a simple detection (experiment 1) and a discrimination (experiment 2) task whilst concurrent EEG was recorded; that is on each trial participants either detected the onset of a target or discriminated target location (up/down). A cue-target interval (800 ms) was chosen that was long enough to diminish any overlap of EEG activity elicited by the cue onto target ERPs. Cues were non-predictive of the subsequent target location and were lateralized taps presented either to the hand the target was presented to (valid trials) or to the opposite hand (invalid trials). For behavioural responses we predicted IOR in the detection task whilst diminished or no IOR in the discrimination task. The aim of this study was to investigate the neural correlate of exogenous attention and establish an association between behavioural differences (i.e. strength of IOR) and attentional modulations of somatosensory processing. Based upon studies of visual attention we assumed tactile IOR to be reflected in and around the P100 as this somatosensory component most closely resembles the visual P1. Moreover, based upon previous tactile studies we set out to investigate attentional effects at a series of components modulated by tactile (endogenous) attention, namely the P45, N80, P100, N140 and late sustained negativity (Nd) (see e.g. Schubert et al., 2008). In addition, a bilateral cue was employed to further explore the underlying neural mechanisms of any attention effects found, behaviourally and in the ERPs. These bilateral cues were aimed to be neutral in the sense that attention was not biased to either side. Behaviourally, if validly cued targets were inhibited (IOR) these trials should also be slower compared to the neutral trials, thus reflecting an attentional orienting cost. Further, if response times (RTs) on invalid trials were faster than on neutral and valid trials then conceptually we assumed that the performance on invalid trials would be due to attentional benefits (Forster and Eimer, 2005; Mayer et al., 2004). We hypothesized that in the detection task, processing of targets would be inhibited on valid trials reflecting attentional orienting costs. In the discrimination task no difference was expected between RTs on valid, invalid and neutral trials. In particular we expected no IOR (see Spence and McGlone, 2001; Miles et al., 2008). Moreover, based on the behavioural distinction of costs and benefits we hypothesised that the relative difference between ERP amplitudes on valid and invalid compared to neutral trials would follow the same pattern as in behaviour.

That is, ERP amplitude differences on valid and neutral trials would reflect suppression of target processing (i.e. attentional orienting costs) whilst ERP amplitude differences on invalid and neutral trials would reflect enhancement of processing at target locations (i.e. attentional orienting benefits).

In addition to analyses of behavioural and post-target ERP data, we investigated ERPs elicited by the cues. The cue-target interval has commonly only been explored within endogenous orienting where cue-locked ERP waveforms elicited ipsilateral and contralateral to the cued side are compared. Two main components have been identified and linked to the fronto-parietal orienting system. Firstly, the so-called anterior directing attention negativity (ADAN) is present at around 300–500 ms post cue-onset with enhanced negativity over frontal electrodes contralateral to the cued side. The ADAN has been demonstrated in a number of visual (e.g. Hopfinger and Mangun, 2000), auditory (e.g. Green and McDonald, 2006) and tactile cue (Forster et al., 2009) studies and has been suggested to reflect a supramodal attention mechanism in the frontal areas (Eimer et al., 2002; Eimer and Van Velzen, 2002; Seiss et al., 2007). Following the ADAN an enhanced contralateral positivity to the cued side, the so-called late directing attention positivity (LDAP) is present which has been suggested to originate from occipitotemporal cortex (Mathews et al., 2006; Praamstra et al., 2005). This component has been suggested to reflect attentional orienting mediated and driven by information about external visual space (van Velzen et al., 2006; Eardley and van Velzen, 2011). The above mentioned studies have only used endogenous attention to study ERPs in the cue-target interval. If exogenous and endogenous attention are part of the same orienting networks (Corbetta and Shulman, 2002; Macaluso, 2010) we expected to also find ADAN like waveforms in the cue-target interval following exogenous attention. However, as there was little visual information available (participants' hands were covered), we did not predict the presence of an LDAP.

2. Method

2.1. Participants

Twenty paid participants took part in this study. All participants were right-handed and all gave written, informed consent prior to their participation. Two participants were excluded from analysis due to insufficient number of trials after artifact rejection. The 18 participants (12 female and 6 male) included in the subsequent analyses had a mean age of 26.4 year (range: 19–42 years).

2.2. Stimuli and apparatus

Stimuli and apparatus were identical in the detection and discrimination task. Participants sat in a dimly lit, soundproofed chamber. Tactile stimuli were presented using 12-V solenoids (5 mm in diameter), driving a metal rod with a blunt conical tip to the finger pad of the middle fingers and thumbs. The four solenoids were set in two wooden cubes (65 mm × 50 mm), one for left and one for the right hand. The two cubes were fixated 640 mm apart on a foam mat (approximately 2 cm thick), used for participants' comfort and for reducing any potential noise caused by the tactile stimulators if in direct contact with the table. White noise (58 dB SPL) was continuously present through two speakers, each located in a direct line behind each hand, to mask any sounds made by the tactile stimulators. Tactile cues and targets consisted of a 50 ms single tap, thus, the contact time between rod and skin was 50 ms. Responses were made vocally into a microphone, placed directly in front of the participant. The experimenter coded responses (in the discrimination task) on a keyboard in the adjacent room via an intercom system. A white fixation cross was presented on a monitor located directly in front of the participant. Throughout the experiment, a black cloth covered the participants' hands and forearms.

2.3. Design and procedure

The experiment consisted of 10 blocks. Half of the participants started the experiment with the detection task (5 blocks) followed by the discrimination task (5 blocks), and vice versa for the other half. The discrimination task consisted of a total of 480 trials (96 trials per block) of which 160 were valid (cue and target appeared at the same side), 160 neutral (target was preceded by a bilateral cue), and 160 invalid (cue and target appeared at opposite sides) trials. The detection task (105 trials per block) included the same 480 trials with an addition of 55 catch trials were no target
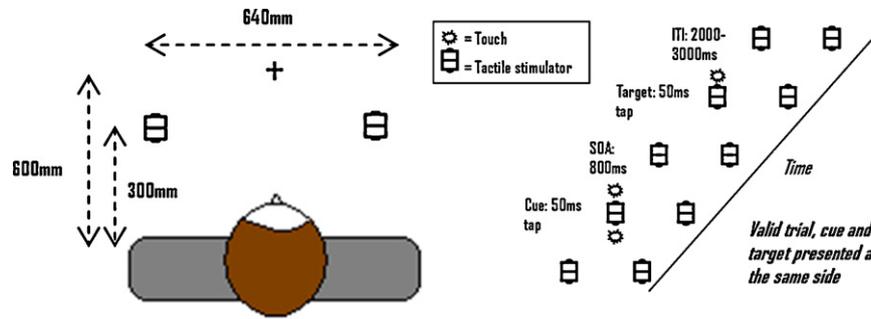
Fig. 1. Left: schematic view of the experimental set-up. The two rectangular boxes in front of subject represent four tactile stimulators held between thumb and middle finger of each hand. Right: schematic representation of events in a valid cue trial. The cubes correspond to the boxes in left figure and the explosions represent tactile stimulation.

was presented after the cue. The catch trials were included to prevent participants anticipating responses. The cue appeared to the left, right, or to both hands with equal probability. Two short practice blocks of 5 valid, 5 neutral and 5 invalid trials (plus 2 catch trials in the detection task only) were presented to the participant prior to each task.

In the discrimination task, each trial started with a 50 ms presentation of the cue which participants were instructed to ignore. Following an inter-stimulus interval of 750 ms (resulting in a SOA of 800 ms) the target was presented for 50 ms from one of the four solenoids. The target was equally likely to appear to the left or right, and equally likely to appear to the middle finger (up) or the thumb (down). The participants were instructed to discriminate the elevation of the target and vocally respond 'up' or 'down' as quickly as possible into the microphone. The onset of the vocal response was measured by a voice key and the response (up/down) was keyed in manually by the experimenter. Following the experimenter's key press there was a random inter-trial interval of 1000–2000 ms before the next cue was presented. The detection task employed the same stimuli and procedure except participants' responded by saying 'pa' into the microphone except for catch trials which required no response. The experimenter was not required to press a response key in the detection task. In order to create approximately similar inter-trial-intervals in both tasks, a longer random interval of 2000–3000 ms was set for the detection task. In both tasks, if the participant did not respond within 1500 ms the trial terminated and a new trial started. Participants were instructed to fixate on a centrally located cross, which was present throughout a block, and avoid eye moments.

2.4. Recording and analysis

Behavioural data were subjected to a repeated measures ANOVA with Task (detection, discrimination), and Cue (valid, neutral, invalid) as factors. Any effect of cue was followed up with post hoc tests. Trials with response times less than 100 ms and greater than 1000 ms were excluded from analysis, resulting in removal of less than 1% of all trials in both detection and discrimination tasks. In addition, in the discrimination task incorrect localizations (e.g. 'up' response when the target appeared to the thumb) were also excluded (3% of all trials).

Electroencephalography (EEG) was recorded using 32 Ag–AgCl electrodes arranged according to the 10–20 system and referenced to the right earlobe. Horizontal electro-oculogram (HEOG) was recorded from the outer canthi of the eyes. Electrode impedance was kept below 5 kΩ, earlobe and ground electrodes below 2 kΩ, and amplifier bandpass was 0.01–100 Hz and digitization rate was 500 Hz. After recording the EEG was digitally re-referenced to the average of the left and right earlobe and filtered with a low pass filter of 40 Hz. Then EEG was epoched offline into 400 ms periods starting 100 ms before and ending 300 ms after target onset for post target analysis. The time window was restricted to 300 ms post target to diminish contamination of the ERPs by behavioural responses. In addition, EEG was also epoched into 900 ms periods starting 100 ms prior to cue onset and ending at target onset, for analysis of the cue-target interval. Baseline correction was performed for both time windows (100 ms period preceding onset of target and cue, respectively). Trials with eye movements or eye-blinks (voltage exceeding ±40 μV relative to baseline at HEOG electrodes) or with other artifacts (voltage exceeding ±80 μV relative to baseline at all electrodes except O1/2 in post target interval) were removed prior to EEG averaging. Further, all trials with behavioural errors were excluded from EEG analysis. This resulted in subsequent ERP analysis for the detection task being based on an average of 100 (SD 22.9) valid trials, 95 (SD 20.8) neutral, and 96 (21.0) invalid trials per participant. The discrimination task ERP analysis was based on an average of 109 (SD 24.5) valid, 101 (SD 23.3) neutral and 108 (SD 24.0) invalid trials per participant. There were minimum of 75 trials available for analysis in each condition. Additionally, the residual HEOG deflections were analysed to make sure no individual had a difference which exceeded 4 μV between cue-left and cue-right trials (Kennett et al., 2007).

For cue-target interval analysis ERPs were averaged separately for task (detection and discrimination) and cue (left and right hand) and analysed at lateral anterior (F3/4, FC5/6, and F7/8), lateral central (C3/4, CP5/6 and T7/8), and lateral posterior

sites (P3/4, P7/8, and O1/2). These sites are commonly used to investigate lateralized cue activity associated with the fronto-parietal attention network (see e.g. Gherri and Eimer, 2008). Mean amplitudes values were computed for two post-cue time windows, that is 400–600 ms, and 600–800 ms (to confirm the presence of the ADAN and LDAP component, respectively). These two time windows were subjected to separate $2 \times 2 \times 2 \times 3$ repeated measures ANOVAs, one for each of anterior, central, and posterior areas, The factors were; Task (detection, discrimination), Cue side (left, right), Hemisphere (electrodes ipsilateral versus contralateral to cue direction) and Electrode Site (F3/4, F7/8, FC5/6 for lateral anterior electrodes; C3/4, CP5/6, T7/8 for lateral central electrodes; and P3/4, P7/8, O1/2 for lateral posterior electrodes).

For post-target ERP analysis epochs were averaged separately for task (detection and discrimination) and cue type (valid, neutral, and invalid cue). ERP mean amplitudes were computed for measurement windows centred on the peak latencies of the somatosensory P45, N80, P100 and N140 components (40–60 ms, 66–96 ms, 96–126 ms and 126–154 ms post-stimulus, respectively). To investigate longer-latency effects of exogenous spatial attention, mean amplitudes were also computed between 154 and 300 ms (Nd) after tactile stimulus onset. Repeated measures ANOVAs for each time window were conducted to compare attentional modulations in the detection and discrimination task with the factors Task (detection, discrimination), Cue (valid, neutral, invalid), Electrode Site (CP1/2, CP5/6, C3/4, FC1/2, FC5/6, T7/8) and Hemisphere (ipsilateral, contralateral). Electrode sites refer to stimuli presented to both left and right hand and trials were averaged in terms of the hemisphere ipsilateral or contralateral to the stimuli. Task × Cue interaction were further broken down into separate analysis for each task. Any interactions including Cue and Hemisphere were further broken down into separate analysis for each hemisphere. Electrode selection for post target analysis was based on electrodes close to and around somatosensory cortex where previous tactile attention modulations have been reported (e.g. Eimer and Forster, 2003). Any effects of Cue were further investigated using post hoc tests to assess attentional effects (valid vs. invalid) as well as costs (valid vs. neutral) and benefits (invalid vs. neutral) of attentional orienting.

Wherever the ANOVA assumption of Sphericity was violated Greenhouse–Geisser adjusted probability levels were reported.

3. Results

3.1. Behavioural performance

Response time analysis showed a significant task difference ($F(1,17) = 94.51$, $p < .001$, $\eta_p^2 = .85$) as on average response times (RTs) were faster in the detection (321.42 ms, standard deviations (SD) 50.34) compared to the discrimination task (437.60 ms, SD 63.32). Further, there was a significant main effect of Cue ($F(2,34) = 13.50$, $p < .001$, $\eta_p^2 = .44$) and a Task × Cue interaction ($F(2,34) = 13.05$, $p < .001$, $\eta_p^2 = .43$) (see Fig. 1). **Q2**

Separate follow-up analysis by Task showed a significant effect of Cue in the detection task ($F(2,34) = 20.97$, $p < .001$, $\eta_p^2 = .55$) and post hoc tests (Bonferroni corrected) showed that this was due to significantly faster ($p < .001$) RTs on invalid (311.82 ms, SD 46.42) compared to valid (337.80 ms, SD 56.09) trials (i.e. IOR), and neutral trials (314.63 ms, SD 46.58) were significantly faster ($p < .001$) than valid trials (Fig. 2).

Analysis of the discrimination task also showed a significant effect of Cue $F(2,34) = 4.35$, $p = .033$, $\eta_p^2 = .20$, however, this was not due to an attention effect (valid vs. invalid) but a significant difference ($p = .01$) between valid (442.98 ms, SD 61.68) and neutral (431.21 ms, SD 61.99) trials.
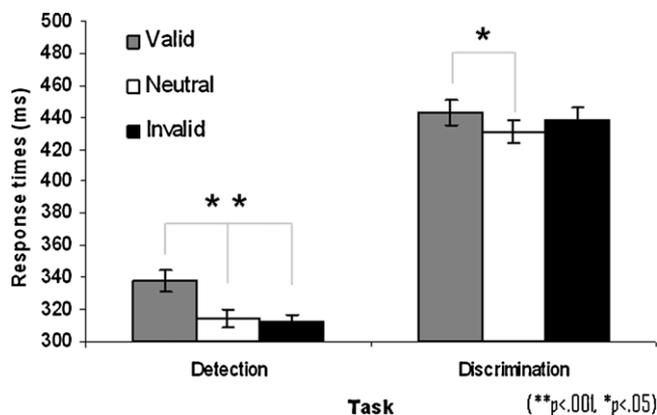
Fig. 2. Reaction times (in ms) and standard errors separately for valid, neutral, and invalid trials for detection and discrimination tasks. Detection task results show inhibition of return whilst there was no difference between valid and invalidly cued targets in the discrimination task.

3.2. ERP results

3.2.1. Effects of exogenous orienting on cue-target interval ERPs

Fig. 3 shows waveforms of the 800 ms cue-target interval for the detection and discrimination task, where black lines represent ERPs contralateral to cue location and grey lines correspond to ERPs ipsilateral to cued side. For both tasks a sustained negativity (upward deflection) at electrodes contralateral compared to electrodes ipsilateral to the cued side (like the anterior directing attention negativity (ADAN) reported during endogenous orienting) starting from about 450 ms after cue onset is present which is spread over central, anterior and also posterior electrodes (Fig. 4, showing topographical maps of the ADAN).
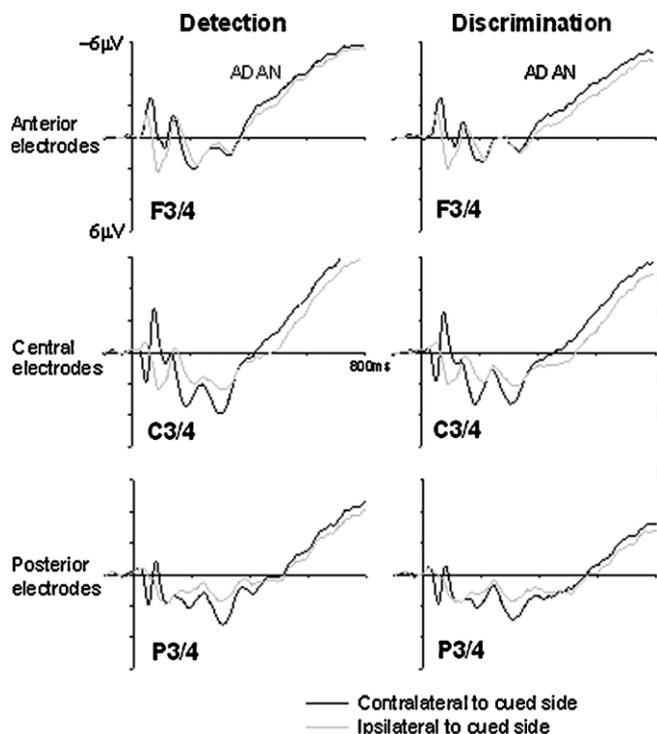

Fig. 3. Grand-averaged ERP waveforms for the cue-target interval in detection (left panel) and discrimination (right panel) task. Black lines represent ERPs at electrodes contralateral and grey lines represent ERPs at electrodes ipsilateral to the cued side. Enhanced negativity (up-ward deflections) for contralateral compared to ipsilateral electrodes (indicating the presence of the ADAN) is demonstrated for both detection and discrimination tasks.
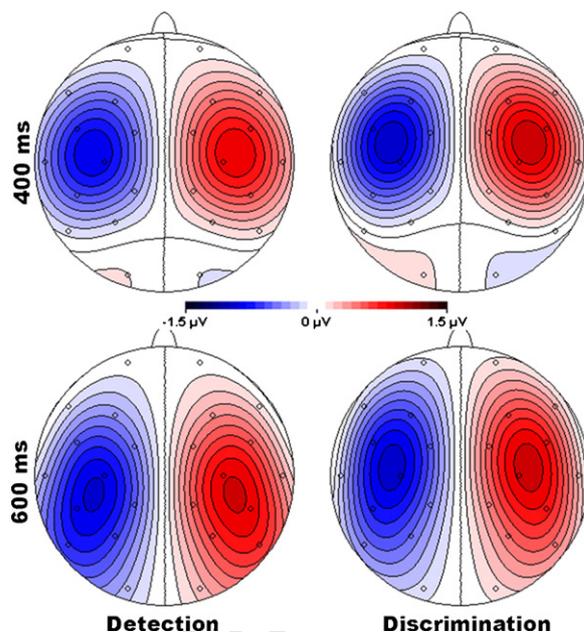

Fig. 4. Scalp distribution of cue-target interval data for the detection (left) and discrimination (right) task 400–600 ms (top) and 600–800 ms (bottom) post cue onset. Maps represent differences between brain activity observed over hemispheres ipsilateral and contralateral to the cued side. The obtained difference waveforms were mirrored to obtain symmetrical but inverse amplitude values for both hemispheres. Each contour line represents 0.05 μV changes (amplitude range between −1.0 and 1.0 μV).

Analysis of the cue-target interval showed a significant Cue × Hemisphere interaction in the 400–600 ms time window at central ($F(1,17) = 36.34$, $p < .001$, $\eta_p^2 = .68$) and anterior ($F(1,17) = 37.03$, $p < .001$, $\eta_p^2 = .69$) electrode sites. In the 600–800 ms time window there was a significant Cue × Hemisphere interaction at posterior ($F(1,17) = 24.17$, $p < .001$, $\eta_p^2 = .59$), central ($F(1,17) = 52.02$, $p < .001$, $\eta_p^2 = .75$), and anterior ($F(1,17) = 25.72$, $p < .001$, $\eta_p^2 = .60$) electrode sites. These Cue × Hemisphere interactions indicated an enhanced negativity contralateral to the cue direction (Figs. 3 and 4). No significant main effect of Task nor Task × Cue × Hemisphere interaction (which would have indicated a difference in lateralized components between the tasks) for each of the time intervals and electrode subsets tested was present (see Table 1 for a summary of main attention orienting effects). Taken together, these results suggest the presence of ADAN in both tasks starting around 400 ms after cue onset over anterior lateral electrode sites. The ADAN continued to be present until target onset over anterior, central and posterior electrode sites. Moreover, absence of an LDAP should be noted which would have been expected at posterior electrode sites at the later analysis time window, whilst in the present study there is a continuation of the ADAN at this stage (see Table 2).   **Q3**

Table 1
Cue-target interval analysis summary.

	400–600 ms	600–800 ms
Lateral posterior electrodes P3/4, P7/8, O1/2	n.s.	$p < .001$
Lateral central electrodes C3/4, Cp5/6, T7/8	$p < .001$	$p < .001$
Lateral anterior electrodes F3/F4, F7/F8, FC5/FC6	$p < .001$	$p < .001$

Note. Summary table of statistical results (*p*-values or non-significance (n.s.) stated) of lateralized cueing effects (i.e. Cue × Hemisphere interactions) for the cue-target interval at three different scalp areas and at two time intervals during which the ADAN and LDAP are commonly observed. No task differences were observed at any time interval and/or electrode site therefore *p*-values are taken from the overall analysis including both tasks.
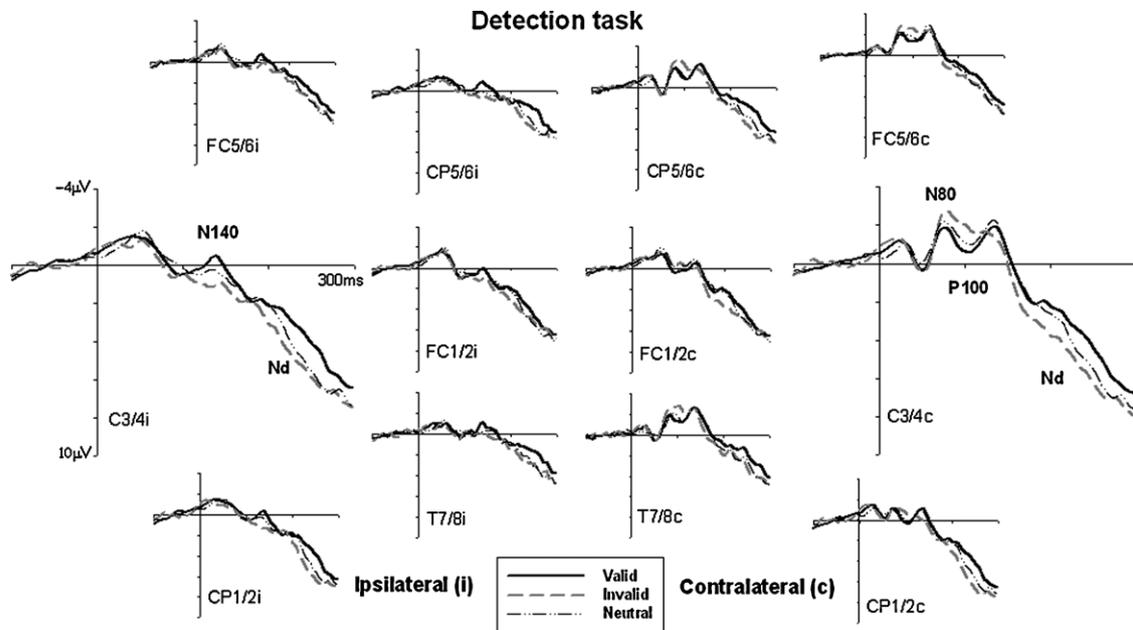
Fig. 5. Detection task grand averaged somatosensory ERPs elicited on valid (solids line), neutral (dashed black lines), and invalid (dashed grey lines) trials in the 300 ms following target onset. The left side shows ERPs over ipsilateral hemisphere and right are ERPs contralateral to target side. The marked out components on C3/4 electrodes denotes if the component was modulated by attention (significant difference between valid and invalid). The C3/4 graphs are enlarged to display the ERP waveforms in more detail.

3.2.2. Effects of exogenous attention on post-target somatosensory ERPs

Figs. 5 and 6 show ERP waveforms elicited by tactile target stimuli on valid (black solid lines), invalid (grey dashed lines) and neutral (black dashed lines) trials in the detection and discrimination task, respectively. The graphs show a similar pattern of post-target ERPs in both tasks with attention effects at the N80, P100, N140, Nd, marked out on the C3/4 electrodes in the figures. The difference between the two tasks lies within the laterality of the P100 attentional modulation; that is the attentional modulation is present over contralateral electrodes (right graph in Fig. 5) in the detection task whilst it is ipsilateral (left graph in Fig. 6) in the discrimination task. This difference in attention effect over contralateral and ipsilateral hemispheres at the P100 component is also demonstrated in Fig. 7 which represents the attention effect at each time window analysed.

3.2.2.1. P45.
No main effect of Cue or interaction involving Cue was present for this analysis window.

3.2.2.2. N80.
There was a contralateral N80 attention effect in both detection and discrimination tasks.

Table 2
Post target ERP attention effects.

Component	Task	Bilateral	Contralateral	Ipsilateral
N80	Both	n.s.	$p = .001$	n.s.
P100	Detection	n.s.	$p = .017$	n.s.
	Discrimination	n.s.	n.s.	$p = .036$
N140	Both	n.s.	n.s.	$p = .033$
Nd	Both	$p = .001$	*	*

Note. Summary table of statistical results (*p*-values or non-significance (n.s.) stated) of attention effects at the somatosensory components analysed for post-target ERPs in the detection and discrimination tasks. Overall main effects of attention (i.e. Cue) are stated in bilateral column. Any Cue × Hemisphere interactions were followed up separately for each hemisphere and effects of Cue reported accordingly. Any interaction involving both Task and Cue were followed up with separate analysis for detection and discrimination tasks. If no Cue by Hemisphere interaction was present no follow-up analysis was performed (denoted with asterisk).

Analysis of post-target ERPs showed a significant Cue × Hemisphere interaction ($F(2,34) = 28.87$, $p < .001$, $\eta_p^2 = .63$) at the N80 component (a significant Cue × Electrode Site × Hemisphere $F(10,170) = 6.93$, $p < .001$, $\eta_p^2 = .29$ was also present). The interaction was followed up with separate analysis for each hemisphere. This revealed a contralateral effect of Cue ($F(2,34) = 5.40$, $p = .018$, $\eta_p^2 = .24$) and post-hoc analysis (Bonferroni corrected) showed only a significant difference between valid versus invalid trials ($p < .001$) with an enhanced negativity on invalid trials. There was also an ipsilateral effect of Cue ($F(2,34) = 3.56$, $p = .04$, $\eta_p^2 = .17$), however, post-hoc tests (Bonferroni corrected) revealed no significant differences between the three levels. Moreover, there were no task differences (in particular no Task × Cue interaction) suggesting the contralateral N80 attention effect was similar in both tasks.

3.2.2.3. P100.
There was a significant contralateral attention effect in the detection task. In the discrimination task the P100 attention effect was present over the ipsilateral hemisphere.

Analysis of the P100 component showed a significant Task × Cue × Electrode Site × Hemisphere interaction ($F(10,170) = 5.06$, $p = .003$, $\eta_p^2 = .23$) and Task × Cue × Hemisphere interaction ($F(2,34) = 8.79$, $p = .001$, $\eta_p^2 = .34$) (other significant interactions including the factor Cue were a Cue × Electrode Site × Hemisphere ($F(10,170) = 11.67$, $p < .001$, $\eta_p^2 = .41$), a Task × Cue × Electrode Site ($F(10,170) = 3.65$, $p = .013$, $\eta_p^2 = .18$), a Cue × Hemisphere ($F(2,34) = 37.80$, $p < .001$, $\eta_p^2 = .69$), and a Cue × Electrode Site ($F(10,170) = 8.34$, $p < .001$, $\eta_p^2 = .33$) interaction). These interactions were followed up by separate analyses for each task. The detection task showed a significant Cue × Hemisphere ($F(2,34) = 28.42$, $p < .001$, $\eta_p^2 = .63$) (as well as Cue × Electrode Site × Hemisphere ($F(10,170) = 10.54$, $p < .001$, $\eta_p^2 = .38$) and Cue × Electrode Site ($F(10,170) = 7.01$, $p < .001$, $\eta_p^2 = .30$)) interaction which was again broken down into analysis of Cue for each hemisphere. Following a significant contralateral Cue × Electrode Site ($F(10,170) = 7.01$, $p < .001$, $\eta_p^2 = .30$) interaction it was revealed the attention effect was located on FC5/6
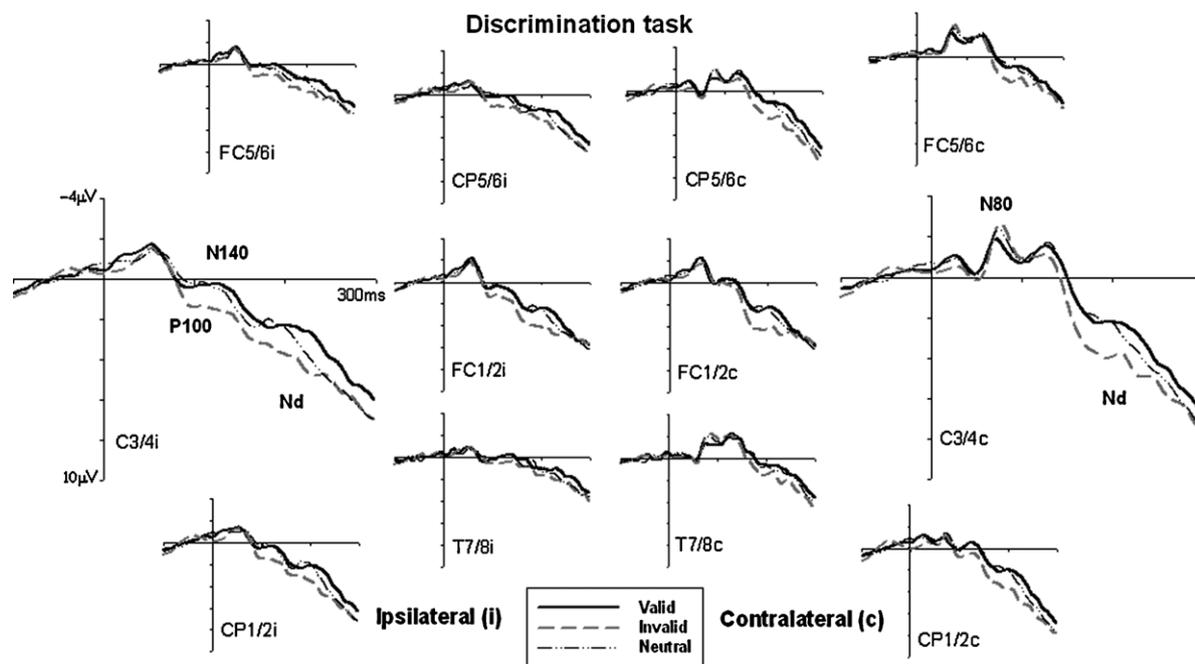
Fig. 6. Discrimination task grand averaged somatosensory ERPs elicited on valid (solids line), neutral (dashed black lines), and invalid (dashed grey lines) trials in the 300 ms time window following target onset. The left side shows ERPs over ipsilateral hemisphere and right are ERPs contralateral to target side. The marked out components denotes if the component was modulated by attention (significant difference between valid and invalid). The C3/4 graphs are enlarged to display the ERPs in more detail.

($p = .017$, Bonferroni corrected) and T7/8 ($p < .001$, Bonferroni corrected) contralateral to the target. Both of these electrodes showed a difference between invalid versus neutral trials ($p < .001$) due to an enhanced negativity on invalid trials suggesting attentional orienting benefits whilst T7/8 also showed a difference between valid versus neutral ($p = .044$, Bonferroni corrected) with a reduced negativity on valid trials suggesting also attentional orienting costs for this time window (see Fig. 5). Analysis of attentional effects for the ipsilateral hemisphere showed a significant Cue × Electrode Site interaction ($F(10,170) = 3.56$, $p = .021$, $\eta_p^2 = .17$). However, follow-up analysis yielded no significant results. Thus, the P100 attention effect in the detection task was located contralaterally, in particular over electrodes FC5/6 and T7/8 contralateral to the target location. Analysis of the discrimination task also showed a Cue × Hemisphere ($F(2,34) = 10.03$, $p < .001$, $\eta_p^2 = .37$, as well as Cue × Electrode Site × Hemisphere ($F(10,170) = 4.74$, $p = .002$, $\eta_p^2 = .22$), and Cue × Electrode Site interaction ($F(10,170) = 3.72$, $p = .011$, $\eta_p^2 = .18$)) which was followed up by effects of Cue for each hemisphere separately. Contralaterally there was a Cue × Electrode Site interaction ($F(10,170) = 5.35$, $p = .001$, $\eta_p^2 = .24$), however, the follow-up yielded no significant effects. Ipsilateral analysis for the discrimination task demonstrated a significant effect of Cue ($F(2,34) = 5.52$, $p = .008$, $\eta_p^2 = .25$). Post-hoc analysis (Bonferroni corrected) revealed that this was due to a significant difference between valid versus invalid trials ($p = .036$) showing the presence of an attention effect and invalid versus neutral trials ($p = .018$) with reduced positivity on invalid trials suggesting that this attention effects was mainly due to attentional orienting benefits (Fig. 6). Thus, the attention effect in the discrimination task was present over the ipsilateral hemisphere, in contrast to a contralateral P100 effect in the detection task.

3.2.2.4. N140. There was an ipsilateral N140 attention effect in both tasks.

Analysis of the N140 component demonstrated significant Cue × Hemisphere ($F(2,34) = 6.03$, $p = .006$, $\eta_p^2 = .26$) and Cue × Electrode Site ($F(10,170) = 3.86$, $p = .012$, $\eta_p^2 = .19$)

interactions. Follow-up analyses for each hemisphere revealed a Cue × Electrode Site interaction ($F(10,170) = 3.46$, $p = .013$, $\eta_p^2 = .17$) for contralateral electrodes, however, follow-up analyses of Cue for each electrode showed no significant attention effect. Ipsilaterally there was a main effect of Cue ($F(2,34) = 5.23$, $p = .01$, $\eta_p^2 = .24$) and Cue × Electrode Site interaction ($F(10,170) = 3.27$, $p = .026$, $\eta_p^2 = .16$). Post-hoc tests showed the main effect of Cue was due to a significant difference between valid versus invalid trials ($p = .033$). Thus, there was an ipsilateral N140 attention effect with enhanced negativity on valid compared to invalid trials (Figs. 5 and 6) and lack of Task × Cue interaction suggested this effect was similar in the two tasks.

3.2.2.5. Nd. There was a bilateral Nd attention effect in both tasks.

Analysis of the late post-target time window showed a significant main effect of Cue ($F(2,34) = 9.51$, $p = .001$, $\eta_p^2 = .36$). Post-hoc tests (Bonferroni corrected) showed there was a difference between valid and invalid trials only ($p = .001$) demonstrating an effect of attention at this late negativity.

3.3. Analysis of links between IOR and post-target ERP attentional modulations

To investigate links between IOR and attentional ERP modulations correlation analysis was conducted. IOR was only present in the detection but not in the discrimination task. Likewise, attentional modulations of ERP waveforms differed between the tasks at the P100 component; that is, in the detection task an attention effect was present over the hemisphere contralateral to tactile targets, whilst the attention effect was ipsilateral in the discrimination task. Therefore, for the time window of the P100 mean amplitude differences between valid and invalid trails were computed at electrodes FC5/6 and T7/8 contralateral to the target side in the detection task and were correlated with the magnitude of IOR (RTs on valid minus invalid trials) for each participant. However, no significant correlation was found ($r = .06$).
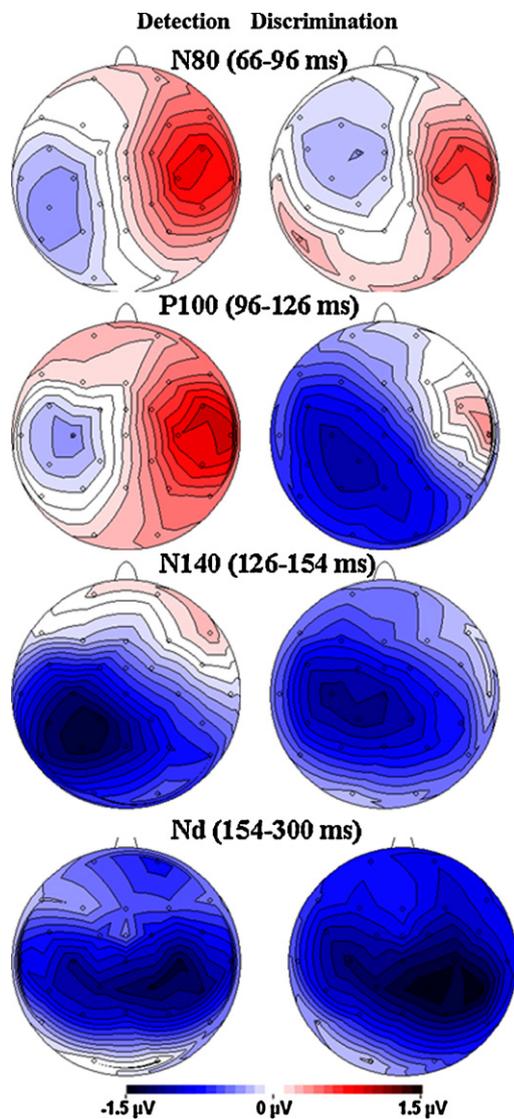
Detection   Discrimination

N80 (66–96 ms)

P100 (96–126 ms)

N140 (126–154 ms)

Nd (154–300 ms)

-1.5 µV   0 µV   1.5 µV

Fig. 7. Topographic maps of the post target attention effects (ERPs on invalid were subtracted from valid trials) at each time window analysed presented for the detection (left panel) and discrimination (right panel) task. The right hemisphere shows attention effect contralateral to the target side and the left hemisphere shows ipsilateral attention effects. The most prominent difference in attention effects between the two tasks is for the time range of the P100 component where the attention effect is contralateral to the target side in the detection task and ipsilateral and reversed in polarity in the discrimination task. This difference was also supported statistically by a Task × Cue × Hemisphere interaction for the P100.

4. Discussion

Attention research has traditionally focused on the visual modality and less is known about the attentional mechanisms of touch, especially exogenous tactile attention. Furthermore, to our knowledge, no previous study has investigated the neural correlates of reflexively orienting to and selecting locations on the body. Therefore, the present study was designed to investigate the behavioural and neural correlates of exogenous tactile attention in a detection and discrimination task. As expected, we found a dissociation between behavioural responses in the two tasks. However, a largely comparable pattern of ERP responses was present during exogenous attentional orienting (cue target interval) and attentional selection (post-target processing), with the exception of attentional ERP modulations of post-target processing at the P100 component possibly suggesting a link between behavioural results and this processing stage. Interestingly, attentional post-target

modulations were already present for the N80 component which is earlier than reported for transient endogenous tactile selection (Eimer and Forster, 2003) and might be specific to exogenous attention.

4.1. Behavioural performance

In line with previous studies on exogenous tactile attention we found IOR in the detection task (Cohen et al., 2005; Lloyd et al., 1999; Poliakoff et al., 2002; Röder et al., 2000, 2002); that is, responses to targets were significantly slower when task irrelevant cues were presented to the hand of the subsequent target location (valid trials) compared to when they were presented to the other hand (invalid trials). In addition, the present study included a neutral cue that was presented to both hands simultaneously. In the detection task the RTs in response to the neutral cue were in accordance with an inhibitory account of validly cued targets. Thus, RTs on neutral trials were no different to invalid trials but significantly faster than valid trials confirming that processing of validly cued targets was inhibited leading to overall IOR. This cost of orienting attention on validly cued trials is in line with what has been demonstrated in exogenous visual studies using bilateral cues (Ayabe et al., 2008; Mayer et al., 2004).

In contrast to the detection task, responses on invalid and valid trials did not differ in the discrimination task. Recent studies have demonstrated a biphasic pattern of inhibition to facilitation with increasing durations between cue and target in tactile discrimination tasks (Miles et al., 2008; Brown et al., 2010). That is, RTs were faster on valid compared to invalid trials at short SOAs (150 and 350 ms; see also Spence and McGlone, 2001), showing facilitation. In contrast, at long SOAs (1000 ms) the opposite was found (i.e. faster responses on invalid compared to valid trials; i.e. IOR) whilst overall no difference between response times on valid and invalid trials was reported for an intermediate SOA (550 ms). In the present discrimination task a SOA of 800 ms was employed and there was no difference between valid and invalid trials. Based upon the biphasic pattern demonstrated in previous tactile discrimination tasks (Miles et al., 2008; Brown et al., 2010) it may be that 800 ms SOA is not long enough for IOR to develop. The lack of difference in the discrimination task for the present cue-target interval could be explained by facilitation and IOR operating as competing mechanisms.[1] Such a competing mechanisms idea may also be supported by our data that showed RTs on neutral trials were significantly faster than valid trials and also faster, albeit not significant, than invalid trials (see Fig. 2). Thus, both valid and invalid trials were to some degree inhibited in the discrimination task compared to the neutral trials, and/or, neutral trials were facilitated to some degree in the discrimination task.

4.2. ERP correlates of exogenous attention

Cue elicited ERP waveforms reflect the neural processes underlying spatial attentional orienting following cue onset. These have been investigated by comparing waveforms elicited by cues directing attention to the left and to the right side. Typically a pattern of a negativity contralateral to the cued direction over anterior electrode sites (ADAN) which is followed by a positivity contralateral to the cued direction over posterior electrode sites (LDAP) has been

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[1] Although there was no overall difference between valid and invalid trials in the discrimination task the hypothesis that competing facilitation and inhibition mechanisms were active in this task was partly supported by analysis of attention effects for individual participants. This showed four participants had significant IOR effect while four participants had a significant facilitation effect (valid RTs significantly faster compared to invalid trials). However, as ten participants did not show a significant effect either way these individual differences were not analysed further.

reported (e.g. Eimer and Van Velzen, 2002). To our knowledge no previous study has investigated cue related ERP modulations during reflexive orienting of attention. One reason for this might be that, in contrast to endogenous orienting where cues are symbolic and presented centrally, under exogenous cueing conditions cues are task irrelevant (i.e. to be ignored) and presented laterally. Therefore, in exogenous attention studies cue direction and cue location are matching and any cue induced ERP modulations could be due either to cue induced orientating of attention or to the physical location of the cue. Nevertheless, correlates of attentional orienting under endogenous attention condition are now well established and the aim of the present study was to reveal whether the same or similar correlates are also present under exogenous attention conditions. In both discrimination and detection tasks an enhanced negativity at anterior electrodes contralateral to the cued side was found suggesting the presence of an ADAN component. Therefore, the present results may indicate that the ADAN component is not limited to endogenous orienting. This in turn may suggest that the anterior attention system is also engaged in exogenous tactile attention. The ADAN in the present study was observed from 400 ms and still present at target onset, 800 ms after cue onset. This is longer than what is typically reported in studies using visual cues where the ADAN diminishes around 500–600 ms after cue onset (Eimer et al., 2002; Hopfinger and Mangun, 2000; Kennett et al., 2007; van der Lubbe et al., 2006; Talsma et al., 2005). Following the ADAN, an LDAP has been shown in the cue-target interval of endogenous visual attention studies (e.g. van Velzen et al., 2006). In the present study, the LDAP was absent which is in line with the suggestion that this later posterior positivity is related to attention processing in visual external space (van Velzen et al., 2006). This may not be surprising as vision was not actively engaged in the present experiments as hands were covered and only tactile stimuli were presented. The presence of an ADAN whilst no LDAP has been demonstrated in endogenous attention studies were vision was not engaged suggesting the LDAP is not required for endogenous orienting (e.g. Eardley and van Velzen, 2011). In an endogenous tactile attention study; Forster et al. (2009) did not find an LDAP and the ADAN was comparably prolonged. This may suggest that in the absence of an LDAP, the ADAN may be present for longer and also more widely spread over also posterior areas as indicated by the topographical maps (see Fig. 4). Importantly, the presence of an ADAN component in this study that is analogous to the ADAN reported in endogenous attention studies may suggests that this component is due to activity of the fonto-parietal attention network rather than the physical location of the cue. Therefore, this suggests that the fronto-parietal attention control network may also be engaged when using an exogenous attention paradigm even though participants were instructed to ignore the cues. However, to further explore whether cue-target waveforms reflect a shared attention network in endogenous and exogenous tactile attention a study directly contrasting the two types of orienting within the same subject would be required.

ERPs time locked to target presentation showed significant attention modulations for the N80, P100, and N140 components and longer latencies (Nd). In both detection and discrimination tasks the earliest somatosensory attention effect was a significantly larger negative amplitude, contralateral to target presentation, for invalid compared to validly cued targets peaking at around 80 ms post target onset. This relatively early attention effect has previously been demonstrated in endogenous tactile attention studies (Eimer and Forster, 2003; Desmedt and Robertson, 1977; Michie et al., 1987). However, in contrast to the present experiment these studies employed a sustained attention task where attention is focused on a location throughout a block and reported an enhanced negativity for validly cued (i.e. attended) compared to invalidly cued stimuli. Therefore, the present study demonstrated for the

first time a modulation of the N80 under transient attention conditions and, further, this modulation of the N80 may reflect specific attention mechanisms related to exogenous attention.

Continuing on from the N80, a P100 attention effect was observed contralateral to target presentation in the detection task. In the discrimination task this contralateral difference was absent. In the time window analysed there was however a difference between valid and invalid trials over ipsilateral hemisphere in the discrimination task. Importantly, the P100 modulation was the only attention effect which was different in the two tasks. In a more descriptive account of the P100 (see Fig. 5) it appears as though the N80 effect in the detection task continues with enhanced negativity for invalid trials in the time window of the P100, whilst in the discrimination task (see Fig. 6) this continuation is not as pronounced. Within the visual domain the P1 component has been the strongest contender as a component directly link to behavioural IOR. However, the visual attention literature does not paint a consistent picture of IOR and the P1, were studies have found a P1 attention modulation but no IOR (e.g. Hopfinger and Mangun, 1998) or IOR but no P1 attention effect (e.g. Prime and Ward, 2006). In the present study, we found IOR in the detection but not in the discrimination task. Examination of topographical attentional difference maps (Fig. 7) of the present study showed a relatively clear distinction of the attention effect at the P100 which is largely contralateral in the detection and ipsilateral in the discrimination task. Based on the present results it could be argued that IOR is linked to a contralateral P100 in touch as IOR was present only in the detection task. Analogously, Tian and Yao (2008) also showed in the visual modality a contralateral P1 attention effect coupled with behavioural IOR. However, in other studies IOR and ipsilateral P1 attention modulation were present (McDonald et al., 1999; Wascher and Tipper, 2004). It should be noted that the Tian and Yao study showed a P1 attention effect at around 100 ms (similar to the present results) whilst in the studies reporting ipsilateral P1 effects linked to IOR, attention effects were present at slightly later time windows (110–190 ms). To further investigate the importance of laterality and attention effects future studies could, for example, employ similar tasks with non-lateralized stimuli. Thus in touch, present stimuli to the body midline to see if there are any differences in the topography of attention effects between detection and discrimination tasks at the P100 when targets are not lateralized. Although tempting to conclude a direct association between IOR and attention modulations at the P100, the present results did not unequivocally demonstrate a link between the P100 and behaviour, in particular, this was evident as there was no correlation between IOR and the attention effect seen in the ERPs. Moreover, if the behavioural data were directly linked to a contralateral P100 then we would expect the waveforms for the invalid and neutral trials to be the same whilst significantly different to the valid trials. However, the neutral ERPs were different to both invalid and valid trials, which is not consistent with the behavioural data for the detection task. Taken together, the presence of behavioural tactile IOR appears to be, if anything, linked to attentional modulations at the somatosensory P100 component when considering separate analysis of behavioural and ERP data; however, on an individual participant level we found no evidence for such a link between behavioural performance and attentional difference at the P100.

At the mid-latency N140 component and longer latency (Nd) an enhanced negativity for stimuli on valid compared to invalid trials was present in both the detection and discrimination tasks (see Fig. 7). The two tasks showed N140 attention effects ipsilaterally whilst the Nd attentional modulation was bilateral for both tasks. The late sustained negativity is assumed to reflect more in-depth stimulus processing. In the present study these waveforms are very similar to ERPs found in endogenous studies of tactile attention with more negative waveforms for valid

compared to invalid trials (e.g. Eimer and Forster, 2003). Importantly though, the behavioural pattern in endogenous studies show facilitation of RTs to validly cued targets rather than inhibition (as in the present study), suggesting no causal link between these later ERP modulations of attention and behavioural effects.

In the present study, the ERP analysis included a neutral cue in order to perform cost/benefits analyses. That is, the aim of the neutral cue was to shed light on whether attention effects (i.e. differences between valid and invalid trials) were due to attentional orienting costs on valid trials or, benefits on invalid trials, or both. At the P100, ERPs on invalid trials were different from neutral trials in both tasks indicating attentional orienting benefits. However, in the detection task there were also some attentional orienting costs as ERPs on valid were different from neutral trials. Our behavioural results suggest attentional orienting cost only in the detection and no attentional orienting benefits in either task. There appears to be no clear relationship between cost/benefit analysis in our behavioural and ERP measures. A bilateral cue was used in the present experiment to act as a neutral cue and, unlike the lateralized cues, it should have not biased attention to either side. However, where attention was deployed during this "neutral" orienting is not clear. Attention may have, for example, been deployed equally to both sides, focused in the middle, or elsewhere. To further explore costs and benefits of attentional orienting, different neutral cues could be employed and compared such as centrally located cues, or no cue at all with only pure reaction times to targets (see e.g. Cohen et al., 2005).

In sum, behavioural responses showed IOR in the detection whilst no difference between responses on valid and invalid trials in the discrimination task, which is in line with previous studies of exogenous attention. ERP correlates of exogenous attention in touch showed an early contralateral attention modulation at the N80 component with an enhanced negativity on invalid compared to valid cue trials regardless of task. This early modulation most likely reflects processes specific to exogenous attention. The subsequent P100 attention modulation was only present over contralateral electrodes in the detection task whilst this contralateral modulation was absent in the discrimination task. Based on vision research the P1/P100 was predicted as the most likely component associated to IOR and this is what was also found in the present study. Although the findings may be along the same lines as some visual literature on IOR there is not yet conclusive evidence that the P100 is directly linked to IOR, especially as there was no correlation between ERP and behavioural effects. Finally, in the cue-target interval an ADAN component was found analogous to the ADAN previously reported in endogenous attention studies. The presence of this cue-target interval component may suggest that exogenous attention activates, at least in part, the same attention control network.

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