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Citation: Jones, A. & Forster, B. (2014). Neural correlates of endogenous attention, exogenous attention and inhibition of return in touch. *European Journal of Neuroscience*, 40(2), pp. 2389-2398. doi: 10.1111/ejn.12583

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Cite as: Jones, A., & Forster, B. (in press). Neural correlates of endogenous attention, exogenous attention and inhibition of return in touch. *European Journal of Neuroscience*. doi:10.1111/ejn.12583

Title page

Title

Neural correlates of endogenous attention, exogenous attention and inhibition of return in touch

Authors

Alexander Jones¹ & Bettina Forster²

¹Middlesex University London

²City University London

Corresponding author

Dr Alexander Jones
Psychology Department
School of Health and Education
Middlesex University
Hendon Campus
The Burroughs
London NW4 4BT

Room: TG68
tel: +44 (0) 2084116328
a.j.jones@mdx.ac.uk

Keywords: Tactile attention, ERP, somatosensory, voluntary, automatic, IOR

Abstract

Selective attention helps process the myriad of information constantly touching our body. Both endogenous and exogenous mechanisms are relied upon to effectively process this information, however, it is unclear how they relate in the sense of touch. In three tasks we contrasted endogenous and exogenous ERP and behavioural effects. Unilateral tactile cues were followed by a tactile target at the same or opposite hand. Clear behavioural effects showed facilitation of expected targets both when the cue predicted targets at the same (endogenous predictive task) and opposite hand (endogenous counter-predictive task), and these effects also correlated with ERP effects of endogenous attention. In an exogenous task, where the cue was non-informative, inhibition of return (IOR) was observed. The electrophysiological results demonstrated early effects of exogenous attention followed by later endogenous attention modulations. These effects were independent in both the endogenous predictive and exogenous tasks. However, voluntarily directing attention away from a cued body part influenced the early exogenous marker (N80). This suggests that the two mechanisms are interdependent, at least when the task requires more demanding shifts of attention. The early marker of exogenous tactile attention, the N80, was not directly related to IOR, which may suggest that exogenous attention and IOR are not necessary two sides of the same coin. This study adds valuable new insight into how we process and select information presented to our body, showing both independent and interdependent effects of endogenous and exogenous attention in touch.

Introduction

Our largest organ, the skin, is constantly bombarded with an endless stream of tactile information. Endogenous attention helps us focus on what information is relevant and to predict upcoming sensory events. On the other hand, when something touches our body unexpectedly (e.g., a mosquito on our ankle), we rely upon exogenous attention to process this new and unexpected information. In everyday life there is naturally an interplay between endogenous and exogenous orienting. However, it is less clear of how, or to what extent, these mechanisms relate.

A common way to explore endogenous and exogenous spatial attention is using a cue-target paradigm (e.g., Posner, 1980) whereby the cue predicts the location of a target (endogenous task) or the cue is unrelated to where the upcoming target will appear (exogenous task). The typical behavioural outcome is faster response times (RTs) to attended compared to unattended targets in endogenous tasks. In an exogenous task the opposite pattern may be found with slower RTs for cued compared to uncued targets, known as inhibition of return (IOR). This effect is only present in vision if the interval between cue and target is longer than about 300 ms. On the contrary, in touch, IOR has been observed at intervals as short as 100 ms (Lloyd et al., 1999). IOR is a behavioural effect by nature and found in all modalities (see Klein, 2000 for review) and often taken as a measure of exogenous attention, that attention is inhibited to return to a previously attended location (e.g., Posner et al., 1985). However, IOR has also been attributed to a range of other perceptual and cognitive processes (e.g., motor inhibition) (Berlucchi, 2006). It is becoming more evident that, although IOR may in part be driven by exogenous orienting, IOR is not synonymous with exogenous attention. Further, it is not known how endogenous attention may influence and relate to exogenous orienting or IOR in touch.

To understand how the triad of endogenous attention, exogenous attention and IOR relate, event-related potentials (ERPs) can add valuable information of the underlying processes in addition to behavioural outcome. Directing endogenous attention to the body has shown to affect somatosensory ERPs (P100, N140, Nd), typically with larger amplitude for the attended compared to unattended tactile stimuli (e.g., Eimer & Forster, 2003; Forster & Eimer, 2004; Zopf, et al., 2004). Much less is known about the neural correlates of IOR and exogenous attention in touch. We recently investigated this (Jones & Forster, 2012) and found an exogenous cueing effect as early as the N80 (potentially primary somatosensory cortex). Moreover, we demonstrated a difference between cued and uncued trials at the P100 when IOR was present and no effect when absent. What is not known is how voluntarily directing our attention influences the way we process exogenous stimuli.

We used three tasks to investigate how endogenous attention influences exogenous attention and/or IOR. The cue was presented to either the left or right hand and the target appeared at either the same (cued) or

opposite hand (uncued). In the exogenous task, the cue did not indicate the target location ($p=.50$). In an endogenous-predictive task the cue predicted targets to appear at the same location ($p=.80$) whilst in a third endogenous counter-predictive condition, the cue predicted the target at the opposite hand. Behaviourally we predicted IOR in the exogenous task and facilitation of RTs in the endogenous tasks. The ERP predictions were less specific but broadly we expected exogenous attention to influence early somatosensory ERPs and endogenous attention to influence later components. Importantly, contrasting our three tasks allowed us to isolate exogenous from endogenous effects, both in terms of underlying neural correlates and also behavioural performance. In other words, our aim was to detangle how endogenous attention, exogenous attention and IOR operate in touch.

Methods

Participants

12 paid participants (10 right-handed) took part in this study and all gave written informed consent prior to their participation. The study conformed with ‘The Code of Ethics of the World Medical Association’ (Declaration of Helsinki) and ethical approval was granted by City University London ethics committee. There were seven males and five females with a mean age of 25.6 years (range: 20-37 years).

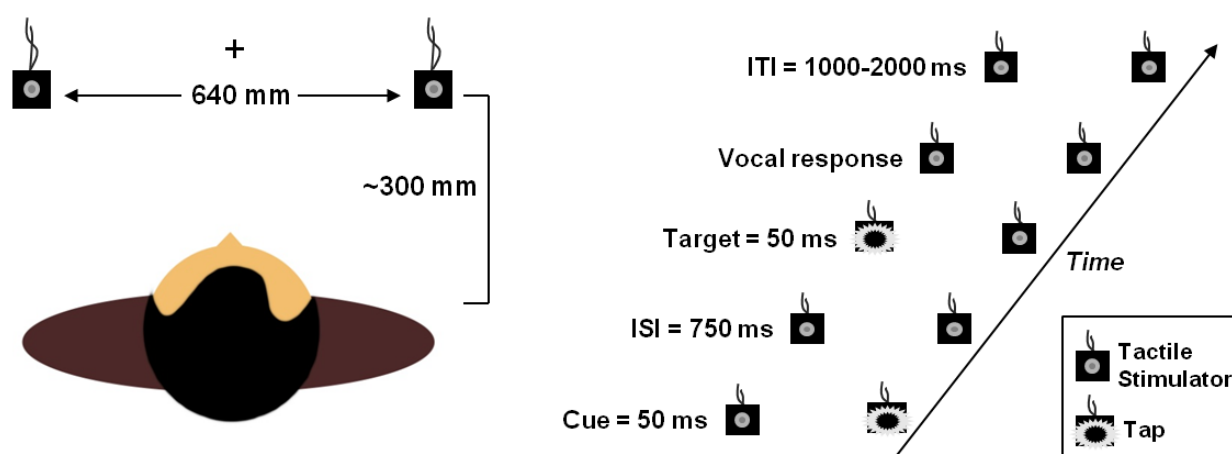


Figure 1 Experimental set-up and stimuli presentation. *Left*: Schematic view of the experimental set-up. The two boxes in front of subject represent two tactile stimulators attached to the index finger of each hand. *Right*: Schematic representation of events in a trial where cue and target are presented at opposite sides (uncued trial). In the exogenous task the schematic view represents an uncued trial, in the endogenous predictive task an unexpected trial, and in the endogenous counter-predictive task the trial would be expected.

Stimuli and apparatus

Stimuli and apparatus were identical in the exogenous, endogenous predictive and endogenous counter-predictive tasks. Participants sat in a dimly lit, sound attenuated Faraday cage. Tactile stimuli were

presented using 12-V solenoids (5 mm in diameter). The two tactors were fixed (using medical tape) to the left and right index finger and the hands were 640 mm apart (see Figure 1 for schematic view of experimental set-up). 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. Responses were made into a microphone, placed directly in front of the participant. A white fixation cross was presented on a monitor located directly in front of the participant and a black cloth covered the participant's hands to avoid any visual information of the tactile stimulation. Stimuli were presented using E-Prime software on a PC in the adjacent room to the Faraday cage. From this PC triggers were also sent to a second PC which recorded the EEG data using Brain Vision Recorder (Brain Products Inc.).

Design and Procedure

The experiment consisted of 13 blocks, 5 for each of the two endogenous tasks and 3 blocks for the exogenous task. The task order was counterbalanced across participants. The participant also completed a practice block of each task.

In the endogenous predictive task, each block consisted of 112 trials out of which in 80 trials, the cue and target appeared to the same side (expected trial) and in 20 trials the target appeared to the opposite side to the cue (unexpected trial) and 8 catch trials where there was no target but only a cue (4 left cues and 4 right). A further 4 trials per block were 'fast filler trials' where the cue target interval was 400 ms for two trials and 500 ms for two, rather than 750 ms as in all other cue-target trials. These trials served to reduce participant's expectation of the target appearing at exactly 750 ms after cue presentation. These four trials were all expected with cue and target appearing at the same location, two to the left and two to the right. Disregarding filler and catch trials, the weighting between expected and unexpected trials was 80% vs. 20%. In the endogenous counter-predictive task there were the same number and ratio of trials as the endogenous predictive task. However, in this task the cue predicted the target to appear at the opposite hand to the cue in 80% of the trials and in 20% of the trials cue and target appeared at the same hand. In the exogenous task there were the same number of trials as the endogenous tasks (112), although in this task cued (cue and target appeared at the same location) and uncued trials (cue and target appeared at opposite location) were equally weighted, 50 cued and 50 uncued trials in each block. As in the other two tasks there were 8 catch trials and 4 'fast filler trials'.

Table 1. Design and terminology of cue and target conditions in the three tasks

Task	Cue and Target locations	
	Cued (same side)	Uncued (opposite sides)
Endogenous predictive	Expected* (80%)	Unexpected (20%)
Endogenous counter-predictive	Unexpected (20%)	Expected* (80%)
Exogenous	Cued (50%)	Uncued* (50%)

Note. Summary of the likelihood of the target appearing at the same or opposite side as the cue in the three tasks. The percentages refer to the likelihood of the target appearing at the location predicted by the cue. So, when a cue appeared to the left in the endogenous counter-predictive task then there was an 80% likelihood that the target would appear to the right hand. The conditions with an asterisk are those predicted to be fastest within each task. In the endogenous tasks this is due to facilitation of expected targets and in the exogenous task, uncued trials are expected to be faster than cued due to IOR.

The stimuli presentation procedure for each trial was the same for all three tasks (see Figure 1). Each trial started with a 50 ms cue. This was followed by a 750 ms inter-stimulus interval before a 50 ms target. The participant was instructed to respond as quickly as possible by saying *pa* into a microphone as soon as the target appeared. Following their response there was a random inter-trial-interval (ITI) of 1000-2000 ms. If no response was made within 1500 ms the trial terminated and the next trial began after the ITI. In the endogenous tasks the participant was instructed about the probabilities of the target appearing at expected compared to unexpected locations and to use this information to speed up RTs. In the exogenous task the participant was informed that the cue would not predict the target location and therefore to ignore the cue completely.

Behavioural analysis

Behavioural data (mean response times) were submitted to a 2x3 repeated measures ANOVA with the factors Task (endogenous predictive, exogenous, endogenous counter-predictive), and Cue (cued, uncued). A Task*Cue interaction was followed up by separate analysis for each task. To detangle facilitation and inhibition on a behavioural level in the different tasks, the three conditions expected to be fastest were subjected to an ANOVA with factor Cue (endogenous predictive cued (expected), exogenous uncued, endogenous counter-predictive uncued (expected)) (see Table 1). Similarly the predicted three slowest conditions were subjected to a repeated measures ANOVA with factor Cue (endogenous predictive uncued (unexpected), exogenous cued, endogenous counter-predictive cued (unexpected)). These predictions of fastest and slowest conditions were based upon well established behavioural research showing facilitation for endogenously attended over unattended targets and IOR in an exogenous task (e.g., Lloyd et al., 1999). Wherever the ANOVA assumption of Sphericity was violated, Greenhouse-Geisser adjusted probability levels were reported. The same adjustments were also made for the subsequent ERP analysis. Trials with RTs less than 100 ms were excluded from analysis, resulting in a removal of 5% of trials in the endogenous predictive, 3.7% in the exogenous and 6.0% in the endogenous counter-predictive task.

ERP recording and analysis

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 k Ω , earlobe and ground electrodes below 2 k Ω , 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. The average earlobe reference is preferred with low density recordings because an average reference (mean of all recorded electrodes) is not as accurate under such conditions (Handy, 2005; Nunez & Srinivasan, 2006). Data was filtered with a low pass filter of 40 Hz. Then EEG was epoched offline into 300 ms periods starting 100 ms before and 200 ms after target onset for post target analysis. The time window was restricted to 200 ms post target to diminish contamination of the ERPs by behavioural responses. Baseline correction was performed in 100 ms period preceding onset of target. Trials with eye movements (voltage exceeding $\pm 40\mu\text{V}$ relative to baseline at HEOG electrodes) or with other artifacts (voltage exceeding $\pm 80\mu\text{V}$ relative to baseline at all electrodes) were removed prior to EEG averaging. Additionally, the residual HEOG deflections were analysed to make sure no individual had a difference which exceeded $4\mu\text{V}$ between cue-left and cue-right trials (Kennett, van Velzen, Eimer, & Driver, 2007). Further, all trials with behavioural errors, as well as catch and filler trials, were excluded from EEG analysis. This resulted in subsequent ERP analysis for the endogenous predictive task and endogenous counter-predictive being based on an average of 346 and 313 expected trials, respectively. For unexpected predictive and counter-predictive analysis was based upon 85 and 81 trials per participant, for each task respectively. The exogenous task analysis was based on an average of 130 cued and 128 uncued trials per participants.

ERP analysis epochs were averaged separately for task (endogenous predictive, exogenous, and endogenous counter-predictive) and cue type (cued, uncued). ERP mean amplitudes were computed for measurement windows centred around the peak latencies (averaged across all conditions) of the somatosensory P45, N80, P100 and N140 components (38-58 ms, 68-88 ms, 90-122 ms and 130-160 ms post-stimulus, respectively). To investigate longer-latency effects of spatial attention, mean amplitudes were also computed between 160-200 ms (Nd) after tactile stimulus onset. The time windows were based upon the components width and are comparable with previous studies from different labs investigating somatosensory ERPs (e.g., Eimer et al., 2003; Jones and Forster, 2012). A repeated measures ANOVA was conducted to compare attentional modulations with the factors Task (endogenous predictive, exogenous, endogenous counter-predictive), Cue (cued, uncued), Electrode Site (CP1/2, CP5/6, C3/4, FC1/2, FC5/6, T7/8) and Hemisphere (ipsilateral, contralateral). The electrode selection was based on electrodes close to and around the somatosensory cortex where tactile ERPs are found and attention effects on tactile processing were expected (e.g., Eimer et al., 2003; Jones and Forster, 2012 & 2013b).

Any significant attention modulations were correlated with behavioural RT effects to further investigate any relationship between the two measures. The ERP effect was the average amplitude difference between cued versus uncued trials at each component. The RT effect was similarly calculated as a difference in ms between cued and uncued trials for each participant. Correlations were only analysed for components which demonstrated a significant attention modulation. Moreover, if the attention effect was over contralateral electrodes, then only contralateral electrodes would be correlated with RTs.

Significant Cue*Electrode site interactions are only reported when warranting follow-up analyses. That is, when the effect of Cue was significant and also a Cue*Electrode site interaction, then this interaction was not investigated further. Whilst a non-significant effect of Cue and a significant Cue*Electrode site interaction were further analysed, applying a Bonferroni correction. Partial eta squared (η^2_p) effect sizes are reported.

Results

Behavioural performance

Analysis of participants' RTs to target stimuli showed there was a significant Task*Cue interaction ($F(2,22)=36.82$, $p<.001$, $\eta^2_p=.77$) indicating RTs for cued and uncued trials were not the same across the three tasks. However, we were specifically interested in investigating facilitation and IOR effects in each task separately as opposite effects were predicted (Lloyd et al., 1999). Analysis of the exogenous task demonstrated IOR as RTs for cued trials (338.71 ms, Standard Error of the Mean (SEM) 24.99) were significantly slower compared to uncued trial (319.06 ms, SEM 22.80) ($t(11)=-2.37$, $p=.037$, $\eta^2_p=.34$). For the endogenous predictive task, RTs to cued targets (315.32 ms, SEM 28.25) were significantly faster compared to uncued targets (439.17 ms, SEM 45.54) ($t(11)=4.26$, $p=.001$, $\eta^2_p=.62$). Analysis of the endogenous counter-predictive task showed that RTs to uncued targets (285.78 ms, SEM 20.13) were significantly faster compared to cued targets (450.93 ms, SEM 38.10) ($t(11)=5.64$, $p<.001$, $\eta^2_p=.74$) (see Figure 2). That is, endogenous orienting facilitated RTs at the expected location in both endogenous predictive and counter-predictive tasks. Errors were overall low, with slightly more errors in the endogenous counter-predictive task as expected. Responses to catch trials (false alarms) were 10% in the endogenous predictive, 16% in the endogenous counter-predictive, and 11.5% in the exogenous task. Trials in which no response was made (missed targets) were 1.6% in the endogenous predictive, 3.2% in the endogenous counter-predictive, and 1.7% in the exogenous task.

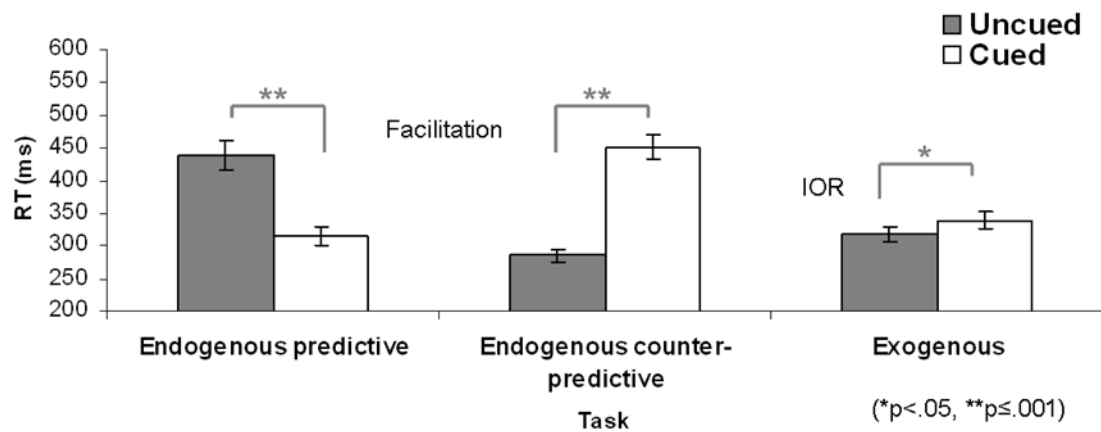


Figure 2 Average response times (RTs in ms) and standard error bars displayed for each task. The white bars represent RTs for cued trials where cue and target were presented to the same hand. Uncued trials are when cue and target were presented to different hands (grey bars). In the endogenous predictive task the cued trials were expected and uncued unexpected. In the endogenous counter-predictive task the uncued trials were expected and cued trials unexpected. In both endogenous tasks, attention significantly facilitated RTs at expected locations. The exogenous task showed IOR as cued trials were significant slower compared to uncued trials.

To explore the nature of facilitation and inhibition, and if these are separate or competing mechanisms, further analyses of the RTs were conducted (for similar analysis see e.g., Chica et al., 2006). The three conditions expected (see Table 1) to show the slowest RTs in each task were compared (i.e., exogenous cued, endogenous predictive uncued, and endogenous counter-predictive cued conditions). Overall the three conditions were significantly different ($F(2,22)=4.34$, $p=.047$, $\eta^2_p=.28$). More specifically, exogenous cued trials (338.71 ms) were significantly faster ($p=.001$, Bonferroni corrected) compared to endogenous counter-predictive cued trials (450.93 ms). Exogenous cued trials (338.71 ms) were not significantly faster ($p=.23$, Bonferroni corrected) compared to endogenous predictive uncued trials (439.17 ms), although a similar effect size. It can be concluded that exogenous inhibition (IOR) does not inhibit RTs as much as in voluntary inhibition, which may not be surprising. Comparison of the three conditions predicted to show fastest RTs within their respective tasks were compared to explore the effects facilitation, and these three conditions showed no significant difference ($p=.41$). In particular, the comparison between expected trials in the two endogenous tasks (endogenous predictive cued vs. endogenous counter-predictive uncued) showed no significant difference ($p=.48$, Bonferroni corrected) and no sign of IOR for unexpected trials (endogenous predictive uncued vs. endogenous counter-predictive cued; $p=1$, Bonferroni corrected). This suggested IOR did not affect or interact with endogenous attention, even when informative cues are presented laterally. Taken together, the behavioural data showed no presence of IOR at expected or unexpected locations.

Effects of attentional orienting on ERPs

Figure 3 shows ERP waveforms in the exogenous task elicited by tactile target stimuli on cued (black line) and uncued trials (grey line). The attention effect here was present at the N80 component with enhanced amplitude for uncued compared to cued trials at electrodes contralateral (right panel) to target location (marked out on the C3/4c electrode). Figure 4 and 5 show ERP waveforms elicited to targets at expected (black line) and unexpected locations (grey line) in the endogenous tasks. In the endogenous predictive task (Figure 4), the N80 effect was similar to that in the exogenous task with larger negativity for cued compared to uncued targets at electrodes contralateral to target location. Following on from the N80 there was a P100 attention effect in the endogenous predictive task, present at T7/8 electrodes contralateral to target presentation. In the endogenous counter-predictive task (Figure 5), the earliest attention effect was also seen at the N80 component. However, this effect was opposite to the other two tasks with enhanced negativity for uncued compared to cued trials (marked out on electrode C3/4i, left panel in Figure 5). Following early somatosensory attention effects, both endogenous tasks showed modulations at N140 and Nd with larger negativity for expected compared to unexpected trials. For topographical maps of the effects see Figure 6.

P45

No significant main effects or interactions involving the factor Cue were found for the P45 analysis window.

N80

Analysis of the N80 time window showed a Task*Cue*Hemisphere interaction ($F(2,22)=21.39$, $p<.001$, $\eta^2_p=.66$; as well as a Cue*Hemisphere $F(1,11)=7.40$, $p=.02$, $\eta^2_p=.40$ interaction). This interaction was broken down further and each task was analysed separately.

The exogenous task showed a significant Cue*Hemisphere effect ($F(1,11)=29.51$, $p<.001$, $\eta^2_p=.73$) and separate follow-up analyses for each hemisphere showed a significant effect of Cue ($F(1,11)=10.01$, $p=.009$, $\eta^2_p=.48$) over electrodes contralateral to target location whilst no attention effect was seen over ipsilateral electrodes. There was no correlation between contralateral attention modulation and RT effect ($r=.04$, n.s.). In other words, there was no indication that larger attention modulation of the N80 related to a larger RT effect across participants.

In the endogenous predictive task there was a Cue*Hemisphere ($F(1,11)=12.00$, $p=.005$, $\eta^2_p=.52$) interaction and separate follow up analyses for each hemisphere showed an attention effect over electrodes contralateral to target presentation only (Cue: $F(1,11)=5.19$, $p=.044$, $\eta^2_p=.32$). There was no significant correlation between the contralateral attention modulation and RT effect ($r=.52$, n.s.).

The endogenous counter-predictive task also demonstrated a significant Cue*Hemisphere interaction ($F(1,11)=12.97$, $p=.004$, $\eta^2_p=.54$) and separate follow-up analyses of each hemisphere demonstrated the N80 attention effect to be present only at electrodes ipsilateral (Cue: $F(1,11)=6.97$, $p=.023$, $\eta^2_p=.39$) to target location. There was no significant correlation between ipsilateral attention modulation and RT effect ($r=.32$, n.s.).

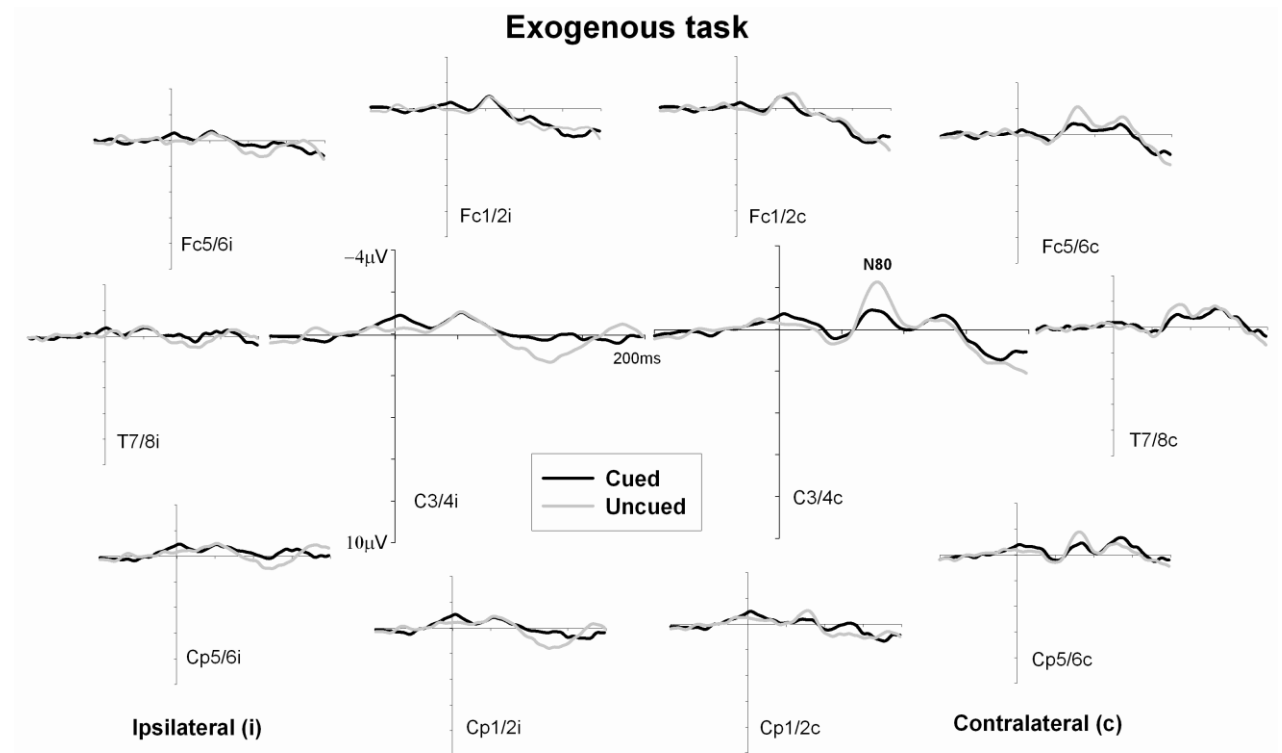


Figure 3 Exogenous task grand averaged somatosensory ERPs elicited on cued (black line) and uncued (grey lines) trials in the 200 ms following target onset. The left side shows ERPs over ipsilateral (i) hemisphere and right are ERPs contralateral (c) to target side. The N80 label on C3/4c indicates the significant difference between cued and uncued trials at the N80 component over contralateral electrodes. No other components showed significant cueing effects.

P100

The overall analysis including all three tasks at the P100 time window demonstrated a significant Task*Cue*Hemisphere interaction ($F(2,22)=8.47$, $p=.002$, $\eta^2_p=.44$; as well as Cue*Hemisphere $F(1,11)=15.95$, $p=.002$, $\eta^2_p=.59$) and follow-up analyses were conducted for each task separately. The exogenous task showed a significant Cue*Hemisphere ($F(1,11)=12.25$, $p=.005$, $\eta^2_p=.53$) interaction. However, separate follow-up analysis revealed no significant effect of attention at either hemisphere. In the endogenous predictive task there was a Cue*Hemisphere $F(1,11)=14.54$, $p=.003$, $\eta^2_p=.57$ interaction and separate follow-up analyses for each hemisphere showed a Cue*Electrode site interaction at contralateral electrodes ($F(5,55)=7.07$, $p=.001$, $\eta^2_p=.39$). This interaction was further broken down and separate attention

analysis for each electrode pair was conducted demonstrating the P100 attention effect was present over contralateral T7/8 ($t(11)=-3.48$, $p=.03$, Bonferroni corrected). Analysis of ipsilateral electrodes showed no P100 attention effect. A correlation of the ERP attention modulation and behavioural effect showed no significant relationship ($r=.25$, n.s). Analysis of the endogenous counter-predictive task showed no significant effects involving the factor Cue.

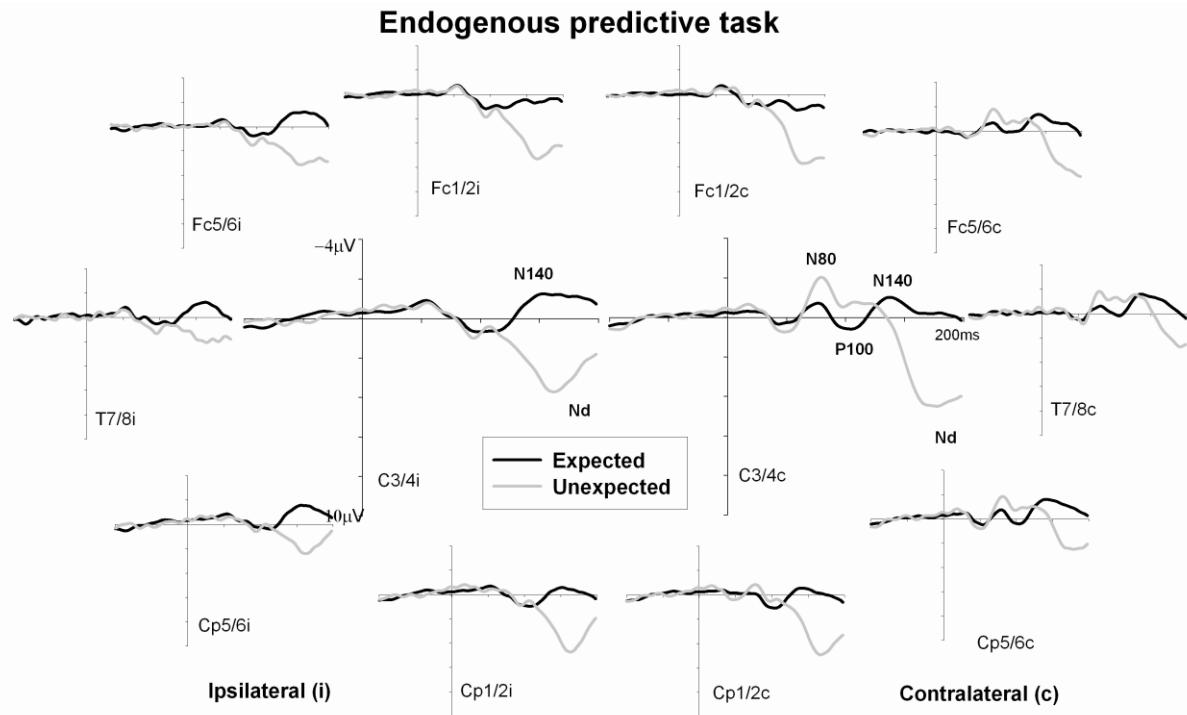


Figure 4 Endogenous predictive task grand averaged somatosensory ERPs elicited on expected/cued (black lines), and unexpected/uncued (grey lines) trials in the 200 ms following target onset. The left side shows ERPs over ipsilateral hemisphere and right are ERPs contralateral to target side. The component labels on the C3/4 electrodes denote if the component was significantly modulated by attention (significant difference between expected and unexpected trials).

N140

There was a Task*Cue*Hemisphere interaction ($F(2,22)=7.05$, $p=.004$, $\eta^2_p=.39$), as well as a main effect of Cue ($F(1,11)=20.87$, $p=.001$, $\eta^2_p=.66$) and Cue*Hemisphere interaction ($F(1,11)=16.27$, $p=.002$, $\eta^2_p=.60$). The significant interaction was further broken down into separate analysis for each task.

Exogenous task analysis of the N140 showed a significant Cue*Electrode site*Hemisphere interaction ($F(5,55)=3.34$, $p=.029$, $\eta^2_p=.23$) which was broken down into separate analyses for each hemisphere. However, there were no significant effects including the factor Cue at electrodes ipsilateral or contralateral to the target presentation, indicating no attention modulation at the N140 in the exogenous task.

Analysis of the endogenous predictive task revealed a significant main effect of Cue ($F(1,11)=16.95$, $p=.002$, $\eta^2_p=.61$) and also Cue*Hemisphere interaction ($F(1,11)=21.53$, $p=.001$, $\eta^2_p=.66$). The interaction was broken down revealing a significant effect of Cue, both for ipsilateral ($F(1,11)=26.66$, $p<.001$, $\eta^2_p=.71$) and contralateral electrodes ($F(1,11)=8.77$, $p=.013$, $\eta^2_p=.44$) and both these effects showed enhanced negativity for expected compared to unexpected trials (the interaction was driven by larger effect size over ipsilateral compared to contralateral hemisphere) (see Figure 4). That is, the N140 attention effect in the endogenous predictive task was present over both hemispheres. Moreover, and importantly, there was a significant correlation between the ERP attention modulation and the behavioural RT effect, with larger amplitude difference between expected and unexpected conditions for each participant relating to larger RT attention effect ($r=.69$, $p=.013$) (see Figure 7 for a scatter plot of this relationship).

The endogenous counter-predictive task revealed the attention effect was, similar to the endogenous predictive task, bilateral as there was a significant effect of Cue ($F(1,11)=5.16$, $p=.044$, $\eta^2_p=.32$). There was no significant correlation between ERP attention modulation and RT effect ($r=.32$, n.s.).

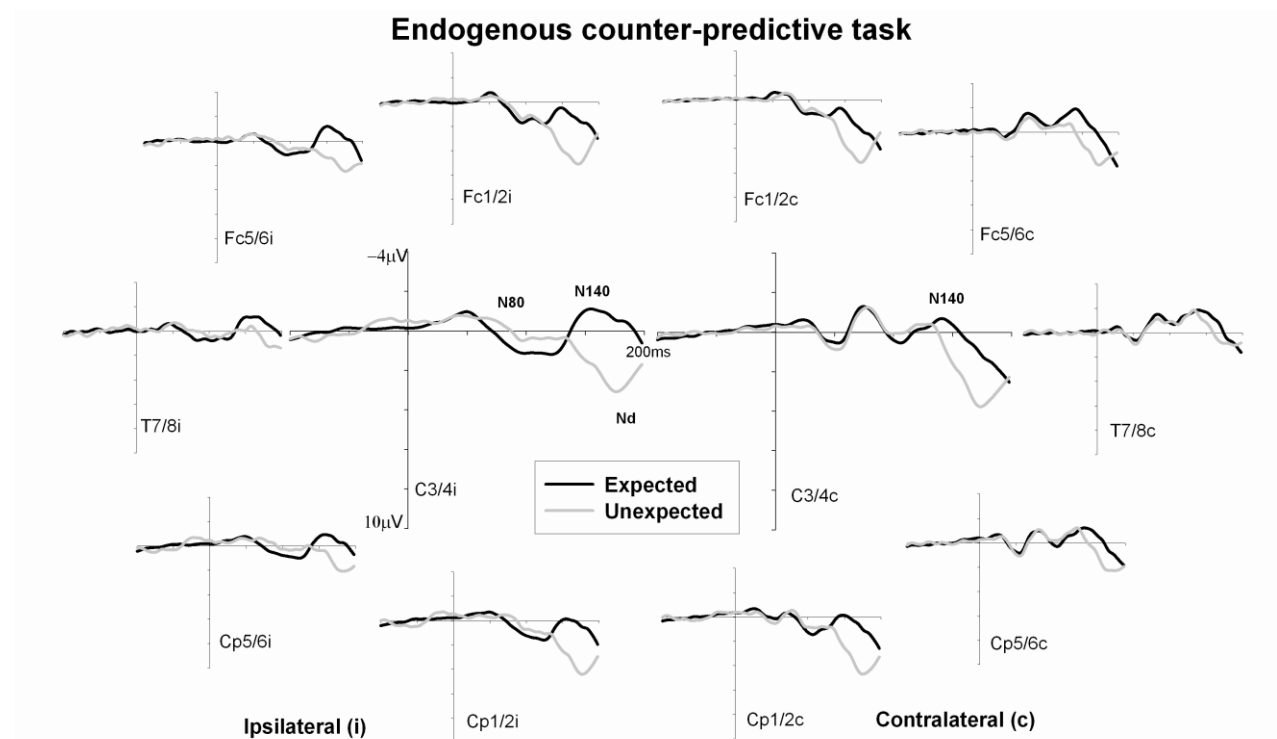


Figure 5 Endogenous counter-predictive task grand averaged somatosensory ERPs elicited on expected/uncued (black lines), and unexpected/cued (grey lines) trials in the 200 ms following target onset. The left side shows ERPs over ipsilateral hemisphere and right are ERPs contralateral to target side. The component labels on the C3/4 electrodes denote if the component was significantly modulated by attention (significant difference between expected and unexpected trials). In the counter-predictive task the early (N80) effect is ipsilateral to the target but contralateral to the cue.

Nd

At this last analysed time window the overall task analysis demonstrated a Task*Cue*Hemisphere interaction ($F(2,22)=8.29$, $p=.002$, $\eta^2_p=.43$, and also; Cue $F(1,11)=11.02$, $p=.007$, $\eta^2_p=.50$) and subsequently each task was analysed separately.

The exogenous task revealed a Cue*Hemisphere interaction ($F(1,11)=8.57$, $p=.014$, $\eta^2_p=.44$). However, separate follow-up analyses for contralateral and ipsilateral hemisphere yielded no significant effects of Cue.

The endogenous predictive task demonstrated an Nd effect which was over both hemispheres (Cue: $F(1,11)=15.33$, $p=.002$, $\eta^2_p=.58$). Moreover, there was a significant positive correlation between attention modulation and behavioural effect ($r=.81$, $p=.001$) (see Figure 7 for a scatter plot of this relationship).

The Nd in the endogenous counter-predictive task was seen over electrodes ipsilateral to target location (Cue $F(1,11)=5.48$, $p=.039$, $\eta^2_p=.33$), following a significant Cue*Hemisphere interaction ($F(1,11)=12.80$, $p=.004$, $\eta^2_p=.54$). Furthermore, there was a significant positive correlation between the ipsilateral attention modulation and RT effect ($r=.60$, $p=.041$) (see Figure 7).

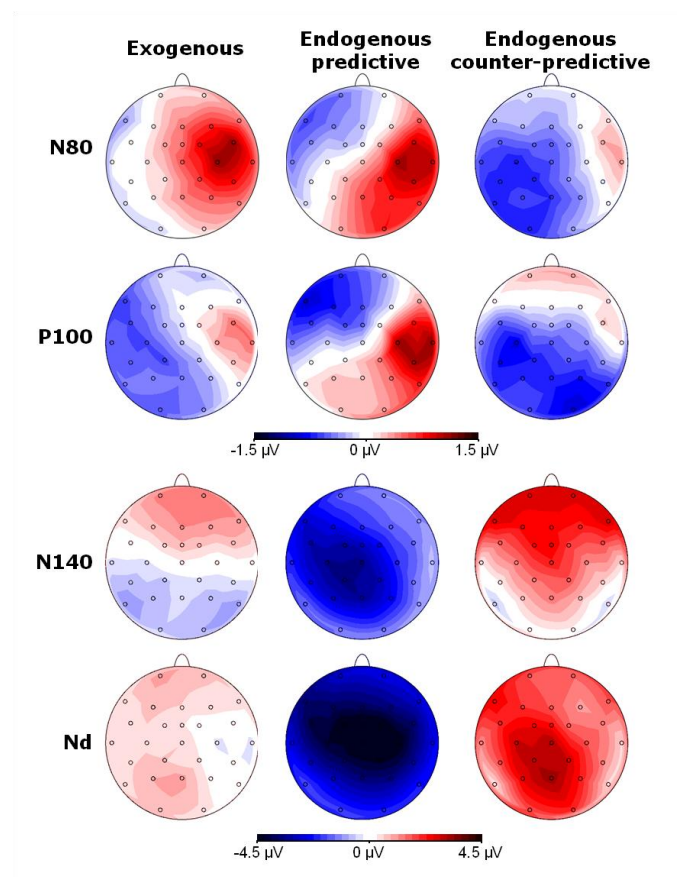


Figure 6. Topographic maps of the attention effects at each somatosensory component. In all three conditions uncued were subtracted from cued trials. The right hemisphere shows attention effects contralateral to the target side and the left hemisphere shows ipsilateral attention effects. The N80 component showed larger negativity over contralateral hemisphere for uncued trials in the endogenous predictive and exogenous task. The N80 effect for the endogenous counter-predictive task is reversed with larger negativity for cued over uncued trials, this effect present over ipsilateral hemisphere. The scaling for the N80 and P100 effect is -1.5 to 1.5 μV and for the N140 and Nd the amplitude ranges between -4.5 to 4.5 μV .

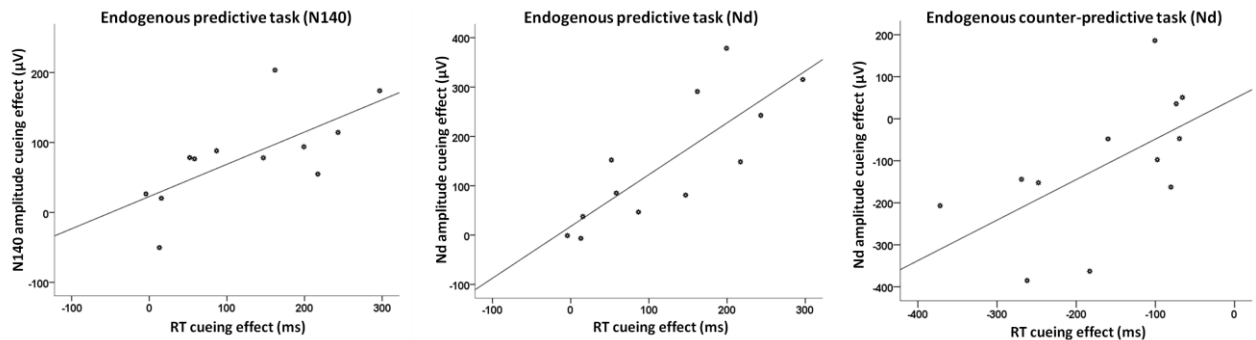


Figure 7. Scatter plots of the relationship between attention effects shown behaviourally and in the somatosensory ERPs for each participant. The *y*-axis shows the difference between uncued and cued trials averaged over somatosensory electrodes. The *x*-axis shows the mean RT effect between uncued and cued trials. The endogenous predictive task demonstrated a positive correlation between the RT effect and cueing effect at the N140 and Nd components. In the endogenous counter-predictive task the correlation was observed at the Nd component only. In other words, both endogenous tasks showed that larger behavioural effect of attention correlated positively with a larger ERP effect of attention.

DISCUSSION

This study looked at how endogenous orienting influences exogenous attention and/or IOR in touch. As predicted, the behavioural data showed facilitation of RTs for expected compared to unexpected targets in both endogenous tasks whilst IOR in the exogenous task (see Figure 2). Interestingly, there was no indication of IOR at either expected or unexpected locations suggesting IOR did not influence endogenous orienting. This suggests that IOR and endogenous attention are not, when behaviour is concerned, interrelated mechanisms. The ERPs revealed both early effects of exogenous (N80) and late effects of endogenous attention (N140 and Nd). Although IOR and endogenous attention were not interrelated at a behavioural level, endogenous orienting affected exogenous cueing effects. That is, endogenous attention influenced early exogenous processing, whilst there was no evidence of an exogenous effect on endogenous processing. Moreover, the N80 cueing effect, demonstrated in the endogenous predictive and exogenous tasks, did not seem to relate to IOR, suggesting a dissociation between IOR and exogenous attention. We predicted that endogenous attention would affect later stages of processing. We did not only demonstrate endogenous attention modulations at these late components (N140 and Nd), but for the first time showed a direct relationship between neural correlates of endogenous tactile attention and behavioural performance.

In other words, the endogenous attention effects shown in the ERP data strongly correlated with RT effects providing compelling evidence for a direct link between behaviour and underlying neural processes. These findings are discussed in more details below.

The behavioural results are in line with previous studies of tactile attention showing IOR in the exogenous task (Cohen et al., 2005; Lloyd et al., 1999; Jones & Forster, 2012), facilitation of attended targets in the endogenous predictive task (Cohen et al., 2005; Lloyd et al., 1999; Jones & Forster, 2013a) and endogenous counter-predictive task (Chica, Sanabria, Lupiáñez, & Spence, 2007). We did not demonstrate a presence of IOR during endogenous attention, in accord with previous tactile studies with a similar paradigm (Chica et al., 2007). Specifically, there was no difference between cued and uncued targets for expected or separately for unexpected trials in the two endogenous tasks. Studies exploring visual stimuli have suggested IOR to be independent of endogenous orienting and these do not interact, at least when task demands are low (e.g., Berger, Henik, & Rafal, 2005; Lupianez et al., 2004). Our behavioural results do not confirm nor disconfirm this idea of independent effects. However, our findings are that IOR does not automatically exert an effect on endogenous attention when using peripheral cues and targets, but is either absent or masked during endogenous orienting.

A better insight into how the triad of endogenous attention, exogenous attention, and IOR interact may be gained from closer inspection of the ERPs, together with the behavioural data. The first notable result was that we did not find an ERP effect which directly represented IOR. Based on IOR studies in visual attention (McDonald, Ward, & Kiehl, 1999; Prime & Ward, 2004, 2006; Tian & Yao, 2008; Wascher & Tipper, 2004, van der Lubbe, Vogel, & Postma, 2005; Prime & Jolicoeur, 2009) as well as our own previous tactile study (Jones & Forster, 2012) we predicted, if anything, the P100 to show an effect associated with IOR. However, there was no cueing effect at the P100 in the exogenous task (see Figure 3). As our exogenous task was a near replication of our previous study (Jones & Forster, 2012, detection task) we can conclude that the P100, at least on its own, is not a marker of IOR. The inability to replicate the P100 effect in the present exogenous task could be extended to the visual literature and highlight that the P1 cueing effect may not be a direct marker of IOR (e.g., Prime & Ward, 2006). That no study has yet shown a correlation between P1 cueing effects and RTs reflecting IOR also highlights this point. The exogenous task did demonstrate an earlier exogenous attention effect on the N80, with larger negativity for uncued compared to cued targets (Figure 3). A very similar modulation was also present in the endogenous predictive task (Figure 4). As these two tasks demonstrated opposite behavioural effects, yet similar N80 modulations, it suggests this is not a marker of IOR. Moreover, comparing the behavioural performance, in the two endogenous tasks showed no presence of IOR whilst they showed an N80 cueing effect, further suggesting the N80 effect is simply not a marker of IOR masked by endogenous attention. While the N80 effect may not be a marker of IOR, we suggest it to be a marker of exogenous attention. A dissociation of IOR from

exogenous visual attention has previously been argued (e.g., Berlucchi, 2006). For example, using fMRI, Mayer et al. (2004) found exogenous attention (facilitation) and IOR activated different brain areas. Furthermore, Fuchs and Ansorge (2012) showed that an unconscious cue that exogenously captures attention does not lead to IOR. It is likely that IOR is the end-results of several cognitive, perceptual and/or motor processes, affecting multiple components. That IOR is not simply an attentional phenomenon has more recently been reported in visual attention literature (e.g., Satel et al., 2013). However, before drawing parallels to other modalities it remains to be established whether IOR is a supramodal or modality specific phenomena. To note is that touch is a purely proximal sense and therein different to other modalities.

The N80 component has been proposed to originate from primary somatosensory cortex contralateral to the stimuli (Hari et al., 1984; Inui et al., 2004; Mima et al., 1998). In the endogenous counter-predictive task the effect was absent at the contralateral N80 component, whilst there was a reverse effect over the ipsilateral hemisphere (Figure 5 & 6). That is, there was larger negativity for cued compared to uncued targets in the counter-predictive task. This suggests that the early exogenous marker was influenced by instructing people to orient their endogenous attention. Put differently, had the N80 been an exogenous effect completely independent of endogenous orienting and task demands then we would expect to find the same pattern in all three tasks. This contrasts in part a visual attention study by Chica and Lupianez (2009) who concluded that the early exogenous effect on the P1 (which they attributed to IOR) was not influenced by endogenous attention. Although there may be several reasons which could explain differences between the studies, our results do not go against the suggestion that IOR and endogenous attention are independent mechanisms (e.g. Berger et al. 2005, Lupianez et al., 2004). A clear conceptual difference is that we found our exogenous marker (N80) to be influenced by orienting endogenous attention in the counter-predictive task, whilst Chica and Lupianez found that their marker of IOR to not to be affected by endogenous attention. Therefore, it may be that IOR is independent from endogenous orienting whilst exogenous effects are not. Taken together, comparing and contrasting the N80 in different conditions led to two main conclusions. First, the N80 cueing effect to likely be a neural correlate of exogenous attention and not directly related to IOR, further supporting the idea that IOR is not synonymous with exogenous attention. That being said, to establish the independence between exogenous attention and IOR more research is needed, in particular where the neural markers of IOR can be observed, something which is yet to be reliably established in any modality. The second conclusion from the N80 was that this early exogenous effect, possible primary somatosensory cortex, can be influenced by orienting voluntary attention suggesting an interaction between endogenous and exogenous attention at early stages of processing tactile information.

Somatosensory components independently modulated by endogenous attention followed the early exogenous N80 effect. In the endogenous predictive task there was a P100 effect with larger positive

amplitude for attended compared to unattended stimuli, an effect corroborating previous tactile attention studies (Eimer & Forster, 2003; Zopf et al., 2004). The strongest indicators of endogenous orienting were seen at the following N140 and Nd components, which have also demonstrated attention effects in previous tactile studies (Eimer & Forster, 2003; Forster & Eimer, 2004; Zopf et al., 2004). Importantly, and previously not demonstrated, is the presence of strong correlations between behavioural and ERP attention effects in both endogenous attention tasks (see Figure 7). That is, participants with larger behavioural attention effects also demonstrated relatively larger ERP amplitude effects between expected and unexpected trials. This expands on a previous study (Forster & Eimer, 2005) which indirectly suggested a similar link by showing analogous weighing of attentional orienting cost and benefits in RTs and these later latency attentional ERP modulations. The endogenous correlations developed slightly earlier in the endogenous predictive task at the N140 ($r=.69$) which probably reflects the additional time to orient attention from one hand to the other, compared to keep focusing attention on the same hand. The following late negativity (Nd) showed strong correlations in both endogenous predictive ($r=.81$) and counter-predictive ($r=.60$) tasks. This indicates that increasing task and attention demands, orienting from one hand to the other instead of attention remaining on the same hand, delays the development of endogenous attention markers in the ERP trace. Interestingly, this delay was not reflected in the behavioural performance where there was no difference between the two endogenous tasks. As a whole, the pattern of early exogenous effects of attention (N80), followed by later markers of endogenous attention (N140 and Nd) is consistent with behavioural accounts based on visual attention proposing that exogenous attention develops faster than endogenous attention (Muller and Rabbitt, 1989). Future research may wish to further explore the exact nature and relationship between behavioural performance and neural markers of attention in touch. For example, it should be noted that the present study only used one SOA (800 ms), an interval chosen as IOR has previously been observed here in touch (Jones & Forster, 2012; Cohen et al., 2005; Lloyd et al., 1999). Unlike in vision, facilitation of exogenously cued targets has not been observed with short cue-target intervals in a detection task (Lloyd et al., (1999) found IOR with a 100 ms SOA). However, similar to vision, the biphasic facilitation-IOR pattern has been demonstrated when targets are discriminated instead of simply detected (for visual discrimination task see Lupianez et al., 1997; and in touch see Miles, Poliakoff, and Brown, 2008). What would therefore be interesting for future research is using a range of SOAs in a discrimination task to investigate how endogenous attention influences both exogenous facilitation and IOR in touch. Moreover, this would additionally provide further insight into whether exogenous attention and IOR are independent or interrelated mechanisms.

In summary, behavioural performance showed facilitation of expected targets in the endogenous tasks and IOR in the exogenous task. The electrophysiological results demonstrated early effects of exogenous attention followed by later endogenous attention modulations. These effects were independent in both the endogenous predictive and exogenous tasks. However, voluntarily directing attention away from a cued

body part influenced the early exogenous marker (N80). This suggests the two mechanisms are interdependent, at least when task demands require more demanding shifts of attention. The early marker of exogenous tactile attention, the N80, was not related to the IOR effect shown behaviourally. Although the neural markers of IOR remain elusive, at least in regard to the sense of touch, we conclude exogenous attention and IOR are not necessary two sides of the same coin.

Abbreviations

Event related potential (ERP), Inhibition of return (IOR), Response time (RT), Stimulus onset asynchrony (SOA)

Acknowledgements

The authors have no conflict of interests to declare.

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