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Neural Correlates of Tactile Attention

Behavioural measures and event-related brain potentials of inhibition of
return, exogenous and endogenous attention in touch

John Alexander Jones

Thesis submitted for the degree of Doctor of Philosophy

**City University London
Department of Psychology**

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THESIS DECLARATION

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ABSTRACT

The studies presented in this thesis investigated the neural correlates of attention in touch. In particular, the electrophysiology of exogenous tactile processing and inhibition of return (IOR) - an area previously unexplored. In all studies a variation of the Posner cue-target paradigm was used. Typically, a cue was presented to the left or right hand. Following a stimulus onset asynchrony of 800 ms, a target would appear at the same or opposite hand. Behavioural results consistently demonstrated IOR when employing a simple target detection task, showing that IOR is a reliable phenomenon in touch. The concurrently recorded event related potentials (ERPs) demonstrated an early attention modulation of the N80 in all studies presented in this thesis, regardless of the presence or absence of IOR. This early component likely reflects processing of the exogenous lateralized cues. Following the N80, the attention modulations varied across studies. The conclusion to be drawn from this thesis is that not one particular ERP component is directly associated with IOR. Analysis of endogenous tactile attention (Chapter V) demonstrated modulations at the N140 and Nd components. Moreover, correlation analysis showed that larger ERP attention modulation was associated with a larger behavioural effect, demonstrating a novel relationship between ERP modulations and response time effects. Analysis of the cue-target interval has previously only been investigated during endogenous orienting. Here, and for the first time, an anterior directing attention negativity (ADAN) was demonstrated during exogenous orienting. This ADAN was unaffected by varying posture suggesting exogenous tactile attention and IOR are somatotopically coded. Indications of an external frame of reference were only demonstrated during shifts of endogenous attention, as indicated by the presence of a late directing attention positivity (LDAP) (endogenous counter-predictive task presented in Chapter V). The final study of this thesis (Chapter VI) demonstrated that varying visual perceptual load influenced tactile processing. Specifically, high perceptual load led to elimination of IOR. Moreover, the P100 for irrelevant tactile stimuli was significantly reduced in high versus low load condition. This suggests perceptual load may suppress irrelevant tactile stimuli relatively early (around 100 ms post stimuli onset) during tactile processing. Taken together, this thesis presents a series of experiments which map out effects of endogenous and exogenous attention and how these mechanisms interact, both through behaviour and underlying neural correlates.

OVERVIEW AND AIMS OF THESIS

Attention research has distinguished between voluntary (endogenous) and automatic (exogenous) orienting (e.g., Klein, 2004). Endogenously attending to a particular spatial location generally leads to enhanced processing of stimuli presented there. Exogenous attention may lead to more diverse effects. An exogenous stimulus at a particular location may facilitate further processing. However, if two consecutive stimuli appear at the same location then the first stimulus may also inhibit processing of the subsequent stimulus. This is known as inhibition of return (IOR) (Posner & Cohen, 1984). Particular areas within the broad field of attention have been more or less explored. First, visual attention has by far been the most investigated modality, followed by auditory attention. However, how we attend in touch has been less researched. Moreover, out of the two types of orienting, endogenous attention has typically been investigated, with much less focus upon mechanisms of exogenous attention.

The general aim of this thesis was to explore an area which has seen little previous research, namely exogenous tactile attention. A few studies have explored the behavioural effects of exogenous tactile attention (see Spence, 2002, for a review of tactile attention) and a handful of studies have investigated the neural correlates of endogenous tactile attention (see Sambo & Forster, 2011, for a review). This thesis therefore aimed to investigate the unexplored area of the neural correlates of exogenous tactile attention. In particular, to investigate the ERP pattern underlying IOR in touch. IOR is by nature a behavioural effect. In order to investigate the neural correlates of this phenomenon it was therefore imperative to first establish IOR at a behavioural level. In all experiments in this thesis behavioural response times were collected on every trial. The aim was to provide two measures of attention and the possibility to link behaviour to neural processes.

The ERP studies in this thesis aimed to investigate tactile attention selection and attention control processes. In a Posner cue-target paradigm the neural correlates during the cue-target interval are suggested to reflect attentional control processes. Importantly, the cue-target interval has not previously been investigated during exogenous orienting but only

during shifts of endogenous attention. The aim was therefore to explore the ERP waveforms in the cue-target interval in exogenous paradigms. To investigate tactile attentional selection the aim was to investigate the ERPs in and around somatosensory areas in the period directly following the target. To paint a fuller picture of the relationship between neural processes and observed behaviour (response times), the attention modulations in the post-target time window were correlated with observed behavioural effects. Correlating response time effects with ERP modulation is a novel method of analysis – at least in the field of tactile attention.

The first study of this thesis (Chapter II) aimed to investigate the behavioural effects of whether exogenous attention interacts with endogenous orienting. Specifically, to investigate whether irrelevant exogenous cues automatically influence behavioural response times during an endogenous task. The second study (Chapter III) aimed to explore the underlying neural correlates when IOR was present versus absent. Different behavioural and ERP effects were elicited by employing a detection and discrimination task. The study presented in Chapter III has been reviewed and re-submitted to *Biological Psychology* and appears as submitted. The study presented in Chapter IV addressed whether IOR is somatotopically or externally coded and how posture influenced tactile processing. The fourth study (Chapter V) aimed to investigate and contrast the neural correlates underlying exogenous and endogenous orienting. This chapter aimed to directly compare the ERPs elicited during exogenous and endogenous attention. To investigate whether informative lateralized cues were also influenced by exogenous attention effect, an endogenous predictive and counter-predictive paradigm was used in Chapter V. The final ERP study (Chapter VI) addressed how varying perceptual load influenced the processing of irrelevant tactile stimuli. Finally, a summary of the findings of the experiments in this thesis and suggestions of future directions are presented in Chapter VII.

The same stimuli onset asynchrony was used in all ERP studies (Chapters III-VI) and all studies included a simple target detection task. The reasoning was to provide results which could be compared across studies. This aimed to establish the reliability of any observed effects, an issue which is often overlooked in ERP research.

CHAPTER I

Attention in touch

1.1 Introduction

Imagine trying to cross a road in a busy area in central London. You need to selectively focus your attention on the traffic whilst ignoring irrelevant information around you such as fellow shoppers. To help direct your attention more specifically, on the ground in front it says *Look left*. You then focus your attention upon gaps in the oncoming traffic from the left. You selectively listen and look and then cross the road. You are in this case drawing upon your endogenous attention. This top down attention control is based upon internal goals (crossing the road safely) and cues (e.g., the writing on the ground) to decide where to focus your attention. Environmental events and stimuli which capture our attention are also important for us to cross the road safely. The appearance of a speeding car in our periphery will in this case attract and activate our exogenous attention. This bottom-up system is driven by external events and is an automatic process. The distinction between endogenous and exogenous spatial attention is supported by a large volume of behavioural evidence in healthy individuals (e.g., Funes, Lupiáñez, & Milliken, 2005; Klein, 2004, for reviews), and brain damaged patients (see Bartolomeo & Chokron, 2002; Losier & Klein, 2001, for reviews), and also evidence from electrophysiology and neuroimaging studies suggesting different neural substrates (see Corbetta & Shulman, 2002; Macaluso, 2010, for reviews).

The first part of the introduction will focus on behavioural measures and the effects of attention, in particular on inhibition of return (IOR) which is the underlying theme throughout this thesis. The main debated theories and empirical evidence which underlie this behavioural phenomenon will be reviewed. The next section of this introduction will explore the neuroscience of attention. This section will concentrate upon evidence from ERP studies of attention as this is the method used in Chapters III-VI, but relevant findings from other areas of neuroscience will also be included. The majority of research has investigated endogenous and exogenous attention separately, and the research reviewed will reflect this accordingly. Additionally, the last section will review paradigms and

findings investigating how these mechanisms interact. In particular, to what extent irrelevant stimuli are processed and can capture our attention when we are focused elsewhere. How we perceive and attend to touch is the basis of this thesis. The majority of research, in particular that involving neuroscientific techniques, has investigated visual and auditory attention. In consequence this is reflected by the theories and models proposed on attention reviewed in this introduction.

1.2 Measuring endogenous and exogenous attention using the Posner paradigm

The most common method to investigate the effects of endogenous and exogenous attention in a laboratory based setting is the use of a Posner paradigm, first developed by Posner (1978, 1980). In a typical endogenous version of this paradigm a participant would be seated in front of a monitor. In the centre of the monitor a cue would appear, typically an arrow. This would indicate to which side of the screen the target is most likely to appear and in turn the participant should direct their covert attention, which means not moving their eyes or head. A target would typically appear at the side predicted by the cue 75-80 % of times (valid trials), or at the opposite side 20-25% of the time (invalid trials). The typical Posner (1980) paradigm may also involve a neutral condition where a cue does not indicate the target location. The participant then responds to the target vocally or by pressing a button. Behaviour, such as response times and accuracy, has shown to be facilitated at the attended compared to the unattended location (e.g., Jonides, 1981; Posner, Snyder, & Davidson, 1980). Endogenous attention is suggested to develop gradually with an initial broader focus of attention followed by narrowing of attention. Shepherd and Müller (1989) found the broadest focus of attention at an interval between cue and target of 150 ms and the focus to be at its narrowest when the interval was 500 ms.

In the exogenous version of the Posner paradigm, the central informative cue is replaced by a non-informative peripheral cue. A typically example is that the participant is focused at the centre of the monitor. A peripheral cue briefly flashes to either the left or right of a central fixation. Importantly the participant is instructed to ignore this cue as it will not indicate where the upcoming target will appear. Following a peripheral target the participant responds as rapidly as possible. In contrast to the time course of endogenous attention, Shepherd and Müller (1989) showed a narrow facilitation effect at 50 ms when cue and target appeared at the same location (valid trial). After approximately 250 ms, the early facilitation effect is replaced with inhibition of validly cued targets. In other words,

response times are slower if the target appears at the same location as the cue (valid trial) compared to a novel (invalid trial) location. This behavioural effect is known as inhibition of return (IOR) (Posner & Cohen, 1984).

1.3 Inhibition of return and underlying theories

IOR - which is the slowing of responses to targets at a previously cued location compared to novel locations - has been demonstrated in visual (see Klein, 2000, for a review), auditory (e.g., Schmidt, 1996; Tassinari & Campara, 1996), tactile modality (Cohen, Bolanowski, & Verrillo, 2005; Lloyd, Bolanowski, Howard, & McGlone, 1999; Röder, Spence, & Rösler, 2000; Röder, Spence, & Rösler, 2002) and between all modality pairings (Ferris, Sarter, & Arbor, 2008; Roggeveen, Prime, & Ward, 2005; Spence, Pavani, & Driver, 2000; Spence, Lloyd, McGlone, Nicholls, & Driver, 2000). Despite considerable research into IOR, the underlying mechanism(s) for this phenomenon remains debated. The most commonly held view of IOR is that the phenomena is attributed to the attention system (Posner, Rafal, Choate, & Vaughan, 1985). The exogenous cue attracts attention and IOR reflects a mechanism which inhibits attention returning to the previously attended site. However, other areas have been proposed to be a part of the slowing of response times at previously cued locations. The principle accounts of IOR, in addition to the attention theory, are that the slowed response times can instead also be explained by sensory, perceptual, and/or motor stages of processing.

1.3.1 Sensory inhibition

The widely held view that IOR is attributed to an attentional effect was first proposed by Posner et al. (1985). In contrast, the pioneering study by Posner and Cohen (1984) which coined the phrase, suggested IOR to be a sensory rather than attention effect. Posner and Cohen (1984) demonstrated the biphasic pattern with facilitation for validly cued targets at short stimulus onset asynchrony (SOA) followed by IOR at long SOA. The hypothesis suggests that attention is initially drawn to the cue. If the target appears within approximately 300 ms then target processing is facilitated. After around 300 ms, exogenous attention is withdrawn from the cued location and subsequently inhibited to return. Posner and Cohen also investigated the effects of a bilateral cue followed by a unilateral target. In this task they found no early facilitation effect whilst the IOR was still present. They reasoned that attention cannot be split between opposite locations and therefore concluded IOR to be a sensory rather than an attentional effect. In other words, IOR arises because the

response of the visual system to the target is reduced due to previous stimulation of the cue, regardless if attention was deployed to the cued location or not.

More recent support for a sensory aspect of IOR comes from a study by Mele, Savazzi, Marzi, and Berlucchi (2008). They presented participants with visual cues which were either high luminance (supraliminal) or low luminance below subjective threshold (subliminal), followed by high luminance targets. When the cue was visible the typical biphasic pattern of early facilitation (150 ms SOA) followed by IOR (750 ms SOA) was observed. When the cue was subliminal there was no early facilitation but only IOR. Mele and colleagues proposed the lack of initial facilitation demonstrated that the cue did not attract attention. If the cue did not attract attention, then attention cannot be withdrawn and subsequently inhibited to return to the cued location. The cue acted outside the influence of attention. They ascribe the slowed response time effect to a self-inhibitory mechanism which is not influenced by attention. However, the lack of early facilitation period can be explained by the rapid disengagement hypothesis rather than that the cue did not capture attention (Ivanoff & Klein, 2003). This hypothesis suggests that the early facilitation period is not present because attention is disengaged rapidly from the cue. As withdrawal of attention has already occurred, the target appears in a time period influenced by both facilitation and early inhibition, resulting in no difference. In other words, the cue does attract exogenous attention but for subliminal stimuli the time course is much faster (see Mulckhuysse & Theeuwes, 2010, for a review of the effects of subliminal exogenous stimuli). Moreover, attributing IOR to a sensory/ perceptual pathway stimulated by the cue seems unlikely as IOR has been demonstrated to occur between modalities possibly suggesting that encoding occurs in a multimodal structure (Ferris et al., 2008; Spence, Lloyd, et al., 2000).

1.3.2 Manual response inhibition

IOR has also been attributed to inhibition of motor processing. The attentional account suggests that inhibition to the target appears because attention is inhibited to return to the cued location where attention has been deployed (e.g., Posner et al., 1985). It has been suggested that the cue elicits an automatic motor programme, and inhibiting a response to the cue leads to slowed response times to a target at the same location (Klein & Taylor, 1994). In other words, holding back a response to the cue evokes IOR. Several studies have investigated this hypothesis by comparing results from a cue-target task to a target-target

task. A target-target task requires the participant to respond to both the cue and the target. This is in contrast with the more common cue-target paradigm where the response is only made to the target. The key point is that in the target-target task a response is not withheld whilst in the cue-target task it may be. Behavioural results consistently demonstrate IOR to be more pronounced in a cue-target task compared to a target-target task. Advocates of the response inhibition account argue that this is due to a cue-target task effect which is a combination of attention inhibition and motor inhibition which arises from withholding a response to the cue (Coward, Poliakoff, O'Boyle, & Lowe, 2004; Poliakoff, Spence, McGlone, & Cody, 2002; Tassinari, Campara, Benedetti, & Berlucchi, 2002).

However, Welsh and Pratt (2006) proposed that the response inhibition account is insufficient when interpreting the reduced IOR in a target-target compared to a cue-target task. They demonstrated in their study that cue-target and target-target tasks show similar magnitude of IOR if the target is discriminated rather than simply detected. In a discrimination task the response is still required to be withheld to the cue suggesting this response inhibition cannot solely account for the difference seen in target-target and cue-target tasks. They propose a response repetition effect as an explanation for the reduced IOR in target-target tasks. The difference in magnitude may therefore be explained by the fact that duplicating the response in the target-target task facilitates response times, and in turn reduces the IOR.

1.3.3 Oculomotor inhibition

In addition to an attention effect, IOR has been suggested to also be driven by activation of the oculomotor (eye movement) system. The oculomotor theory proposes that a peripheral visual cue reflexively attracts our attention. Additionally, the cue also activates the saccadic system which automatically programs an eye movement to the cued location. This hypothesis proposes that even if no eye movements are required, the peripheral cue produces an automatic activation of an eye-movement to that location, which generates in IOR (Rafal, Calabresi, Brennan, & Sciolto, 1989).

Contrasting evidence that IOR is linked to the eye-movement system comes from a study investigating IOR in the blind. Röder et al. (2000) demonstrated that congenitally blind participants and participants with no eyes demonstrated tactile IOR, indicating that IOR can appear without oculomotor control. Taylor and Klein (2000) suggested that when the

oculomotor system is dormant then the attention system contributes to IOR. When the oculomotor system is active, then IOR is generated by both attention processing and oculomotor processing. In a recent study, Chica, Taylor, Lupiáñez, and Klein (2010) demonstrated that these two flavours of IOR operate independently.

The hypothesis that oculomotor programming is linked to IOR is consistent with the theory that the superior colliculus (SC) plays an important part in generating IOR (e.g., Dorris, Klein, Everling, & Munoz, 2002). The SC is one of the oculomotor pathways involved in programming eye-movements (Schiller, 1977). The link between oculomotor programming and IOR is supported by studies demonstrating patients with SC damage show reduced or no IOR (e.g., Posner et al., 1985; Rafal, Posner, Friedman, Inhoff, & Bernstein, 1988; Sapir, Soroker, Berger, & Henik, 1999). Moreover, one study showed a patient with visual cortex damage but intact SC demonstrated IOR in his blind visual field (Danziger, Fendrich, & Rafal, 1997). Although it has been established that neurons in the SC reflect IOR, it is not clear whether it is the SC itself generates IOR or whether the SC receives reduced activity from other brain areas. It has further been suggested that the parietal area, which has strong connections with the SC, may underlie the reduced input to the SC during IOR (Tipper et al., 1997).

1.3.4 Attention inhibition

Although several mechanisms have been suggested and have challenged the early attention inhibition account of IOR, this remains the most favourable explanation (Berlucchi, 2006). Initial research suggested that IOR occurred in detection but not in discrimination tasks (e.g., Tanaka & Shimojo, 1996; Terry, Valdes, & Neill, 1994). This observation fuelled theories such as the response inhibition or sensory inhibition accounts, suggesting IOR was less of a phenomenon of attention processing. However, it has now been demonstrated that IOR occurs in visual discrimination tasks, although, the onset of IOR is around 700 ms rather than 300 ms as shown in detection studies (e.g., Lupiáñez, Milán, Tornay, Madrid, & Tudela, 1997). When a target has to be discriminated a response cannot easily be prepared in advance. This suggests that slowed response times at cued locations cannot be attributed to slowed preparation of a particular response. Moreover, discrimination of a target requires a decision. This suggests IOR does not affect early sensory processing, but later stages of decisional processing. The presence of IOR in discrimination tasks has been taken as evidence that IOR is an attentional effect (Lupiáñez et al., 1997). In favour of the attention

account, Klein (2000) proposed IOR may also be viewed and explained through an evolutionary perspective. Efficient foraging for food (or other desirable objects) involves selectively attending to locations of interest for further inspection or a place to return to, relying on our endogenous attention. In contrast, locations which have been searched containing nothing of interest should be remembered to be avoided. IOR serves as an automatic process which encourages searching novel locations rather than returning to already explored sites. IOR has also been reported in visual search tasks suggesting IOR acts as a foraging facilitator (Thomas et al., 2006).

1.4 IOR in touch

The views and theories surrounding the IOR phenomena have largely been based upon research conducted in vision. Touch differs from vision and hearing as it is a proximal sense (Gibson, 1966) and therefore IOR may be different in touch compared to vision. When investigating tactile exogenous attention and IOR an adapted version of the Posner paradigm used in vision has commonly been adopted (e.g., Cohen et al., 2005; Lloyd et al., 1999; Poliakoff et al., 2002; Poliakoff et al., 2003; Röder et al., 2000; Röder et al., 2002). A typical trial to elicit IOR in touch would consist of an exogenous tap (a non-informative cue) presented to either the left or right hand. Following a SOA, a second tap (the target) would appear to either the same or opposite hand, to which a response is made. In touch, IOR has been demonstrated for SOAs between cue and target between 100 ms (Lloyd et al., 1999) up to 6 seconds (Cohen et al., 2005) and contrary to the visual modality, no early facilitation period for simple target detection has been shown. Within vision, a lack of an early facilitation period has been taken as evidence that IOR is due to sensory inhibition rather than inhibition of attention (e.g., Mele et al., 2008; and section 1.3.1). In other words, there is no evidence that attention is initially drawn towards the cue and then disengaged, so it can be inhibited. It may be that exogenous attention in touch has a shorter time course compared to vision and facilitation is replaced by IOR at a SOA of 100 ms, the shortest SOA tested.

However, recently IOR has also been demonstrated using tactile discrimination tasks. Miles, Poliakoff, and Brown (2008) presented participants with non-informative tactile cues to either their left or right hand. Following a variable SOA, participants discriminated whether a target appeared to the thumb or index finger. In accordance with visual detection (e.g., Klein, 2004) and discrimination studies (e.g., Lupiáñez et al., 1997), a biphasic

facilitation-to-inhibition pattern was demonstrated. At the short SOAs tested (150 & 350 ms), validly cued targets were faster compared to an invalid target (see also Spence & McGlone, 2001). At the long SOA (1000 ms), IOR was present whilst at the intermediate SOA (550 ms) there was no difference between valid and invalid trials (see also Brown, Danquah, Miles, Holmes, & Poliakoff, 2010, for similar results). The presence of this biphasic pattern may be taken as evidence that IOR reflects attention rather than simply sensory inhibition in touch. The debate whether IOR is attributed to response or attention inhibition has also been investigated using tactile stimuli. In a study by Poliakoff et al. (2002) participants responded to both the cue and target (target-target task), or only to the second tap (cue-target task). They found IOR to be smaller in the target-target compared to cue-target task which agrees with findings from visual attention research (e.g., Coward et al., 2004). Whether this demonstrates response inhibition to be a part of IOR or whether the reduced effect is due to a response repetition effect remains unresolved (see section 1.3.2). However, what this does suggest is that tactile IOR is, at least partly, an attention phenomenon.

1.5 Neuroscience of attention

Understanding the underlying mechanisms involved in attention has been approached from several directions, such as patient, neuroimaging, and electrophysiological studies. The subsequent sections review the neuroimaging and particularly the ERP literature surrounding selective attention. Although the research on patients will not be reviewed in any great detail here, a very generalized finding from neuropsychological studies is that patients with right parietal lesions show impaired attention (Karnath, Berger, Küker, & Rorden, 2004). Using a Posner paradigm it was demonstrated that when participants were cued to the right (ipsilesional side) and the target appeared to the left (contralesional side) patients performed poorly. This led to suggest that the parietal cortex is important when re-orienting attention, as would be required on an invalid trial (Mesulam, 1999; Posner, Walker, Friedrich, & Rafal, 1984).

Neuroimaging and electrophysiological studies, with humans and single unit recordings with monkeys, have demonstrated that attending to a location can bias the sensitivity of particular neurons (Motter, 1993). That is, increasing the sensitivity for neurons that are responsive to relevant stimuli and decreasing the sensitivity for irrelevant stimulus features. Neuroimaging techniques such as functional magnetic resonance imaging (fMRI) and

positron emission topography (PET) have particularly been useful to study the brain areas involved in attention. The top-down bias of attention on neuronal sensitivity has been proposed to originate from a fronto-parietal attention control network involved in orienting and maintaining attention (see Macaluso, 2010, for a review; and see section 1.7 for more details).

Event related potentials (ERPs) have been an important method used in understanding the neural basis of attention effects on different information processing stages. Using a Posner paradigm the ERPs can be time locked in relation to the cue or the target. Cue-locked ERPs have made it possible to study attention mechanisms which in behavioural paradigms can typically only be inferred by observing the responses to targets. To investigate the attentional shifts, studies have typically compared ERPs for the hemisphere contralateral and ipsilateral to the attended side. Enhanced processing at contralateral over ipsilateral electrodes is then suggested to reflect orienting and maintaining the focus of attention. This will be reviewed in more detail in Section 1.7 below.

Investigating the ERP waveforms following the target has been the more common method and is suggested to reflect attentional selection processes. The ERP pattern elicited by sensory stimulus consists of a series of positive and negative peaks in the time window following the onset of the stimulus. In vision, these components are named in order of appearance and whether the peak was positive or negative; P1, N1, P2 etc. The concept of sensory gain suggests selective attention increases neuronal activity at the attended areas. Incoming information in attended pathways would elicit stronger neuronal responses with a higher signal-to-noise ratio than in unattended pathways (Posner and Driver, 1992). Early studies with animals (e.g., cats) showed that the amplitude for sensory evoked responses were enhanced when the attention was directed towards the stimulus and reduced when directed away from the stimulus (e.g., Hernandez-Peon, Scherrer, and Jouvet, 1956).

The two early components, the P1 and N1, have in particular been demonstrated to be related to attention. The amplitude of these components is typically enhanced for attended compared to unattended stimuli (see Hillyard, Vogel, and Luck, 1998, for a review). It was originally suggested that these two components reflected a sensory gain effect. However, it is now suggested that the P1 and N1 reflect qualitatively different mechanisms (e.g., Luck et al, 1994; Talsma, Slagter, Nieuwenhuis, Hage, and Kok, 2005). It was proposed that the

P1 amplitude was reduced in invalidly cued trials compared to endogenous valid trials, as well as non-informative “neutral” trials. On the other hand, the N1 amplitude was enhanced for validly cued trials, as compared to endogenous invalid and non-informative trials. Broadly speaking, this suggested that the P1 amplitude reflected suppression of irrelevant stimuli whilst the N1 reflected enhancement of attended stimuli. These findings, and the attached models and theories, have been based on primarily the visual modality.

The ERP waveforms following a tactile stimulus are similar to visual components with positive and negative peaks. However, in addition to the polarity of the components they are also named more specifically as to when the peak appeared post tactile onset such as P45, N80, P100, and N140. For example, the N80 component refers to a negative peak around 80 ms post stimuli onset. Following these early to mid-latency effects a ‘negative difference’ (Nd) is commonly observed in tactile attention studies (see Sambo & Forster, 2011, for a review). Although there are differences between the timings of somatosensory and visual components, the P1 and N1 closely resemble the P100 and N140 in touch. Moreover, the P100 and N140 have consistently been demonstrated to reflect tactile selective attention with generally larger amplitude for attended (valid) compared to unattended (invalid) trials. The somatosensory ERPs and attention will be reviewed in more detail in Section 1.9 below.

1.6 Neuroimaging studies of IOR, exogenous and endogenous attention – a frontal-parietal attention network

Neuroimaging studies have highlighted different networks related to endogenous and exogenous attention in vision (see Corbetta & Shulman, 2002; Macaluso, 2010, for reviews). A set of areas around the posterior parietal cortex and precentral sulcus collectively known as the dorsal fronto-parietal (dFP) network have been associated with interpreting the cue and endogenously shifting and maintaining attention (e.g., Kelley, Serences, Giesbrecht, & Yantis, 2008; Yantis et al., 2002). In the Posner paradigm this activation would occur in the cue-target interval, in the time period where attention is oriented. Following the cue, the target can then appear at the attended or an unattended location. If the target appears at the attended location, the dFP network representing endogenous attention has also been suggested to feed back and modulate the activity in occipital visual cortex. The retinotopic area representing the attended location showing increased activation. In other words, an attentional selection occurs and heightens the

sensory representations of attended stimuli over unattended stimuli (Hopfinger, Buonocore, & Mangun, 2000; Martínez et al., 1999).

If the target appears at an unexpected location then a more ventral fronto-parietal network (vFP; such as inferior parietal cortex (temporal parietal junction; TPJ) and inferior pre-motor regions (inferior frontal gyrus (IFG) and frontal operculum) is activated (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000). Although the vFP network is sometimes referred to in relation to exogenous attention, it is only activated in response to unexpected (invalid) targets in an endogenous task. Kincade, Abrams, Astafiev, Shulman, and Corbetta, (2005) compared to the more conventional definition of endogenous and exogenous attention whereby endogenous cues are informative and exogenous cues are not (the definition also used throughout this thesis). They found more activation of the dFP network following predictive over non-predictive cues, which was in line with the dFP network being involved in endogenous attention. They found endogenous invalid cues activated the vFP network whilst non-informative cues did not trigger this network (see also Indovina & Macaluso, 2007, for similar results). An important behavioural aspect of the study by Kincade et al. (2000) was that although the exogenous cues were non-informative they resulted in facilitation of validly cued targets rather than IOR. The comparison between the two mechanisms was therefore between endogenous facilitation and exogenous facilitation.

In line with the findings presented above, Mayer, Dorflinger, Rao, and Seidenberg (2004) found different brain regions activated when comparing endogenous versus exogenous orienting, when the exogenous cue led to facilitation of validly cued targets. In contrast, when they compared fMRI activity in response to endogenous facilitation and exogenous IOR they found largely similar brain areas activated. Mayer and colleagues proposed the similarity of neuronal areas involved in endogenous facilitation and IOR may suggest similar neuronal resources are employed to limit exogenous facilitation from dominating visual attention. In other words, endogenous attention is employed to selectively attend to relevant information out of the stream of information bombarding our sensory system. Similarly, IOR is a mechanism used to save attention resources and reduce the influence of irrelevant stimuli.

Taken together, the main findings from neuroimaging studies have suggested that endogenous orienting activates a dFP network. Via feedback signals this process may

facilitate processing of attended stimuli in the sensory areas. The vFP network is a system which allows interruption from the endogenous control when unexpected (but relevant) stimuli occur outside our focus of attention. Exogenous stimuli which are not relevant fail to activate the dFP or the vFP networks to the same extent as endogenous attended or endogenous unattended stimuli. However, largely similar brain regions are activated when comparing orienting to attended locations and when the exogenous task elicits IOR.

1.7 ERP correlates of an attentional control network – the cue-target interval

The fronto-parietal attention network demonstrated in neuroimaging studies has also been investigated using ERPs. It has been suggested that the activation of this attention network can also be demonstrated using ERPs. In the cue-target interval, a series of components have been proposed to reflect activation of the fronto-parietal network. More specifically, lateralized ERP differences between waveforms contralateral and ipsilateral to the attended side are thought to reflect activation of the attention network. Initial reports of these lateralized effects were presented in a study by Harter, Miller, Price, LaLonde, and Keyes (1989). They presented a central visual arrow indicating to which side the participant was to orient their covert attention to detect an upcoming peripheral target. Three main components were found and suggested to reflect successive stages of attentional processes. An ‘early directing attention negativity’ (EDAN) was present over posterior electrodes. That is, there was enhanced negativity for electrodes contralateral compared to ipsilateral to the attended side. However, more recent evidence suggests the EDAN is not directly linked to control of attentional shifts but instead processing asymmetrical properties of the cue, such as left and right pointing arrows (van Velzen & Eimer, 2003). The EDAN is also absent when auditory cues are used to direct endogenous visual attention suggesting the visual cue itself is more important than the attentional orienting (Eimer & van Velzen, 2002).

At around 350 ms post cue onset a contralateral negativity has been demonstrated over anterior electrodes termed; ‘anterior directing attention negativity’ (ADAN). This lateralized negativity contralateral to the attended side has been demonstrated in a number of visual (e.g., Hopfinger & Mangun, 2000), auditory (e.g., Green & McDonald, 2006) and tactile studies (Forster, Sambo, & Pavone, 2009). The ADAN has been suggested to reflect supramodal attention mechanism in the frontal areas (Eimer, van Velzen, & Driver, 2002; Seiss, Gherri, Eardley, & Eimer, 2007).

Following the ADAN, a ‘late directing attention positivity’ (LDAP) has been demonstrated over posterior electrodes at around 500 ms post cue onset (Mathews, Ainsley Dean, & Sterr, 2006). This enhanced positivity at contralateral compared to ipsilateral electrodes has been suggested to reflect attentional orienting mediated by external visual space (van Velzen, Eardley, Forster, & Eimer, 2006).

The ADAN and LDAP may reflect the same fronto-parietal network demonstrated in neuroimaging studies. However, this hypothesis is more based on a common consensus in the research literature rather than on any studies directly investigating how the ADAN/LDAP reflect the same attentional network as that concluded from neuroimaging studies. Moreover, the cue-target ERP components have only been investigated during endogenous orienting. The lack of research comparing cue-target ERP modulations between endogenous, exogenous shifts of attention and during IOR limits the conclusion which can be drawn comparing neuroimaging and ERP results.

1.8 Tactile frames of reference

The ADAN and LDAP components have been suggested to reflect functionally distinct attentional control mechanisms anchored in different reference frames (Eimer, Forster, Fieger, & Harbich, 2004). When something touches our body we can localize the stimuli in two ways, where on the skin or where in external space the stimuli appeared. The primary somatosensory cortex (SI), located along the postcentral gyrus, is generally organized in a somatotopic manner (Penfield & Boldrey, 1937). The areas in the SI are organized in the order they appear on the skin such as the hand being represented next to the arm. Localizing relative to the skin surface is not always sufficient, but localising one’s body in external space is also important (see introduction to Chapter IV for a more detailed discussion on the brain areas involved in somatotopic and external frames of reference). For example, if an insect lands on our leg it is not only important to know where on the leg the insect is (somatotopic frame of reference), but also where the leg is in external space (external frame of reference). Once we know both these spatial coordinates we can for example prepare a hand movement to accurately swat the insect.

A method of investigating the different frames of reference is to compare perception and attention effects when the hands are crossed over the body midline versus in a “typical”

uncrossed position. The logic behind this method is that crossing the hands may cause a conflict between the somatotopic and external frame of reference. Behavioural evidence suggest slower response times for crossed compared to uncrossed posture due to the conflict between the spatial codes (Nicoletti, Anzola, Luppino, Rizzolatti, & Umiltà, 1982; Riggio, Gawryszewski, & Umiltà, 1986).

That the ADAN and LDAP are anchored in different frames of reference is supported by studies upon varying posture. Eimer, Forster, and van Velzen (2003) presented participants with a central arrow indicating to which side a tactile target would appear. They recorded ERPs when the hands were in a crossed and uncrossed posture. Eimer and colleagues found the polarity of the ADAN was reversed and also with a delayed onset when hands were crossed compared to uncrossed. That is, the ADAN showed enhanced negativity contralateral to the anatomically stimulated hand rather than contralateral to the externally attended space which was stimulated. However, the LDAP was unaffected by variations in hand posture. They concluded that the ADAN is somatotopically based whilst the LDAP relies on external spatial coordinates.

The conflict between external and somatotopic codes when the hands are crossed has also shown to affect attention modulations of tactile selection. In the uncrossed posture Eimer, Forster, et al. (2003) found enhanced amplitudes for the P100 and N140 for tactile stimuli presented to the attended compared to unattended hand. In the crossed hand posture these components were not modulated by attention. The crossed hand posture did not see an attention modulation until the late negativity (Nd) component. Moreover, the difference between attended and unattended trials at the Nd was also smaller in the crossed compared to uncrossed hands posture. Eimer and colleagues concluded the delayed attention modulation of somatosensory processes in the post-target time window demonstrated a conflict between external and anatomical coordinates. Thus, the attentional selection of one hand over the other is strongly affected by varying posture.

It has been suggested that crossing the hands over the body midline may induce qualitatively different processing requirements compared to how spatial coordinates are typically processed (Heed & Röder, 2010). Eimer et al. (2004) investigated the effects of having the hands near or far apart, without crossing the midline. They found the ADAN was not affected by posture which is in line with previous findings, indicating the ADAN is

somatotopically anchored. However, the LDAP was attenuated in the condition when hands were close together compared to far apart, demonstrating the LDAP is modulated by external space. The somatosensory ERPs elicited by the target found an enhanced attention effect of the N140 component when hands were far apart compared to close together. This demonstrates further evidence that tactile attention is linked to two different spatial frames of reference and these two reference frames are separable even though they are not in direct conflict (as when crossing the hands).

1.9 Post-target somatosensory ERPs

All ERP studies presented in this thesis include neural correlates elicited by exogenous tactile stimuli, in particular IOR (Chapter V also directly investigates neural correlates of endogenous tactile attention). Although there have been a handful of electrophysiological studies investigating exogenous attention in vision and audition, comparing ERP modulations and findings across modalities has limitations. Recent ERP studies suggest that the neural mechanisms underlying tactile spatial endogenous attention differ in comparison to the other senses (Forster & Eimer, 2005; Forster & Gillmeister, 2010). Although there are no previous ERP studies investigating exogenous tactile attention and IOR, there are now an increasing number of studies which have investigated endogenous tactile attention using ERPs (see Sambo & Forster, 2011, for a recent review).

Research into endogenous attention has distinguished between sustained and transient attention. In a sustained attention paradigm a participant is typically instructed to attend to a body location (e.g., the hand) for a prolonged period of time, usually an experimental block lasting a few minutes. Early studies presented electrical stimuli to the hands and participants endogenously attended (by counting the number of tactile stimuli presented) or directed their attention elsewhere (Desmedt & Tomberg, 1989; Garcia-Larrea, Lukaszewicz, & Mauguier, 1995; Michie, 1984; Michie, Bearpark, Crawford, & Glue, 1987). The attention was focused throughout a whole block towards the stimuli, employing a sustained attention paradigm. These studies found early and mid-latency components (Michie et al., 1987 - N80; Desmedt & Tomberg, 1989 - P100; Desmedt & Tomberg, 1989; Garcia-Larrea et al., 1995; Michie, 1984; Michie et al., 1987 - N140) were modulated by attention with larger amplitudes for attended versus unattended stimuli at each of the components.

Similarly, more recent studies of sustained attention using mechanical tactile stimuli found attention modulations at the N80 (Eimer & Forster, 2003a), P100 (Eimer & Forster, 2003a; Zopf, Giabbiconi, Gruber, & Müller, 2004), and N140 (Eimer & Forster, 2003a; Forster & Eimer, 2004; Zopf et al., 2004). The studies showed enhanced amplitude for the attended over the unattended hand. These studies also showed an Nd effect following the N140, with enhanced negativity for attended over unattended stimuli. More specifically, the N80 has been suggested to originate from the primary somatosensory cortex (SI), contralateral to the stimulated side (Allison, McCarthy, & Wood, 1992; Allison et al., 1989; Forss & Jousmäki, 1998; Hari & Forss, 1999; Hari et al., 1984; Inui, Wang, Tamura, Kaneoke, & Kakigi, 2004; Mima, Nagamine, Nakamura, & Shibasaki, 1998). The P100 has been proposed to originate from the secondary somatosensory cortex (SII), both in ipsilateral and contralateral hemispheres to the target side (Frot, Garcia-Larrea, Guénot, & Mauguière, 2001; Mauguière et al., 1997; Zhu, Disbrow, Zumer, McGonigle, & Nagarajan, 2007). Precisely where the N140 component originates from is not entirely known but the SII and frontal areas have been particularly suggested (Allison et al., 1992; Hari et al., 1993, 1984; Kakigi et al., 2000; Mima et al., 1998). The time course of the effects suggest attentional selection occurs relatively early and attention modulates sensory specific areas, namely the SI and SII.

ERP effects of endogenous attention have also been studied using a transient paradigm whereby a cue indicates where to direct attention on a trial by trial basis (Forster & Gillmeister, 2011; Forster et al., 2009). Eimer and Forster (2003a) investigated differences in sustained and transient tactile attention. They found attention modulated early somatosensory processing (the N80 - with enhanced negativity for attended over unattended stimuli) only in their sustained attention task. In the transient attention task they found a bilateral attention modulation of the P100. Eimer and Forster concluded that sustained and transient attention affect different somatosensory areas, and transient attention affecting somatosensory processing beyond SI.

If tactile selective attention is similar to visual selective attention then we may predict the P100 and N140 reflect qualitatively different mechanisms, as the P1 and N1 have been proposed to do (e.g., Luck et al., 1994; Talsma et al., 2005). That is, the P100/P1 would reflect suppression of irrelevant stimuli whilst the N140/N1 would be specifically related to enhancement of attended stimuli. Further evidence that the P1 may be related to

suppression of irrelevant stimuli comes from exogenous attention studies investigating the ERP pattern of IOR.

1.10 ERP correlates of IOR

Research into the ERP pattern relating to IOR has previously only been explored within vision and no studies have investigated the neural correlates of IOR in touch. The N1 peak has been discussed in relation to IOR. A few studies have found a significantly enhanced valid negativity (Prime & Ward, 2004, 2006; Tian & Yao, 2008) whilst other studies have found a significant enhancement of invalid over valid trials (Eimer, 1994; Hopfinger & Mangun, 1998; McDonald, Ward, & Kiehl, 1999). The N1 has previously been flagged as a potential “IOR component” as it has been found in studies which also showed behavioural IOR. However, the visual attention literature now seems to suggest that the diversity of results in studies of the N1 and IOR exclude this component as a direct link to behavioural IOR (Prime & Ward, 2006).

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 (Chica & Lupiáñez, 2009; McDonald et al., 1999; Prime & Jolicoeur, 2009; Prime & Ward, 2004, 2006; Tian & Yao, 2008; Wascher & Tipper, 2004). Moreover, the P1 has been suggested to be directly linked to behaviour, with larger amplitude of the P1 associated with enhanced behaviour (Luck et al., 2000). The reasoning is that the larger amplitude for invalid over valid trials reflects the faster response times for invalid over valid trials. However, the link between attention modulations at the P1 components and behavioural IOR is not clear. Other studies have demonstrated a reduction in amplitude on valid trials without a behavioural IOR effect (Doallo et al., 2004; Hopfinger & Mangun, 1998) or a significant IOR effect but no P1 attention modulation (Prime & Ward, 2006). Prime and Ward (2006) conclude that the P1 and IOR are likely to be associated, since 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.

1.11 Cueing tactile attention

The type of cue in an exogenous Posner paradigm is typically not very varied. It is usually similar to the target in terms of features and also location. However, the cue in endogenous attention has, and can be, more diverse. The cue in the study by Eimer and Forster (2003)

described earlier, was a visual arrow directing tactile attention to the left or right hand (see also Eimer, Forster, et al., 2003; Eimer et al., 2004; Forster & Eimer, 2005; for auditory cues directing endogenous attention see: Eimer, van Velzen, Forster, & Driver, 2003). The cue modality has been shown to influence tactile processing. Chica, Sanabria, Lupiáñez, and Spence (2007) presented unilateral tactile or visual cues followed by tactile or visual targets. They found behavioural endogenous attention effects were larger when cue and target were presented in the same sensory modality compared to intermodal presentation. Forster et al. (2009) compared the neural correlates of tactile attention following either visual (intermodal) or tactile cues (pure tactile condition). The tactile cues were bilateral tactile vibrations indicating to which hand the tactile target was most likely to appear. The visual cues were flickering lights presented bilaterally close to the hands. The results showed attentional differences between intermodal and pure tactile condition in both the cue-target and post-target interval. Forster and colleagues concluded that the engagement of the visual system alters several stages of endogenous tactile spatial attention.

An important development in the study by Forster et al. (2009) was the use of bilateral tactile cues to induce endogenous attention. Previous studies investigating pure tactile attention employed unilateral tactile cues to direct attention to one hand or the other (Cohen et al., 2005; Lloyd et al., 1999). For example, a cue to the left hand indicated a target was most likely to appear to the same location. However, when using unilateral cues it is difficult to disentangle whether any observed effects are due to exogenous or endogenous mechanisms (see introduction of Chapter V for a more detailed discussion of this issue). An informative unilateral tactile cue may in theory lead to facilitation of a target at that location via endogenous orienting but a cue and target presented to the same location may also elicit IOR.

A way of isolating the orienting processes may be achieved by using a counter-predictive condition where the cue indicates the most likely target location to be at the opposite side to the cue (Chica & Lupiáñez, 2009; Chica et al., 2007; Posner, Cohen, & Rafal, 1982). Chica et al. (2007) used a paradigm where unilateral tactile cues predicted the target to appear to the same location (predictive task). They also measured the behavioural effects when the cue predicted the target to appear to the opposite side (counter-predictive task). Overall they found that expected targets were faster compared to unexpected target. There was no difference in attention effects between the predictive and counter-predictive tasks

suggesting that IOR did not influence response times in their endogenous tasks. Employing paradigms which separate any interactions between endogenous and exogenous attention are important for the understanding of how these mechanisms work and what neural correlates can be pinned to a certain type of orienting. However, it is difficult to imagine everyday situation were the attention mechanisms operate in complete isolation but rather, they constantly interact.

1.12 Endogenous and exogenous interaction

1.12.1 Double cueing-paradigm

Investigating how endogenous and exogenous attention interact has been explored using different paradigms. One way is to combine the two versions of the Posner paradigm into a double-cueing paradigm (see also Chapter II). This paradigm includes an endogenous and exogenous cue in the same trial. An endogenous cue initially indicates where to attend, for example using a central arrow directing attention to a peripheral location. When attention is engaged, an exogenous cue, which is irrelevant to the task, appears. Following the exogenous cue a target appears, typically to the same or opposite location to the exogenous cue. Early studies showed that when endogenous attention is fully engaged, the exogenous cue does not affect the behaviour (Theeuwes, 1991; Yantis & Jonides, 1990). In other words, engaging endogenous attention can lead to filtering out irrelevant stimuli from reaching our awareness. More recently, using a double-cueing paradigm van der Lubbe and Postma (2005) presented participants with a central arrow directing attention to one side or the other (endogenous cue), followed by a irrelevant peripheral flash (exogenous cue), and then a peripheral target. They demonstrated faster response times when the exogenous cue was at the same side as the target, thus suggesting the irrelevant stimuli captured attention, even when endogenous attention was engaged. Moreover, they found the same effect with an auditory exogenous cue indicating that irrelevant cues attract attention even in a highly focused state in a multisensory setting. However, that an exogenous cue can attract attention when the endogenous system is engaged does not necessarily indicate how the two mechanisms interact.

In a series of experiments, Berger, Henik, and Rafal (2005) investigated whether the two mechanisms interact or operate independently. They found endogenous cues to facilitate response times at attended compared to unattended location. Moreover, they found that the exogenous cue could elicit IOR for validly cued targets. Although these two effects were

opposite, meaning that the target was facilitated by endogenous attention and at the same time inhibited by IOR, they did not interact. In other words, the effect of exogenous attention was the same regardless of whether the target appeared at an endogenously attended or unattended location. However, this was only true when the target was to be detected. When they increased the task difficulty, Berger and colleagues demonstrated that endogenous and exogenous mechanisms interacted. They concluded that the attention mechanisms operate independently under low task demands. Increasing task demands leads to an interaction as the two types of attention compete for shared resources (see introduction to Chapter II for a more detailed discussion).

1.12.2 Assessing the automaticity of exogenous attention

The effects of task demand upon attention have also been researched using a dual task paradigm. Typically a participant will engage in one task and the ability of concurrently presented irrelevant stimuli will be measured to see whether they capture attention. Such a paradigm intuitively relates to situations commonly encountered in our everyday lives. It is easy to imagine how focusing on one task, for example reading this introduction, influences how well irrelevant stimulus such as a buzzing fly attracts our attention. It has been especially demonstrated that varying the attentional, perceptual and cognitive load in one task affects the ability for exogenous stimuli to enter our awareness (see Santangelo & Spence, 2008, for a review).

The load theory of selective attention suggests perception is a limited capacity process. The perception of exogenous stimuli will only proceed as long as sufficient attentional resources remain available (Lavie, 1995; Lavie, Hirst, de Fockert, & Viding, 2004). Under a high perceptual load condition where our attentional capacity is fully engaged in processing task relevant information, then there is no spare capacity to process irrelevant stimuli. On the contrary, when we engage in a task with low perceptual load, any capacity which has not been utilized in the relevant task is left over to automatically process task irrelevant stimuli. It should be highlighted that the load theory of attention distinguishes between perceptual and cognitive load. Increased perceptual load, as mentioned above, leads to decreased processing of irrelevant stimuli. However, cognitive load (sometimes also referred to as working memory load) has the opposite effect. That is, increased cognitive load in a central task (for example memorizing a larger set of numbers during a trial) leads to the increased distracting effect of irrelevant stimuli compared to during low

cognitive load (Lavie, 2005). This thesis will however focus on perceptual and attentional load rather than cognitive or working memory load.

The load theory of selective attention also provides a model for the longstanding debate of when selective attention occurs. Whether attentional selection affects the perceptual process at an early (Broadbent, 1958) or a late stage (Deutsch & Deutsch, 1963). In other words, early selection suggests that unattended stimuli are filtered out at an early stage of processing allowing only selected stimuli to be perceived and recognized. Late selection proposes that all incoming sensory events receive equal perceptual processing and attention operates at a late stage of processing to regulate information into our awareness. The load model incorporates both early and late views as it suggests that attentional selection is an adaptive filtering mechanism which is not fixed at early or late stages of processing. The bottleneck of selection varies according to the amount of concurrently presented information and attentional load. In other words, the theory proposes high load to filter out irrelevant stimuli early in the selection process. When load is low it result in a late selection process (Lavie, 1995; Lavie et al., 2004).

Santangelo and Spence (2007) investigated the effects of varying visual perceptual load upon the influence of irrelevant tactile stimuli (see Chapter VI for a similar paradigm). Tactile stimuli were delivered to the hands - an exogenous tactile cue to the left or right was followed by a target to the same or opposite hand (a typical tactile exogenous version of the Posner paradigm). In one task the participant simply had to respond to the tactile target whilst viewing a centrally located fixation cross. In a second task the fixation cross was replaced with a string of letters presented on a screen (a rapid serial visual presentation; RSVP). Embedded in the letters was a number which served as a visual target. The participant in this task had to detect a visual and tactile target. This dual task involved a higher load placing more demand on our endogenous attention. Santangelo and Spence found the exogenous tactile cue only influenced response times in the low load task (with no RSVP stream). When participants' load was increased by including searching for a number embedded in a string of letters, then the exogenous cue had no effect upon response times. It was concluded that the exogenous cue was filtered out in the condition where perceptual processing demand was high. Employing an RSVP stream to manipulate perceptual load has also demonstrated similar effects where high load reduces the influence of how well irrelevant visual (Santangelo, Botta, Lupiáñez, & Spence, 2011) and auditor

stimuli (Santangelo, Ho, & Spence, 2008) capture attention. In other words, increased load may lead to filtering out exogenous stimuli.

1.12.3 To what extent are irrelevant stimuli filtered out during varying load?

In the behavioural studies, the reduced attention effect in the high compared to low load tasks is taken as evidence that the exogenous cue fails to capture attention. This is due to the high attentional demands required in the central task. In behavioural tasks a target is needed in addition to the exogenous cue, as otherwise there is no way of measuring the effect of the irrelevant stimuli (the cue). Investigating the ERPs allows us to directly investigate how irrelevant stimuli are processed when perceptual load is high or low. For example, O'Connell, Schneider, Hester, Mattingley, and Bellgrove (2011) presented participants with a central RSVP stream as well as flashing irrelevant visual stimuli in the periphery. O'Connell and colleagues found the amplitude for the P2 and P3 components elicited by the irrelevant stimuli decreased as a function of increasing load. Thus, indicating that the peripheral stimuli processing is diminished with increasing central load. Similar findings have also been demonstrated in neuroimaging studies (e.g., Rees, Frith, & Lavie, 1997; Schwartz et al., 2005). Using fMRI, Schwartz et al. (2005) presented participants with a central RSVP stream of letters. The activation in the primary visual cortex (V1) for task-irrelevant checkerboard stimuli in the periphery was decreased by higher perceptual load in the central task. The effect of load also increased for successive extra striate areas (V2, V3, and V4). This has been taken as evidence that higher perceptual load, which in turn increases the attentional demands, filters out irrelevant stimuli early in the perceptual process (Lavie, 1995).

Although perceptual load studies typically do not use the terminology exogenous and endogenous attention it seems logical that perceptual load research concerns similar processes. That is, the focus on a central task through high versus low perceptual load varies the endogenous attention, and the task irrelevant peripheral stimuli are exogenous. The load theory proposes that higher perceptual load increases the attentional demands which in turn decreases the ability of irrelevant stimuli to capture our attention (Lavie, 1995). A central task (e.g., an RSVP stream) will engage our endogenous attention. Increased endogenous attention leads to reduced influence of exogenous attention (van der Lubbe & Postma, 2005). In other words, the load theory proposes how endogenous and exogenous attention may interact.

1.13 Summary

Attention can be oriented endogenously or exogenously. The most common behavioural paradigm to investigate these two mechanisms is to use the cue-target paradigm developed by Posner (1978, 1980). Behavioural results demonstrate that cueing attention to a location facilitates information processing at the attended location. In the exogenous version of the Posner paradigm the cue may lead to facilitation or inhibition of a target at the same location. The common thread throughout this thesis is IOR, which features in all experiments. IOR is a behavioural phenomenon and has been demonstrated within and between all sensory modalities. Precisely what underlies this effect is debated, although the most widely accepted theory is that it is a phenomenon which reflects inhibition of attention. Neural correlates of IOR have been investigated in vision. The P1 has demonstrated to be the main contender associated with IOR, but no direct relationship has been demonstrated. Neuroimaging studies have proposed a fronto-parietal network to reflect orienting of attention. ERP studies have proposed the cue-target interval components, the ADAN and LDAP, to reflect activation of the fronto-parietal attention network. The post-target ERPs are proposed to reflect attentional selection processes. A series of components following a target have been highlighted to reflect attentional selection (in particular the P100 and N140). The attention modulations have repeatedly demonstrated enhanced amplitude for tactile stimuli presented at attended over unattended locations. This pattern is also demonstrated in other sensory modalities. Endogenous and exogenous attention have not only been investigated separately but also how they interact. Different paradigms have been employed (e.g. double-cueing paradigm and high versus low perceptual load tasks) and have established that varying the level of endogenous attention and/or perceptual load influences how well exogenous stimuli attract our attention.

1.14 Novelty of paradigms, exploring an uncharted area, and main questions addressed in this thesis

In all ERP studies presented in this thesis (Chapter III-VI) behavioural data was concurrently recorded and participants provided a response on each trial (except catch trials). It is common in ERP studies to record behavioural performance, but typically not on every trial. For example, in an attention paradigm participants may respond to an infrequent target to make sure they are directing attention to the instructed location. This is because

the muscular activity elicited by behavioural responses may cause confounding potentials in the time window following the stimuli (although see the ADJAR method for a way to circumvent this problem; Woldorff, 1993). By not collecting behavioural data on each trial the conclusions drawn from the ERP data can only be inferred rather than linked to behaviour. In the ERP studies of this thesis it was possible to record both types of data on each trial as the ERP effects of interest were those present shortly after stimuli onset. The time window of interest was approximately within the first 200 ms after stimuli onset, which was short enough not to be contaminated by response artifacts. Recording both ERP and behavioural data leads to the additional possibility of investigating any relationship between observed effects. Any behavioural attention effects can therefore be correlated to ERP modulations of attention. Correlating ERP and behavioural effects aimed to add a new and more direct insight into the relationship between ERPs and behaviour.

Chapter IV addresses whether IOR is somatotopically or externally coded and how posture influences tactile processing. The study presented in Chapter V contrasts and compares the neural correlates of exogenous and endogenous tactile attention. The final experimental chapter explores how we process exogenous stimuli when our attention is engaged in another task - how perceptual load influences processing of irrelevant tactile stimuli and IOR. How endogenous and exogenous tactile attention interact is also explored behaviourally in Chapter II.

CHAPTER II

Behavioural effects of endogenous and exogenous tactile attention

Endogenous and exogenous attention mechanisms in touch have typically been investigated separately. Previous endogenous tactile studies have employed unilateral tactile cues informing the likely location of an upcoming target. However, when employing unilateral cues it is not possible to isolate whether any observed effects are influenced by also exogenous mechanisms. In Study 1 of this chapter, bilateral tactile cues were used to induce endogenous tactile orienting. The results demonstrated faster response times (RTs) for attended compared to unattended targets. In Study 2 an exogenous cue followed the endogenous cue in a double-cueing paradigm. This second study investigated whether exogenous tactile cues could influence RTs when tactile attention was otherwise engaged. The results from Study 2 showed faster RTs for endogenous attended compared to unattended trials. The exogenous cue demonstrated facilitation of validly cued targets. However, this effect was only present at short (250 ms) stimulus onset asynchrony (SOA) whilst there were no exogenous attention effects at longer SOAs. Moreover, there was no interaction between exogenous and endogenous attention at any SOA tested. That is, any effects of the exogenous cue were the same regardless of whether the target appeared at an attended or unattended location. This suggests that endogenous and exogenous attention mechanisms do not interact, at least when task difficulty is low.

2.1 Introduction

Mechanisms of selective attention help us to focus on information of behavioural relevance from the stream of incoming information from our senses. Attention research distinguishes between reflexive (exogenous) and voluntary (endogenous) orienting of attention. A commonly used paradigm to investigate these types of attention was developed by Posner (1980). Typically in such a cue-target paradigm endogenous attention would be induced by an informative central cue indicating the most likely location for an upcoming peripheral target. Exogenous orienting would be induced by presenting non-informative peripheral cues. The response to targets at the cued or opposite locations would indicate what effect the preceding exogenous cue has elicited, although instructed to be ignored.

Much of the research on endogenous and exogenous attention has studied these two orienting mechanisms separately. However, everyday situations often require activating and combining both types of attention and the relationship between these two mechanisms has been investigated (Berger et al., 2005; van der Lubbe & Postma, 2005; Müller & Rabbitt,

1989; Theeuwes, 1991; Yantis & Jonides, 1990). Much of this research has investigated the effects of exogenous stimuli when our endogenous attention is in a focused state. In other words, to what extent irrelevant stimuli can capture our attention. At one end of the spectrum of how endogenous and exogenous attention interact is that exogenous attention is truly automatic. That is, when stimulation is above sensory threshold it will always capture our attention. At the other end, exogenous stimuli can be filtered out if required. There is some empirical support for the view that abrupt peripheral onset of stimuli outside the focus of attention does not attract attention (Yantis & Jonides, 1990; Theeuwes, 1991). These studies used a double-cueing paradigm which includes both an endogenous and exogenous cue in the same trial. An endogenous cue initially indicates where to attend, for example using a central arrow directing attention to a peripheral location. When attention is engaged, an exogenous cue, which is irrelevant to the task, appears. In the studies by Yantis and Jonides (1990) and Theeuwes (1991), it was demonstrated that presenting a peripheral exogenous stimulus failed to attract attention in the condition when attention was in a highly focused state. Thus, increasing endogenous attention leads to “filtering out” exogenous stimuli reaching our awareness. However, in a more recent study van der Lubbe and Postma (2005) demonstrated exogenous orienting effects when attention was otherwise engaged. They presented an arrow at a centrally located monitor instructing to what side participants were to attend. Following an 800 ms SOA, a brief (50 ms) exogenous visual flash appeared to the left or right, followed shortly (after 200 ms) by a target at the endogenously attended side. The results showed faster RTs for trials where the exogenous cue was at the same side (valid) compared to opposite side (invalid) to the target. Moreover, they found a similar effect when presenting auditory exogenous stimuli to the left and right suggesting irrelevant cues attract attention even in a highly focused state in a multisensory setting.

In a series of experiments, using a range of SOAs, Berger et al, (2005) aimed to establish whether endogenous and exogenous attention mechanisms are separate or if they interact. Employing a similar double-cueing design as described above, in three experiments they also found faster RTs for endogenous valid compared to invalid trials. Moreover, they demonstrated an effect of exogenous attention. There was facilitation of exogenously valid targets at short SOAs (0 ms, 100 ms). At longer SOA (750 ms), the exogenous cue resulted in inhibition of return (IOR) with faster RTs when the exogenous cue was invalid compared to valid. Importantly, they found no interaction between endogenous and exogenous

attention, even though at long SOA the two mechanisms accounted for opposite effects. In other words, the effect of exogenous attention (e.g., IOR at long SOA) was the same regardless of whether the target appeared at an endogenously attended or unattended location. This indicated that exogenous and endogenous attention mechanisms can independently have effects upon behaviour without interacting. To investigate whether endogenous and exogenous attention interact during more demanding conditions, Berger and colleagues increased the task difficulty and participants performed target discrimination rather than simple target detection. In this fourth experiment they found an interaction between endogenous and exogenous attention but only at intermediate SOA where neither exogenous facilitation nor IOR was present. Berger et al. (2005) proposed five different models that could account for the relationship between endogenous and exogenous attention.

First, (1) endogenous and exogenous attention are two modes of action of a single mechanism (e.g., Posner, 1980). (2) Endogenous orienting can influence exogenous attention but not the other way around (e.g., Theeuwes, 1991; Yantis & Jonides, 1990), (3) Exogenous attention can influence endogenous orienting but not vice versa (e.g., Müller & Rabbitt, 1989). (4) Endogenous and exogenous attention are two separate mechanisms capable of mutual interference (Müller & Humphreys, 1991). A fifth option which extends the fourth model; Berger et al. propose this model to best comply with their findings suggesting (5) "... endogenous and exogenous orienting are separate mechanisms that, under low task demand, can lead to independent orienting effects, even under conditions when they contradict each other. Increasing task demands leads to an interaction between the mechanisms as they compete for shared resources" (p. 219).

Evidence that endogenous and exogenous attention are mechanisms operating separately also comes from neuroimaging studies. For example, in a double-cueing paradigm study with endogenous and exogenous cues in the same trial, Natale, Marzi, Girelli, Pavone, and Pollmann (2006) demonstrated faster RTs when the exogenous cue was valid. They concurrently measured fMRI activation and found the ventral fronto-parietal (vFP) areas to be activated in relation to invalid endogenous targets whilst the exogenous cues did not modulate this activity. Although the neural correlates of exogenous and endogenous attention and how they interact are not fully established, the activation of different brain areas suggest some segregation between the orienting systems (see Corbetta & Shulman,

2002; and Macaluso, 2010, for reviews of the neural correlates of endogenous and exogenous attention).

While the majority of experimental studies on spatial attention have been conducted in the visual modality, comparably few studies have investigated tactile attentional selection (see Spence, 2002; and Johansen-Berg & Lloyd, 2000, for reviews of tactile attention studies). Furthermore, most studies investigating tactile attention have not controlled for visual orienting effects on tactile processing. A number of tactile attention studies have used visual cues to direct attention to tactile targets (Chica et al., 2007; Forster & Eimer, 2005; Posner, 1978; Spence, Pavani, et al., 2000) inducing crossmodal orienting effects (Chica et al., 2007; Mondor & Amirault, 1998; Turatto, Benso, Galfano, & Umiltà, 2002), while in other studies (e.g., Cohen et al., 2005; Lloyd et al., 1999) participants moved their eyes to the tactile target location inducing visual overt orienting effects (Rorden, Greene, Sasine, & Baylis, 2002). Other cross-modal paradigms have investigated the automaticity of exogenous tactile stimuli by varying visual perceptual load. For example, Santangelo and Spence (2007) showed that increasing the visual perceptual load in a central task led to reduced influence of peripheral tactile stimuli. Thus, suggesting a higher focused state in a visual task leads to filtering out irrelevant tactile stimuli (see also Chapter VI of this thesis for similar results). To understand the operations of tactile attentional mechanisms and to clarify whether attentional mechanisms are modality specific or operate in the same fashion across modalities, tactile attention studies employing modality specific paradigms (e.g. employing tactile cues and targets) and excluding engagement of other modalities (e.g. vision) are required.

Previous studies investigating pure tactile attention employing tactile cues and targets have typically used peripheral tactile stimuli presented to one of the hands. Similar to vision, peripheral non-informative cues and targets have been used to investigate exogenous attention using variations of the Posner paradigm (Cohen et al., 2005; Lloyd et al., 1999; Röder et al., 2002; Spence & McGlone, 2001). To induce endogenous attention in vision a central informative cue has often been used to direct attention. To employ a central cue is however much more difficult in touch (although see Forster & Gillmeister, 2011 for tactile cue presented on the neck). Presentation of mechanical, tactile cues along the body midline may either induce bone conductance (e.g., when placed on the face or spine) or are difficult to administer (e.g., when placed on the stomach), and are therefore not suitable. To

overcome this methodological problem studies have made unilateral tactile cues informative. That is, a peripheral cue indicates that the target is most likely to appear at that same location (Cohen et al., 2005; Lloyd et al., 1999). However, informative unilateral cues attract both endogenous and exogenous attention which makes it hard to establish the contribution of each attention mechanism to any observed effect (although see Chica et al., 2007; and Chapter V for counter-predictive paradigm to separate endogenous and exogenous effects using unilateral cues).

To overcome the difficulty of disentangling endogenous and exogenous effects following unilateral informative cues the experiments presented in this chapter employed bilateral cues to induce endogenous attention. In Study 1, participants were presented with two different vibrations to both hands as cues to either detect a tactile target (Experiments 1), or discriminate the target location (Experiment 2). In line with previous simple detection (Lloyd et al., 1999; Posner, 1978) and target discrimination (Chica et al., 2007) studies of endogenous tactile orienting we employed informative cues indicating the most likely target location (80% correct). In Study 2 the bilateral vibrations also served as the endogenous cues directing attention to the left or right hand as in the first study. In addition, following the endogenous cue there was a single tap to the left or right which the participant was instructed to ignore, serving as an exogenous cue. Thus, the second study used a double-cueing paradigm. Participants in the second study discriminated whether the target was presented to their middle finger or thumb. Study 2 consisted of two experiments. In the first experiment the SOA between exogenous cue and target was 250 and 850 ms and in the second experiment the interval was either 550 ms or 1350 ms. The two experiments consisted of different participant groups but all procedure and design were identical for experiments 1 and 2 of Study 2.

Study 1 aimed to investigate the ability to use endogenous bilateral cues in the tactile modality. Moreover, it was predicted that orienting effects would be similar to that found in the visual modality with facilitation of validly cued targets. In Study 2 – using a double-cueing paradigm - we aimed to investigate whether exogenous tactile cues could influence RTs when attention is otherwise engaged. Moreover, to investigate whether any interaction effects were the same across varying time intervals between exogenous cue and target.

2.2 Study 1 - Endogenous bilateral cues

2.2.1 Methods

2.2.1.1 Participants

Eight paid participants (5 males and 3 females), aged between 23-27 years old and with a mean age of 24.5 years, took part in Experiments 1 and 2. All participants were right handed and gave written informed consent.

2.2.1.2 Stimuli and materials

Participants were seated in a soundproofed room which was controlled for light, sound, and temperature. 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 index and middle fingers, making contact with the fingers whenever a current was passed through the solenoid. The solenoids were set into two wooden cubes (63 mm x 50 mm), each with two tactile stimulators (2.2 cm between solenoid's tips) for the middle and index finger of the left and 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 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 cube, to mask any sounds made by the tactile stimulators¹. Tactile cues were always presented to both index fingers simultaneously. Two types of vibrations (cycles of switching solenoids ON/OFF) were employed evoking a sensation of 'flutter' (5 cycles of 6 ms ON and 54 ms OFF followed by 2ms ON) or 'continuous' (15 cycles of 2 ms ON and 18 ms OFF followed by 2 ms ON) vibrations each of a duration of 340 ms. Single tap targets consisted of the tactile stimulator being switched ON for 50 ms, while for double tap targets the tactile stimulator was switched ON for 50 ms, OFF for 100 ms and then ON for 50 ms. The participants were blindfolded throughout the experiment.

2.2.1.3 Design and procedure

Each experiment consisted of two practice blocks of 20 trials each with 16 trials indicating the correct target location (valid trials) and on 4 trials cues were misleading (invalid trials).

¹ The white noise settings were checked and tested by attaching tactors to someone else's hand and participants needed to indicate when they heard the sounds of the stimuli being presented or not.

The practice blocks were followed by four experimental blocks of 80 trials each with 64 valid and 16 invalid trials. The trials were randomly presented in each block. At the start of each trial a bilateral cue was presented to the index fingers. For half of the participants a flutter vibration indicated that the left middle finger, and a continuous vibration indicated that the right middle finger, was the most likely target location; for the other half of participants this assignment was reversed. The endogenous cue was followed by a target with 80% likelihood to appear at the valid location and 20% likelihood of being invalid. The appearances of targets to the left and right middle fingers were equally balanced. In other words, the cue was presented to both index fingers simultaneously and the targets to either middle finger. The interval between cue off-set and target on-set was either 300 ms or 800 ms long resulting in SOAs of 640 ms and 1140 ms, respectively.

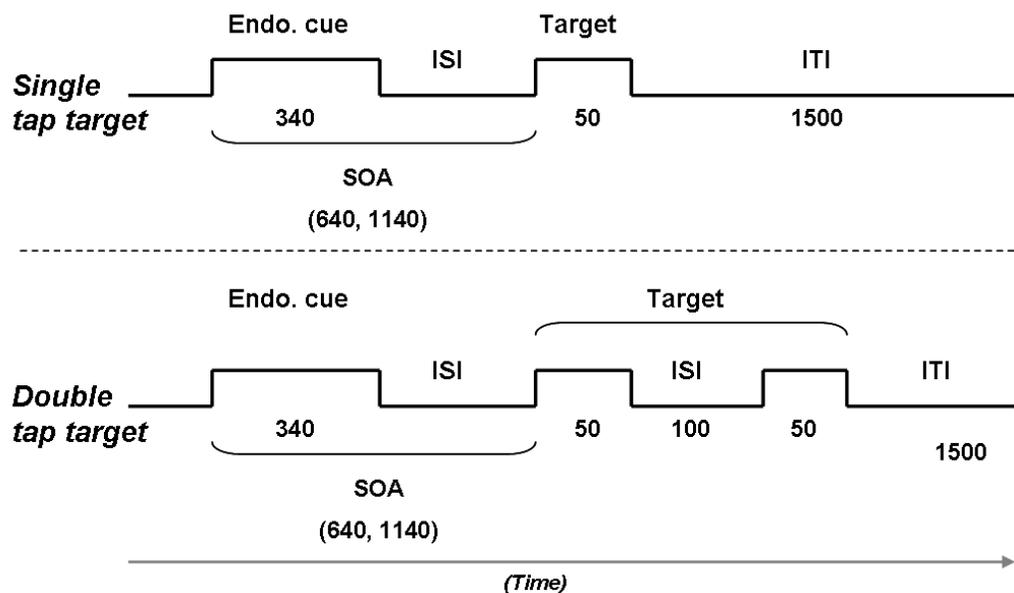


Figure 2.1.1 Stimuli presentation. Timeline in milliseconds of stimuli presentation during a typical trial with either a single or double tap target. The endogenous cue (Endo. cue) was either a flutter or continuous vibration. In the Detection task (Experiment 1) a single tap was always the target. In the Discrimination task (Experiment 2) participants' discriminated between a single and double tap target on each trial. ISI = inter stimulus interval; SOA= stimulus onset asynchrony; ITI = inter trial interval.

In Experiment 1 the participant's task was to press a foot switch as soon as they detected a target (see 'Single tap target' time line in Figure 2.1.1). For half of the participants the foot switch was located under their left foot and for the other half it was located under their right

foot. In Experiment 2 participants discriminated between either a single or double tap on each trial (see Figure 2.1.1). The participant pressed a left foot pedal if the target was a single tap and the right foot pedal if the target was a double tap. This was counterbalanced across participants. On half of the trials targets were single taps and, on the remaining half these were double taps. If no response was registered within 1200 ms of target offset the next trial started after an inter-trial interval of 1500 ms. All participants were blindfolded throughout each experiment and were instructed to gaze at an imaginative point in front of them throughout the experiment. Participants were monitored via a video camera throughout the experiments for any head movements.

Eye-movements were measured using horizontal electro-oculogram (HEOG). HEOG was recorded bipolarly from Ag-AgCl electrodes positioned on the outer canthii of both eyes, together with linked-earlobe references. A Brain-Amps amplifier system and Brain Vision Recorder and Analyzer 1.05 software (Brain Products, GmbH) were used for recording and offline analysis of HEOG data. Impedance was kept below 5 K Ω , amplifier band-pass was 0.01 to 40 Hz, and digitization rate was 500 Hz. In an offline analysis, HEOG epochs were extracted for a period starting 100 ms prior until 600 ms after the onset of the cue for trials with short SOA, and 100 prior and 1100 ms after cue onset for trials with long SOA. Trials with eye-movements (HEOG amplitudes larger than ± 40 mV) were excluded from analysis resulting in removal of on average 30% of trials across all participants in Experiment 1 and 36% in Experiment 2².

2.2.2 Results

Responses faster than 140 ms and slower than 800 ms were excluded from analysis. This resulted in the removal of on average 1% in Experiment 1 (detection task), and 8% in Experiment 2 (discrimination task). This difference in error rates between tasks was also significant ($t(7)=3.15$, $p=.016$). The results were analysed with a 2x2x2 repeated-measures ANOVA with the factors Task (detection, discrimination), SOA (640, 1140 ms), Cue (valid, invalid).

¹A likely reason for this relatively large portion of trials removed is that participants were blindfolded which made it difficult to keep the eyes still as there was no physical point at which to fixate their gaze upon.

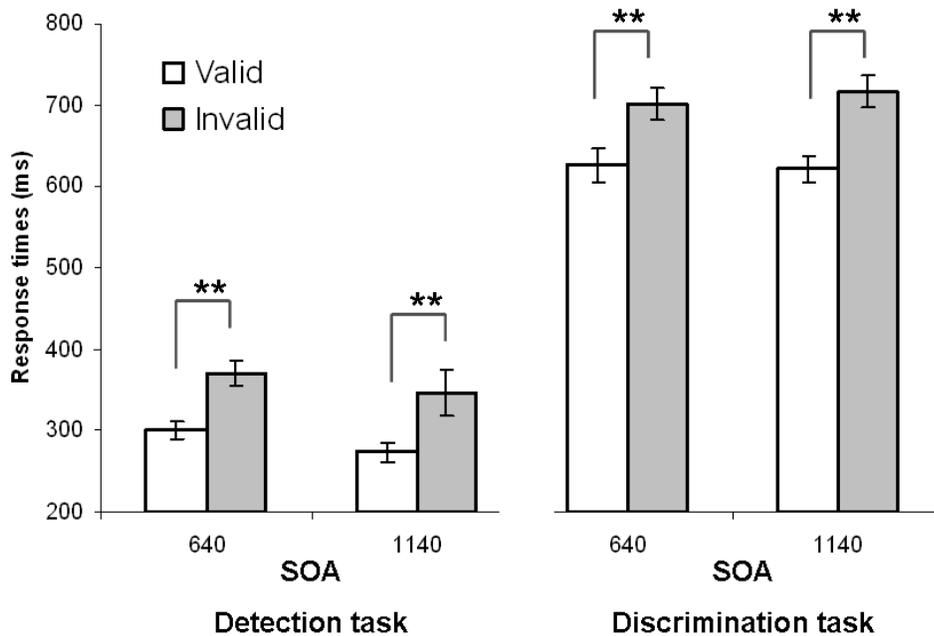


Figure 2.1.2 Behavioural results for Study 1. Mean response latencies (response times in milliseconds) and standard error for detection (Experiment 1) and discrimination (Experiment 2) of tactile stimuli on trials following a valid (white) and invalid (grey) bilateral tactile cue. Both experiments demonstrated significantly (** $p < .001$) faster RTs on valid compared to invalid cue trials. This attention effect was similar for both stimulus onset asynchronies (SOAs) tested.

There was a main effect of Task ($F(1,7)=304.20, p < .001, \eta^2_p=.98$), with significantly faster RTs in the detection (322.12 ms) as compared to the discrimination task (666.29 ms). There was also a main effect of Cue ($F(1,7)=55.78, p < .001, \eta^2_p=.89$) with significantly faster valid (455.39 ms) compared to invalid trials (533.71 ms) (see Figure 2.1.2). This main effect indicated participants were able to endogenously attend to the cued location. There was a significant Task*SOA interaction $F(1,7)=13.83, p=.007, \eta^2_p=.66$. No other main effects or interaction were significant.

2.2.3 Discussion – Study 1

We investigated tactile covert endogenous orienting induced by bilateral tactile cues in simple detection and discrimination tasks. In both experiments participants responded significantly faster on valid compared to invalid trials (Figure 2.1.2), suggesting that participants were able to endogenously attend to the target location predicted by the bilateral cue. In other words, covert endogenous orienting of tactile spatial attention facilitates detection and discrimination of tactile stimuli at attended locations.

2.3 Study 2 – Endogenous and exogenous double-cueing paradigm

2.3.1 Methods

2.3.1.1 Participants

Data were collected from fourteen paid participants in Experiment 1 (7 male and 7 female), and fourteen paid participants in Experiment 2 (6 male and 8 female), all of whom were right-handed and naïve to the purpose of this study. Participants' age ranged from 20 to 42 years old, with a mean age of 25.3 years old. The experiment lasted approximately 60 minutes and all participants provided written informed consent.

2.3.1.2 Stimuli and materials

The apparatus and materials were identical in Experiment 1 and 2. Participants were seated in a soundproofed room which was controlled for light, sound, and temperature. Tactile stimuli were presented using 12-V solenoids (5 mm in diameter), to the finger pad of the middle fingers and thumbs. The solenoids were set into two wooden cubes (63mm x 50mm), each with two tactile stimulators (2.2 cm between solenoid's tips) for the middle finger and thumb of the left and 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 noise caused by the tactile stimulators if in direct contact with the table. The endogenous cue consisted of two different vibrations directing attention to the left or right. The two vibrations (cycles of switching solenoids ON/OFF) evoked a sensation of 'flutter' (5 cycles of 6 ms ON and 54 ms OFF followed by 2 ms ON) or 'continuous' (15 cycles of 2 ms ON and 18 ms OFF followed by 2 ms ON) vibrations each of a duration of 302 ms. The exogenous cue was a 50 ms tap presented simultaneously to both the thumb and middle finger of either the left or right hand. Target stimuli consisted of a rapid 25 ms buzz (5 cycles of ON 3 ms and OFF 2 ms) presented to one of the four possible locations, either up (fingers) or down (thumbs) to the left or right hand. Responses were made into a centrally located microphone which measured RTs. White noise (58 dB SPL) was continuously present through two speakers, each located in a direct line behind each cube, to mask any sounds made by the tactile stimulators. A black cloth was used to cover the participant's hands to deprive all visual information of the stimulated body location. Stimuli were presented and recorded using E-Prime. Participants were monitored via a video camera throughout the experiments for any head movements. An intercom system was used so the

experimenter could hear the participants responses, and in turn code *up* or *down* on a keyboard in the adjacent room.

2.3.1.3 Design and procedure

The design and procedure were identical in Experiment 1 and 2 with the exception that in Experiment 1, the SOA between exogenous cue and target was 250 ms and 850 ms, and in Experiment 2, 550 ms and 1350 ms. Each experiment consisted of three factors; SOA (Experiment 1; 250, 850 ms, Experiment 2; 550 ms, 1350 ms), Endogenous orienting (valid, invalid), and Exogenous orienting (valid, invalid). Each experiment consisted of two practice blocks of 40 trials each with 32 trials indicating the correct target location (valid trials) and on 8 trials cues were misleading (invalid trials). The practice blocks were followed by six experimental blocks of 80 trials each with 64 valid and 16 invalid trials, leading to a “Posnerian” weighting of 80% for endogenous valid trials and 20% for invalid trials. The exogenous cue was weighted 50/50 valid and invalid. In half of the endogenous valid trials (32 trials) the exogenous cue was presented at the same side as the target, thus a trial with a valid endogenous and valid exogenous cue. In the other half of the endogenous valid trials the exogenous cue was presented to the opposite side to the target, thus an endogenous valid and exogenous invalid trial. The exogenous cues were also equally weighted for the endogenous invalid trials. In half the endogenous invalid trials, the exogenous cue was presented to the same side as the target and on the other half the exogenous cue was presented to the opposite side to the target. The presentation of all valid endogenous targets and valid exogenous targets were equally presented to the left and right. Further, on half of all trials the targets were presented to either the left or right middle finger (up), and the other half the targets to the thumbs (down). The endogenous cues were counterbalanced between participants’ so continuous vibration indicated left and flutter vibration indicated right and vice versa for the other half of participants’. All trials were randomly presented in each block.

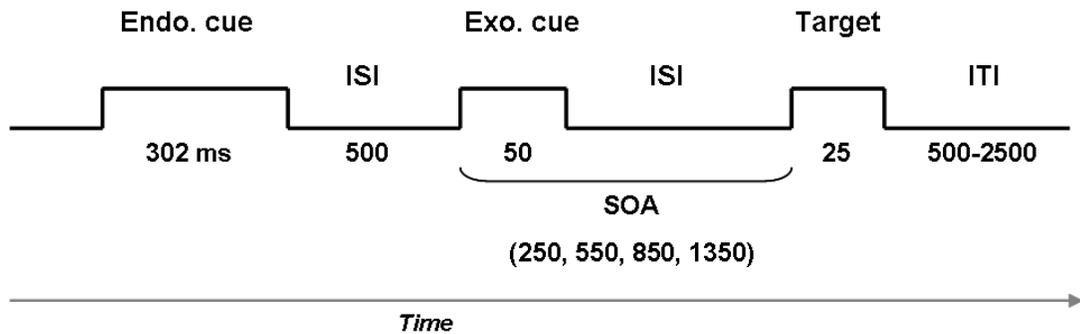


Figure 2.2.1 Stimuli presentation. Timeline in milliseconds of stimuli presentation during a typical trial: The endogenous cue (Endo. cue) was either a flutter or continuous vibration presented bilaterally. The exogenous cue (Exo. cue) was a single tap presented to both the thumb and middle finger of either the left or right hand. The target was a short buzz presented to the thumb or middle finger of the left or right hand. ISI = inter stimulus interval; SOA= stimulus onset asynchrony; ITI = inter trial interval.

Each trial started with one of two vibrations to all four stimulators indicating to which side the participant was to focus their endogenous attention. The endogenous cue was presented bilaterally. Participants' were instructed to focus their covert attention to the side indicated by the bilateral cue whilst fixating their gaze upon a centrally located cross. Following the off-set of the endogenous cue there was an inter-stimulus interval of 500 ms before the presentation of the unilateral exogenous cue (see Figure 2.2.1). The participant was informed that this exogenous cue (or distractor) was to be ignored and appeared at random, equally often to the right and left. Following the off-set of the exogenous cue there was a varied inter-stimulus interval of 200, 500, 800, or 1300 ms prior to the presentation of the target. The participant made a vocal discrimination, saying *up* if the target stimulus appeared to either middle finger, and *down* if the target was presented to either thumb. Via an intercom system, the experimenter then coded their response on a keyboard in the adjacent room. Following the experimenters key-press, there was a random inter-trial interval between a minimum of 500 ms and maximum of 2500 ms before the presentation of the endogenous cue.

2.3.2 Results

The data from Experiment 1 and 2 were analysed using repeated-measures analysis of variance (ANOVA) using SPSS version 14.0. The factors included in the statistical analysis

were Endogenous attention (valid, invalid), Exogenous attention (valid, invalid) and SOA (250 ms and 850 ms in Experiment 1; 550 ms and 1350 ms in Experiment 2). The SOA factor only refers to the time interval between exogenous cue and target. The time interval between endogenous and exogenous cues was always constant (see Figure 2.2.1). Prior to analysis of main effects an error analysis was performed. Errors where participants did not respond were excluded. These errors were likely due to the microphone not recording a response. In Experiment 1 (SOA of 250 ms and 850 ms) less than 1% of trials were due to no responses and 2% of trials across all participants in Experiment 2 (SOA of 550 ms and 1350 ms). Further, discrimination errors, (e.g., participants responded *up* to a target presented to their thumb) accounted for less than 4% of trials across all participants in Experiment 1, and less than 6% in Experiment 2. RTs which were too slow or too fast were also filtered out. This was calculated individually for each participant where RTs greater than 1.96 standard deviations above or below the mean were excluded. This filter led to approximately 6% of trials excluded across all participants in Experiment 1, and approximately 14% of trials were excluded from subsequent analysis in Experiment 2.

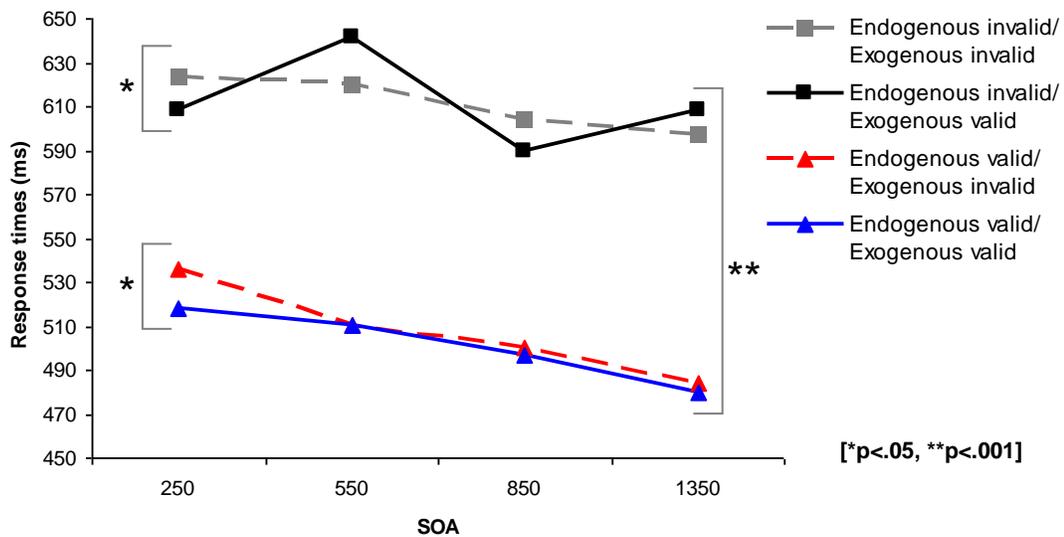


Figure 2.2.2 Behavioural results Study 2. Response times (in milliseconds) to trials were the endogenous cue was valid or invalid, and the exogenous cue was valid or invalid. Experiment 1 included stimulus onset asynchronies (SOAs) between exogenous cue and target of 250 ms and 850 ms, and Experiment 2 included SOAs of 550 ms and 1350 ms. The SOA only refers to the time interval between exogenous cue and target. The time interval between endogenous and exogenous

cues was always constant (see Figure 2.2.1). Endogenous orienting to validly cued target was significantly faster compared to invalidly cued targets (* $p < .001$). There was a significant difference (* $p < .05$) between Exogenous valid and invalid trials, but only for SOA of 250 ms.

There were significant main effects of SOA and Endogenous orienting in both Experiment 1 and 2. In Experiment 1, responses to targets preceded by an 850 ms SOA (mean = 547.74 ms) were significantly faster compared to targets with a 250 ms SOA (mean = 571.53 ms) ($F(1,13) = 8.09$, $p = .014$, $\eta^2_p = .38$). This effect was also present in Experiment 2 where responses to targets preceded by a 1350 ms SOA (mean = 542.53 ms) were significantly faster ($F(1,13) = 10.01$, $p = .007$, $\eta^2_p = .44$) than responses to targets preceded by a 500 ms SOA (mean = 570.20 ms). Thus, the longer SOA in each experiment induced significantly faster RTs in relation to the shorter SOA (see Figure 2.2.2). A main effect of Endogenous orienting was significant in Experiment 1 ($F(1,13) = 67.75$, $p < .001$, $\eta^2_p = .84$) as targets preceded by a valid endogenous cue (mean = 512.69 ms) were significantly faster as compared to endogenous invalidly cued targets (mean = 606.29 ms). Similarly, a significant main effect of Endogenous orienting was present in Experiment 2 ($F(1,13) = 49.14$, $p < .001$, $\eta^2_p = .79$) as validly cued targets (mean = 495.78 ms) were on average faster 121 ms faster compared to invalidly cued targets (mean = 616.95 ms).

Experiment 1 demonstrated a significant effect of cue validity for exogenous orienting ($F(1,13) = 4.72$, $p = .049$, $\eta^2_p = .27$) with faster RTs for exogenously valid (553.16 ms) compared to invalid trials (565.82 ms). Comparisons were also made for Endogenous and Exogenous effects at each SOA separately, as the *a priori* predictions suggested that IOR may vary at short and long SOA. Analysis of the 250 ms SOA trials showed a significant effect of Exogenous attention ($F(1,13) = 6.55$, $p = .024$, $\eta^2_p = .34$) suggesting facilitation of exogenous valid (563.30 ms) compared to invalid trials (579.78 ms). However, there was no Endogenous*Exogenous interaction suggesting the facilitation effect was the same regardless if the target appeared at the attended or unattended side (see Figure 2.2.2). There were no effects of Exogenous cueing, nor Exogenous*Endogenous interactions at any of the three other SOAs. Similar endogenous attention effects were present at all 4 SOAs ($p < .001$).

2.3.3 Discussion – Study 2

The results from Study 2 indicated that when bilateral cues are used to direct endogenous attention then validly cued targets were facilitated, replicating the findings from Study 1. Study 2 additionally demonstrated this endogenous effect continued to be robust at long SOAs between endogenous cue and target as it was present at SOAs over 2 seconds. A facilitation was also demonstrated when exogenous cues were valid, however, this effect was only present at short (250 ms) SOA whilst there was no exogenous attention effect at longer SOAs. Moreover, there was no interaction between exogenous and endogenous attention at any SOA tested suggesting these mechanisms operate independently of each other.

2.4 General discussion

The first study presented in this chapter investigated the use of bilateral tactile cues to induce endogenous orienting. In both a detection and discrimination task participants responded significantly faster on valid compared to invalid trials (Figure 2.1.2). Suggesting that participants were able to endogenously attend to the location predicted by the bilateral cue. A key element of Study 1 was to establish a viable tactile cue to direct attention to a tactile location, without also eliciting exogenous cueing effects and/or influences from other modalities. Previous studies of tactile attention have been unable to disentangle endogenous and exogenous effects due to the use of unilateral cues which may evoke both attention mechanisms (Cohen et al., 2005; Lloyd et al., 1999, although see: Chica et al., 2007; Forster & Gillmeister, 2011); and Chapter V for alternative cueing methods), or using vision to direct attention to tactile targets (Forster & Eimer, 2005; Posner, 1978; Spence, Pavani, et al., 2000). Expanding the findings from Study 1 using these bilateral cues, the second study aimed to investigate the relationship between endogenous and exogenous attention. In Study 2 the endogenous effect from Study 1 was replicated in that participants were able to use the bilateral cues to facilitate RTs at the endogenously attended location. The endogenous facilitation effect was present at all SOAs between exogenous cue and target (250, 550, 850, & 1350 ms; see Figure 2.2.2.) demonstrating an endogenous cueing effect over 2 seconds long. The results from Study 2 showed that the exogenous cue only influenced RTs when the SOA was short (250 ms). Moreover, there was no interaction between endogenous and exogenous attention effects suggesting that endogenous and exogenous attention are separate mechanisms. In other words, the effect of

exogenous attention seen at the 250 ms SOA condition was the same regardless if the target appeared at the endogenously attended or unattended location.

The lack of interaction between endogenous and exogenous attention is partly in line with a similar double cueing study in the visual modality. Similar to the present results, Berger et al. (2005) found that endogenous orienting facilitated RTs at the attended location. Moreover, when there was a short SOA (100 ms) between the exogenous cue and target there was facilitation of exogenously valid targets. At longer SOA the participants' demonstrated IOR, with longer RTs for valid compared to invalid trials. This biphasic pattern of results was the same across all their experiments involving target detection. Their results showed no interaction between the attention mechanisms, even when at long SOA, endogenous and exogenous attention demonstrated opposite effects. However, when they increased task demand and participants' discriminated targets in contrast to simple target detection, an interaction at particular SOAs between the two attention mechanisms appeared. When targets were preceded by either the shortest (100 ms) or longest (1000 ms) SOA, Berger et al. found facilitation and IOR respectively for their exogenous cue. These effects did not interact with the endogenous attention effect. However, at intermediate SOAs (200 ms & 300 ms) there was no effect of exogenous orienting, but importantly, this interacted with endogenous attention. Berger and colleagues concluded that the more difficult discrimination task increased attentional resources required which led to the interaction of endogenous and exogenous attention. They further suggested that there was no interaction at the shortest SOA (100 ms) as endogenous and exogenous attention did not compete. Thus, at short SOA both mechanisms lead to facilitation of validly cued targets. The lack of interaction between endogenous attention and IOR at the long SOA was explained as IOR being an effect too robust to integrate with the endogenous process. A direct comparison between findings from vision research and the present Study 2 - investigating touch - should be made with caution as there are clear differences between the two modalities. For example, in an exogenous cue-target detection task there is an early facilitation period for validly cued targets in vision (SOA less than approximately 250 ms) before IOR becomes apparent. However, this facilitation period is not present in similar exogenous tactile detection tasks (e.g., Lloyd et al., 1999). If the target needs to be discriminated, then the results are more similar across the two modalities. In both vision (e.g., Lupiáñez et al., 1997) and touch (e.g., Miles et al., 2008) there is a biphasic pattern with early facilitation of exogenously valid targets, followed by IOR. The results of Study 2

demonstrated early facilitation period of exogenous valid over invalid trials (see Figure 2.2.2.). However, no inhibition period followed the early facilitation, hence, not demonstrating the biphasic behavioural pattern. Moreover, there was no interaction between endogenous and exogenous attention at the more intermediate SOAs which showed no effect of exogenous attention.

Berger et al. (2005) proposed the interaction between endogenous and exogenous attention appeared due to increased task demand in their discrimination task, and thus increased attentional load. The present second study also employed a discrimination task. Evidence that the present discrimination task was more difficult compared to a detection task also in touch can be taken from Study 1. This was demonstrated by increased RTs and errors for discrimination task compared to the simple target detection. However, it is possible that the discrimination task was not difficult enough in Study 2 to require endogenous and exogenous attention to interact. This simplicity may be indicated by the fact that the error rates were rather low, amounting to on average 5% of all trials. This is in line with the suggestion made by Berger et al. that when the task is simple (detection task in their study) the attentional resources are not exhausted and the two modes of orienting occur in separation, and they interfere only when task demands are higher. In other words, it is possible that the present tactile discrimination task was too simple to elicit any interaction between endogenous and exogenous attention.

Conversely, there was no indication that the longer SOAs in Study 2 elicited IOR. In contrast to the hypothesis that the lack of interaction between endogenous and exogenous attention effects was a result of the task being too easy, it has been suggested that easier discrimination tasks allows for more IOR (Cheal & Chastain, 1999). Moreover, the absence of IOR influences at the longer SOA contrasts recent tactile discrimination studies of exogenous attention. Brown and colleagues (Brown et al., 2010; Miles et al., 2008) demonstrated facilitation at early SOAs (150 ms and 350 ms), no difference at 540 ms, and IOR at 1000 ms. The 1350 ms SOA between exogenous cue and target in Study 2 is well within the time range previously demonstrated to elicit IOR in an exogenous discrimination task. Several possible hypotheses could account for the lack of IOR effect. It could be that endogenously orienting towards a tactile location eliminates and masks any IOR. This would contrast Berger et al.'s (2005) conclusion that IOR is inexorable and not affected by endogenous attention. It may also be possible that endogenously attending delays the

development of IOR beyond the longest SOA measured in the present task. In other words, in previous tactile exogenous discrimination tasks the IOR develops at around 1000 ms post cue onset (Brown et al., 2010; Miles et al., 2008). By including endogenous orienting in the task the additional attention resources required may delay the onset of IOR even further. A range of longer SOAs, above 1350 ms between exogenous cue and target would be required to investigate this hypothesis. A third possibility may be that endogenous attention is completely re-oriented during the time window between exogenous cue and target. Thus, the attention is initially drawn towards the exogenous cue. When the SOA is short (250 ms) there is not sufficient time for the endogenous attention to fully re-orient back to the attended location. This in turn leads to an effect of exogenous attention. At longer SOAs, the irrelevant cue may initially attract attention away from the endogenously attended location. However, there is sufficient time to fully re-orient covert endogenous attention back to the endogenous valid location, and eliminating any effects of exogenous attention.

Berger and colleagues (2005) proposed five different models which can account for the relationship between endogenous and exogenous attention (see introduction of this chapter). They concluded the model which fits their findings best is that endogenous and exogenous attention are separate mechanisms, at least until task demands and attentional load is increased at which point they interact. The results from the present study are in line with the conclusion of separate mechanisms for the two types of orienting also in touch. Whether endogenous and exogenous attention failed to interact due to the simplicity of the task remains unclear. However, increasing task difficulty in the discrimination task may provide an answer.

2.5 Summary and conclusion

The first study demonstrated that endogenous attention can be directed covertly using bilateral tactile cues. The second study demonstrated that presenting irrelevant tactile stimuli during endogenous orienting influences RTs. The effects of an exogenous cue are only present when the irrelevant stimulus is presented shortly before the target (250 ms SOA). However, there is no interaction between the two types of attention mechanisms. Thus, any effects of the exogenous cue are the same regardless of whether the target appears at an attended or unattended location. This suggesting that endogenous and exogenous attention mechanisms do not interact, at least when task difficulty is low.

Chapter III

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

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.

3.1 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 are 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 & Cohen, 1984).

Behaviourally IOR has been demonstrated within the visual (for review see Klein, 2000), auditory (e.g., Schmidt, 1996; Tassinari & Berlucchi, 1995), tactile modality (Cohen, Bolanowski, & Verrillo, 2005; Lloyd, Bolanowski, Howard, & McGlone, 1999; Poliakoff

et al., 2002; Röder, Spence, & Rösler, 2002; Röder, Spence, & Rösler, 2000), and between all modality pairings (Ferris & Sarter, 2008; Roggeveen, Prime, & Ward, 2005; Spence, Lloyd, McGlone, Nicholls, & Driver, 2000; Spence, Pavani, & Driver, 2000). Within the tactile modality IOR has been demonstrated for SOAs between cue and target of 100 ms (Lloyd et al., 1999) to 6 seconds (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 reduces possible response biases influencing results (c.f. Spence & McGlone, 2001). The few studies investigating discrimination of tactile targets (Chambers, Payne, & Mattingley, 2007; Miles, Poliakoff, & Brown, 2008; Santangelo & Spence, 2007; Spence & McGlone, 2001; Brown, Danquah, Miles, Holmes, & Poliakoff, 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, Ward, & Kiehl, 1999; Prime & Ward, 2004, 2006; Wascher & Tipper, 2004; Tian & Yao, 2008; Chica & Lupianez, 2009). Further, Luck, Woodman, and Vogel (2000) suggested that the P1 amplitude difference between valid and invalid trials is usually directly linked to behavioural 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 & Mangun, 1998; Doallo et al., 2004) or a significant IOR effect but no P1 modulation (Prime & Ward, 2006). Nonetheless, Prime and Ward (2006) concluded 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 a proximal sense only informing us of events on our body and not in the external spatial environment (Gibson, 1966). Likewise, recent research suggests that the neural mechanisms underlying tactile spatial endogenous attention differ in comparison to the other senses (Forster & Eimer, 2005; Forster & 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 electrophysiological 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 while 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 has a similar functional significance to 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 effects observed in invalid trials would be due to attentional benefits (Forster & Eimer, 2005; Mayer, Dorflinger, Rao, & Seidenberg, 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. The discrimination task predictions were based upon the hypothesis that the 800 ms SOA used in the experiment may not be long enough to elicit IOR or short enough for facilitation to occur (see 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) while ERP amplitude differences on invalid and neutral trials would reflect enhancement of processing at target locations (i.e. attentional orienting benefits). We hypothesized that the ERP modulations of exogenous attention may be present at one or several of the components previously demonstrated to be modulated by endogenous attention (i.e., the N80, P100, N140, and Nd).

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 & Mangun, 2000), auditory (e.g., Green & McDonald, 2006) and tactile cue (Forster, Sambo & Pavone, 2009) studies and has been suggested to reflect a supramodal attention mechanism in the frontal areas (Eimer, van Velzen, & Driver, 2002; Eimer & van Velzen, 2002; Seiss, Gherri, Eardley, & Eimer, 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, Dean, John, & Sterr, 2006; Praamstra,

Boutsen, & Humphreys, 2005). This component has been suggested to reflect attentional orienting mediated and driven by information about external visual space (van Velzen, Eardley, Forster, & Eimer, 2006; Eardley & 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 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.

3.2 Methods

3.2.1 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).

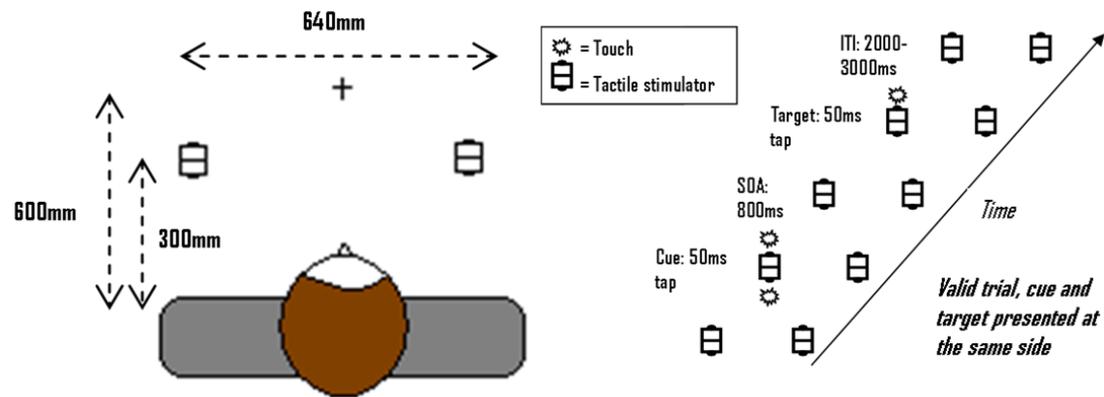


Figure 3.1 Experimental set-up and stimuli presentation. *Left:* Schematic view of the experimental set-up. The two rectangular boxes in front of the subject represent four tactile stimulators held between the thumb and middle finger of each hand. *Right:* Schematic representation of events in a valid cue trial. The cubes represent the tactile stimulators, also depicted in the left figure, and the explosions represent tactile stimulation.

3.2.2 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 x 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. All stimuli were presented using E-Prime software, which also recorded response times. A second PC recorded the EEG data using Analyzer (Brain Vision) and was connected to the E-Prime computer so it could receive digital triggers of when a particular tactile stimulus was presented. This set-up was the same for all subsequent studies in this thesis.

3.2.3 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 where no target 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. The trials were randomly presented within each block. 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 movements.

3.2.4 Recording and analysis

Behavioural data were subjected to a repeated-measures ANOVA with Task (detection, discrimination), 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 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 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 $\pm 40\mu\text{V}$ relative to baseline at HEOG electrodes) or with other artifacts (voltage exceeding $\pm 80\mu\text{V}$ relative to baseline at all electrodes 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 a 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 $4\mu\text{V}$ between cue-left and cue-right trials (Kennett, van Velzen, Eimer, & Driver, 2007).

For cue-target interval analysis ERPs were averaged separately for task (detection and discrimination) and cue (left and right hand) and analyzed 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 & Eimer, 2008). Mean amplitude 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 -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. Where the effect of Cue was significant together with a Cue*Electrode interaction, the interaction was not broken down further to reduce type I error rates induced by additional analyses. However, whereby the effect of Cue was not significant whilst a Cue*Electrode interaction was, the interaction was broken down. Importantly, this further analysis adopted strict Bonferroni correction due to the exploratory nature of this further analysis at specific electrodes. 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 & 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.

3.3 Results

3.3.1 Behavioural performance

Response time analysis showed a significant Task difference ($F(1,17)=94.51$, $p<.001$, $\eta^2_p=.85$) as on average 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 ($F(2,34)=13.50$, $p<.001$, $\eta^2_p=.44$) and a Task*Cue interaction ($F(2,34)=13.05$, $p<.001$, $\eta^2_p=.43$).

Separate follow-up analysis by Task showed a significant effect of Cue in the detection task ($F(2,34)=20.97$, $p<.001$, $\eta^2_p=.55$) 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 (Figure 3.2).

Analysis of the discrimination task also showed a significant effect of Cue $F(2,34)=4.35$, $p=.033$, $\eta^2_p=.20$, 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.

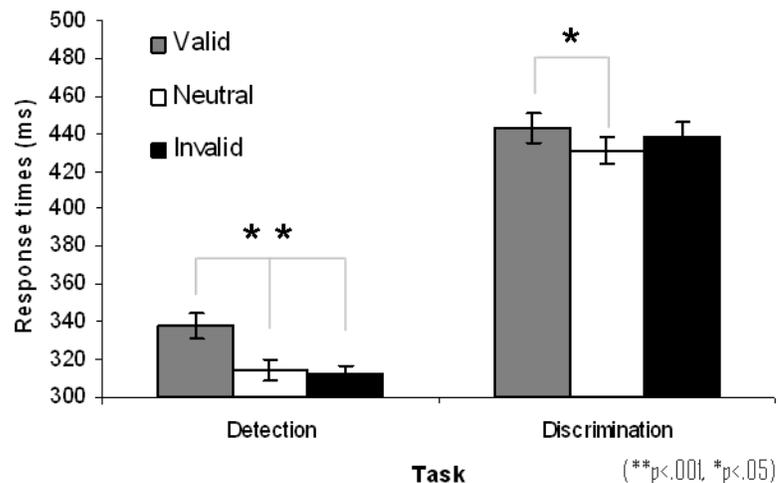


Figure 3.2 Behavioural results. Response times (in ms) and standard errors separately for valid, neutral, and invalid trials for detection and discrimination tasks. Detection task results show significantly slower RTs for valid compared to both neutral and invalid trials demonstrating IOR. There was no difference between valid and invalidly cued targets in the discrimination task indicating no IOR.

3.3.2 ERP results

3.3.3 Effects of exogenous orienting on Cue-Target interval ERPs

Figure 3.3 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 (Figure 3.4, showing topographical maps of

the ADAN). In the subsequent analyses the ADAN is represented by a Cue*Hemisphere interaction.

Table 3.1 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.

Analysis of the cue-target interval showed a significant Cue*Hemisphere interaction in the 400-600 ms time window at central ($F(1,17)=36.34$, $p<.001$, $\eta^2_p=.68$) and anterior ($F(1,17)=37.03$, $p<.001$, $\eta^2_p=.69$) electrode sites. In the 600-800ms time window there was a significant Cue*Hemisphere interaction at posterior ($F(1,17)=24.17$, $p<.001$, $\eta^2_p=.59$), central ($F(1,17)=52.02$, $p<.001$, $\eta^2_p=.75$), and anterior ($F(1,17)=25.72$, $p<.001$, $\eta^2_p=.60$) electrode sites. These Cue*Hemisphere interactions indicated an enhanced negativity contralateral to the cue direction (Figures 3.3 and 3.4). 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 3.1 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.

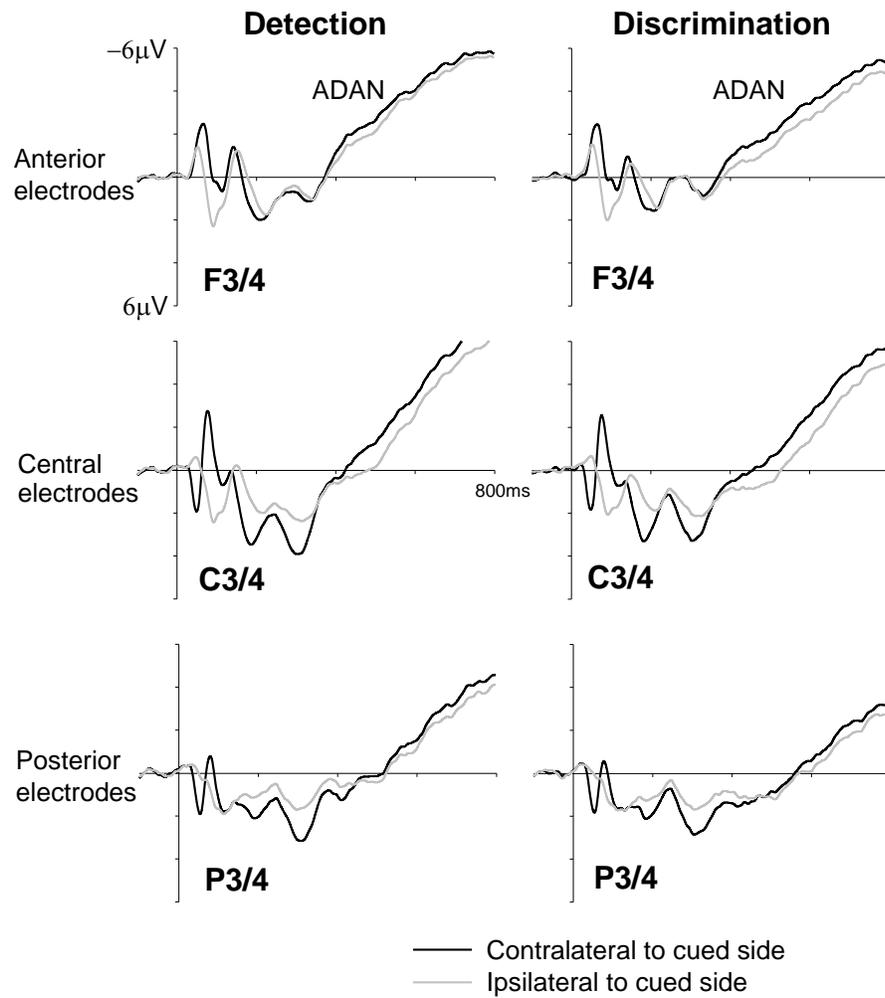


Figure 3.3 Grand-averaged ERP waveforms for the cue-target interval in detection (left panel) and discrimination (right panel) task. Black lines represent ERPs at electrodes contralateral and grey lines represent ERPs at electrodes ipsilateral to the cued side. Enhanced negativity (upward deflections) for contralateral compared to ipsilateral electrodes (indicating the presence of the ADAN) is demonstrated for both detection and discrimination tasks.

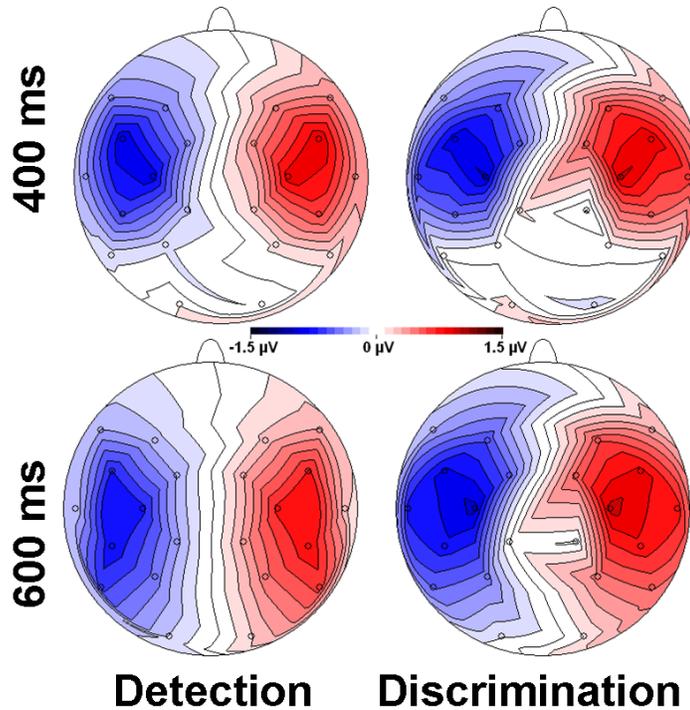


Figure 3.4 Scalp distribution of cue-target interval data for the detection (left) and discrimination (right) task 400-600 ms (top) and 600-800 ms (bottom) post cue onset. Maps represent differences between brain activity observed over hemispheres ipsilateral and contralateral to the cued side. The obtained difference waveforms were mirrored to obtain symmetrical but inverse amplitude values for both hemispheres. That is, the same effect is presented over both left and right hemispheres in the figure. Each contour line represents 0.05 μ V changes (amplitude range between -1.0 and 1.0 μ V).

3.3.4 Effects of exogenous attention on post-target somatosensory ERPs

Figure 3.5 and 3.6 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 Figure 3.5) in the detection task whilst it is ipsilaterally (left graph in Figure 3.6) in the discrimination task. This difference in attention effect over contralateral and ipsilateral hemispheres at the P100 component is also demonstrated in Figure 3.7 which represents the attention effect at each time window analysed. In the subsequent analyses the attention effect is represented by an effect of Cue.

Table 3.2 *Post-target ERP attention effects*

Component	Task	Bilateral	Contralat.	Ipsilat.
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 analyzed 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).

P45

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

N80

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

Analysis of post-target ERPs showed a significant Cue*Hemisphere interaction ($F(2,34)=28.87$, $p<.001$, $\eta^2_p=.63$) at the N80 component (a significant Cue*Electrode Site*Hemisphere $F(10,170)=6.93$, $p<.001$, $\eta^2_p=.29$ was also present). The interaction was followed up with separate analysis for each hemisphere. This revealed a contralateral effect of Cue ($F(2,34)=5.40$, $p=.018$, $\eta^2_p=.24$) and post-hoc analysis (Bonferroni corrected) showed only a significant difference between valid versus invalid trials ($p<.001$) with an enhanced negative amplitude on invalid trials. There was also an ipsilateral effect of Cue ($F(2,34)=3.56$, $p=.04$, $\eta^2_p=.17$), 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 the same in both tasks.

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 ($F(10,170)=5.06$, $p=.003$, $\eta^2_p=.23$) and Task*Cue*Hemisphere interaction ($F(2,34)=8.79$, $p=.001$, $\eta^2_p=.34$) (other significant interactions including the factor Cue were a Cue*Electrode Site*Hemisphere ($F(10,170)=11.67$, $p<.001$, $\eta^2_p=.41$), a Task*Cue*Electrode Site ($F(10,170)=3.65$, $p=.013$, $\eta^2_p=.18$), a Cue*Hemisphere ($F(2,34)=37.80$, $p<.001$, $\eta^2_p=.69$), and a Cue*Electrode Site ($F(10,170)=8.34$, $p<.001$, $\eta^2_p=.33$) interaction). These interactions were followed up by separate analyses for each task.

The detection task showed a significant Cue*Hemisphere ($F(2,34)=28.42$, $p<.001$, $\eta^2_p=.63$) (as well as Cue*Electrode Site*Hemisphere ($F(10,170)=10.54$, $p<.001$, $\eta^2_p=.38$) and Cue*Electrode Site ($F(10,170)=7.01$, $p<.001$, $\eta^2_p=.30$)) interaction which was again broken down into analysis of Cue for each hemisphere. Following a significant contralateral Cue*Electrode Site ($F(10,170)=7.01$, $p<.001$, $\eta^2_p=.30$) interaction it was revealed the attention effect was located on FC5/6 ($p=.017$, 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 a reduced positive amplitude on invalid trials suggesting attentional orienting benefits whilst T7/8 also showed a difference between valid versus neutral ($p=.044$, Bonferroni corrected) with an enhanced positive amplitude on valid trials suggesting also attentional orienting costs for this time window (see Figure 3.5). Analysis of attentional effects for the ipsilateral hemisphere showed a significant Cue*Electrode Site interaction ($F(10,170)=3.56$, $p=.021$, $\eta^2_p=.17$). 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 ($F(2,34)=10.03$, $p<.001$, $\eta^2_p=.37$, as well as Cue*Electrode Site*Hemisphere ($F(10,170)=4.74$, $p=.002$, $\eta^2_p=.22$), and Cue*Electrode Site interaction ($F(10,170)=3.72$, $p=.011$, $\eta^2_p=.18$)) which was followed up by effects of Cue for each hemisphere separately. Contralaterally there was a Cue*Electrode Site interaction ($F(10,170)=5.35$, $p=.001$, $\eta^2_p=.24$), however, the follow-up yielded no significant effects. Ipsilateral analysis for the discrimination task demonstrated a significant effect of Cue ($F(2,34)=5.52$, $p=.008$, $\eta^2_p=.25$). 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 (Figure 3.6). Thus, the attention effect in the discrimination task was present over ipsilateral hemisphere, in contrast to a contralateral P100 effect in the detection task.

N140

There was an ipsilateral N140 attention effect in both tasks.

Analysis of the N140 component demonstrated significant Cue*Hemisphere ($F(2,34)=6.03$, $p=.006$, $\eta^2_p=.26$) and Cue*Electrode Site ($F(10,170)=3.86$, $p=.012$, $\eta^2_p=.19$) interactions. Follow-up analyses for each hemisphere revealed a Cue*Electrode Site interaction ($F(10,170)=3.46$, $p=.013$, $\eta^2_p=.17$) 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 ($F(2,34)=5.23$, $p=.01$, $\eta^2_p=.24$) and Cue*Electrode Site interaction ($F(10,170)=3.27$, $p=.026$, $\eta^2_p=.16$). 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 negative amplitude on valid compared to invalid trials (Figures 3.5 and 3.6) and lack of Task*Cue interaction suggested this effect was similar in the two tasks.

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 ($F(2,34)=9.51$, $p=.001$, $\eta^2_p=.36$). 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.

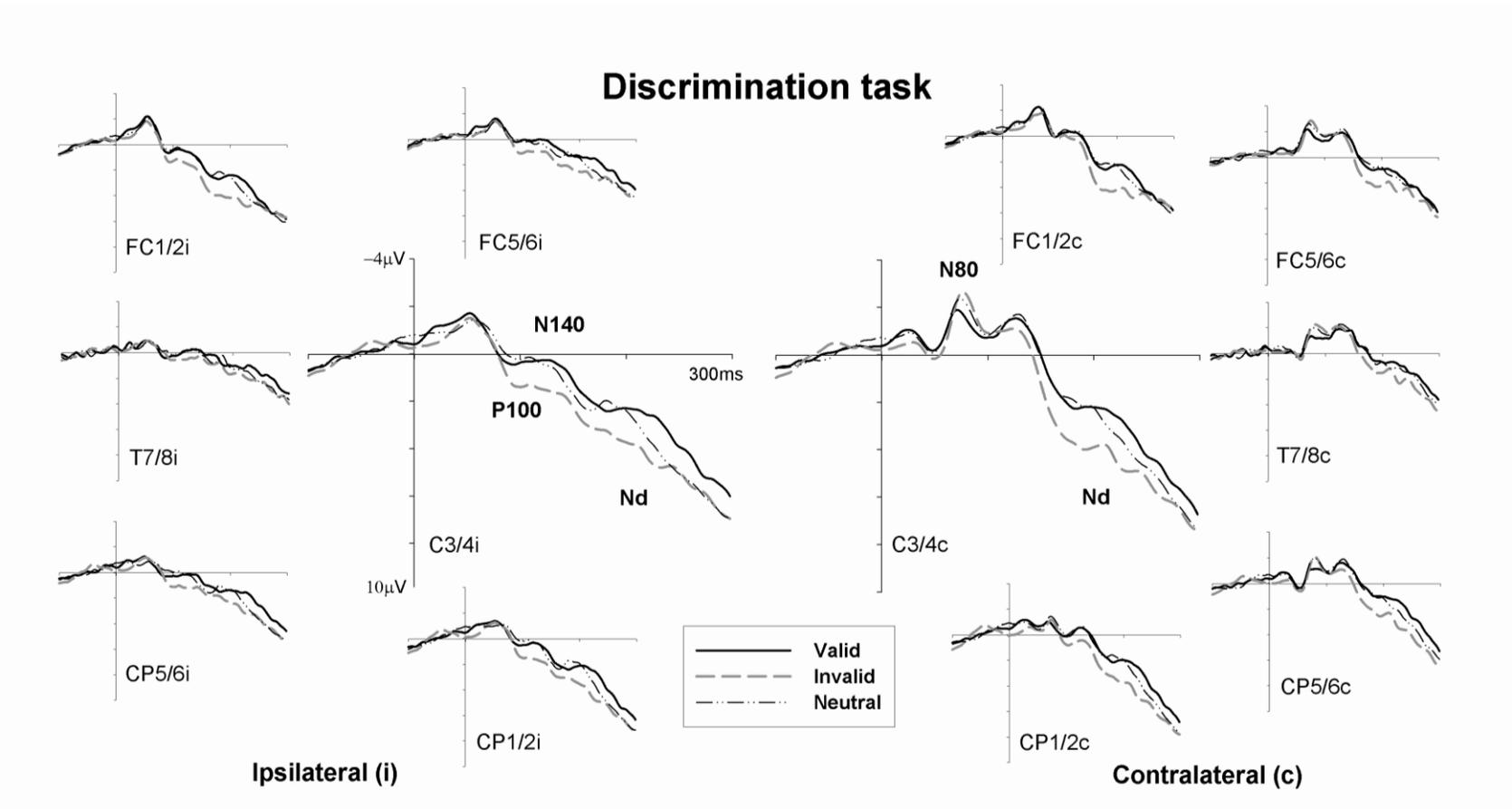


Figure 3.6 Post-target ERPs for the discrimination task. Discrimination task grand averaged somatosensory ERPs elicited on valid (solid line), neutral (dashed black lines), and invalid (dashed grey lines) trials in the 300 ms time window following target onset. The left side shows ERPs over ipsilateral 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.

Detection Discrimination

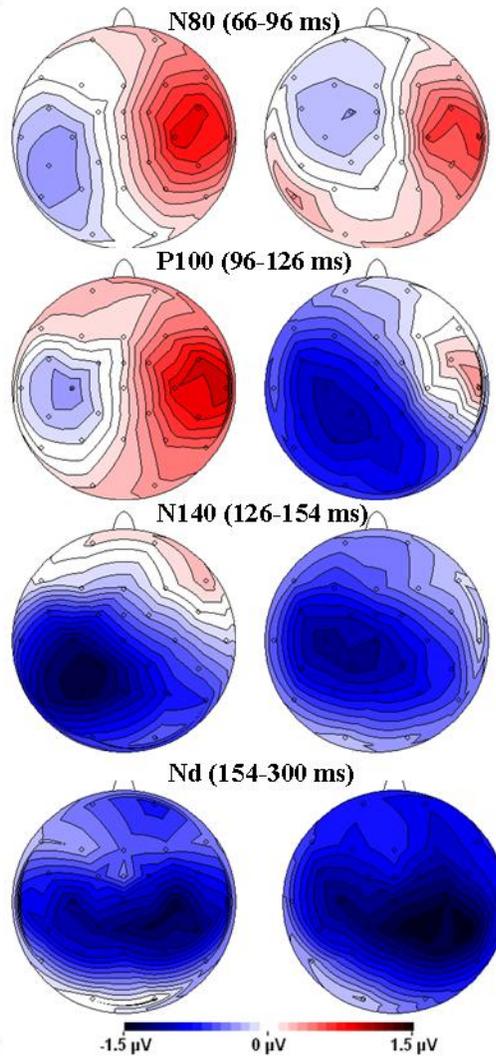


Figure 3.7 Topographic maps of the post-target attention effects (ERPs on invalid were subtracted from valid trials) at each time window analyzed presented for the detection (left panel) and discrimination (right panel) task. The right hemisphere shows attention effect contralateral to the target side 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.

3.3.5 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, while the attention effect was ipsilateral in the discrimination task. Therefore, for the time window of the P100 mean amplitude differences between valid and invalid trials 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 ($r=.06$)

3.4 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 & Forster, 2003) and might be specific to exogenous attention.

3.4.1 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., 2002; Röder et al., 2000); that is, responses to targets were significantly slower when task irrelevant cues were present 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 the mechanisms responsible for the pattern of results observed for validly cued targets. That is, 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 & 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) while 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 mechanisms³. 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 Figure 3.2). 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.

³ 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.

3.4.2 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 reported (e.g., Eimer & 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 orienting 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 & Mangun, 2000; Kennett, van Velzen, Eimer, & Driver, 2007; van der Lubbe, Neggers, Verleger, & Kenemans, 2006; Talsma, Slagter, Nieuwenhuis, Hage, & Kok, 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 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 where vision was not engaged

suggesting the LDAP is not required for endogenous orienting (e.g., Eardley & van Velzen, 2011). In an endogenous tactile attention study, Forster, Sambo and Pavone (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 Figure 3.4). Importantly, the presence of an ADAN component in this study that is analogous to the ADAN reported in endogenous attention studies may suggest that this component is due to activity of the fronto-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 & Forster, 2003; Desmedt & Robertson, 1977; Michie, Bearpark, Crawford, & Glue, 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 Figure 3.5) it appears as though the N80 effect in the

detection task continues with enhanced negative amplitude for invalid trials in the time window of the P100, whilst in the discrimination task (see Figure 3.6) this continuation is not as pronounced. Within the visual domain the P1 component has been the strongest contender as a component directly linked to behavioural IOR. However, the visual attention literature does not paint a consistent picture of IOR and the P1, where studies have found a P1 attention modulation but no IOR (e.g., Hopfinger & Mangun, 1998) or IOR but no P1 attention effect (e.g., Prime & Ward, 2006). In the present study, we found IOR in the detection but not in the discrimination task. Examination of topographical attentional difference maps (Figure 3.7) 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 & 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; Washer & 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 it would be 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 was directly linked to a contralateral P100 then we would expect the waveforms for the invalid and neutral 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, when directly comparing these two effects by means of correlation

then 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 Figure 3.7). 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 these later ERP modulations of attention do not reflect the processing stages affected by the behavioural inhibition caused by the exogenous cue. It may therefore be hypothesized that the exogenous and/or inhibitory effects affect earlier stages of processing.

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, benefits, or both⁴. At the P100, ERPs on invalid trials were different from neutral trials in both tasks indicating attentional orienting benefits. Although, 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, for example; attention may have been deployed equally to both sides, focused in the middle, or elsewhere. To further

⁴ Attentional costs in an endogenous Posner task would reflect invalid trials to be suppressed compared to neutral trials. Attentional benefits are expressed as enhancement of valid trials compared to neutral trials. However, in an exogenous Posner task reflecting IOR, conceptually the costs/benefits analysis would be reversed. That is, if IOR is due to costs then valid trials would be suppressed compared to neutral cues. If IOR was instead due to exogenous attentional benefits then invalid trials would be enhanced compared to neutral trials.

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.

CHAPTER IV

Inhibition of return is coded in a somatotopic frame of reference – Evidence from ERPs and behaviour

To localize a tactile stimulus we can use a somatotopic frame of reference indicating where on the body the stimulus appeared. It may also be important to use an external frame of reference to know where the stimulated body part is located in external space. Previous research has shown endogenous tactile attention and tactile processing to be affected by varying posture. Here we examine the effects of posture on exogenous tactile attention. Participants detected tactile targets with the hands near, far apart, or behind their back. To investigate whether posture affected finger and hand processing differently tactile stimuli was presented to the palms or fingers, separately in each posture. The results demonstrated similar behavioural effects in terms of inhibition of return in all postures, and no difference was observed whether stimuli were presented to the fingers or hands. Behavioural results indicated only a somatotopic frame of reference was used. Concurrently recorded ERPs also demonstrated remarkably similar effects across conditions. An anterior directing attention negativity (ADAN) was observed in all conditions - a cue-target waveform suggested to reflect attention effects relying on somatotopic spatial co-ordinates. ERPs elicited by tactile targets showed exogenous attention modulations at the N80, P100, N140 and Nd1 components. These attention effects were the same in all conditions and not modulated by varying posture. Behavioural and ERP results indicated that exogenous tactile attention is somatotopically coded and not remapped into external spatial co-ordinates.

4.1 Introduction

When something touches our body maybe the most important initial process is to localize where this event happened. The location can be defined in two ways; where on the skin or where in external space did the stimuli appear. How the brain localizes and processes where on the skin surface the tactile stimulation appeared is one of the most researched and well known functions in the brain. Early mapping studies demonstrated that skin representations in the primary somatosensory cortex (SI), located along the postcentral gyrus, are generally organized in a somatotopic manner (Penfield & Boldrey, 1937). This sensory homunculus is an orderly array of brain areas which roughly represents the order of our body parts, such as the hand representation is next to the arm representation also in the brain. Penfield and Boldrey also established that the more sensitive body parts and/or those used more often have larger cortical representation in the SI, often visually depicted as a man with large

hands and lips. However, localizing relative to the skin surface is not always sufficient. Important to know is also the location of one's body in external space. For example, if a mosquito lands on your arm, it is important to know where on the arm the mosquito is (somatotopic frame of reference) as well as where the arm is in space (external frame of reference) in order to accurately swat the insect. Dissociation between the two reference frames has been demonstrated in neurologically damaged patients. For example, Paillard (1999) reported a patient with a peripheral deafferentation who could accurately locate tactile stimuli on the skin surface with her eyes closed but unable to identify the position in external space. That is, demonstrating intact somatotopic representations in somatosensory cortex whilst impaired body posture and external frame of reference.

Postural representations likely involve both visual and proprioceptive input when forming an accurate representation of the limb position in external space (Medina & Coslett, 2010). Based mainly on findings from non-human research, an area proposed to be involved in postural representations is the superior parietal lobe, in particular Brodman's area 5. For example, a single cell recording study by Sakata, Takaoka, Kawarasaki, and Shibutani (1973) involving rhesus monkeys showed neurons in Brodman's area 5 responded preferentially to stimulation of a body part, but only when that body part was in a particular location in external space. In a recent study, Azañón, Longo, Soto-Faraco, & Haggard (2010) demonstrated the role of the parietal lobe in human mapping of touch in external space. Participants had to judge the elevation of touches on their forearms in relation to tactile stimuli to their face, without visual input. Transcranial magnetic stimulation (TMS) was delivered to the posterior parietal cortex (PPC), putatively the ventral intraparietal (VIP) area, and this showed disruption in the remapping of touch into external space. They further suggested that this area is dissociable from the pure proprioceptive (area 5) and somatosensory (SI) localization. Moreover, they suggested a model for tactile remapping whereby initial somatotopic localization of touch occurs in SI and possible secondary somatosensory cortex (SII)⁵. Then the proprioceptive information is gathered specifically in area 5 which converge with the somatotopic information in the VIP cortex to form the tactile mapping.

⁵ The SII is thought to be generally organized according to a body map and there is evidence suggesting this area is also involved in posture, in addition to somatotopic processing (Graziano & Cooke, 2006).

One of the most commonly used methods of investigating external and somatotopic frame of references is to compare tactile processing when hands are crossed over the body midline versus in a more “typical” uncrossed posture. The logic is that crossing the hands may cause a conflict between the somatotopic and external frame of references. For example, temporal order judgement tasks (TOJ) have demonstrated that crossing the hands over the body midline leads to worse performance compared to tactile stimuli presented in an uncrossed position, demonstrating this conflict between external and somatotopic frame of reference (Shore, Spry, & Spence, 2002; Yamamoto & Kitazawa, 2001).

The role of vision in understanding spatial reference frames has been studied comparing sighted with blind people. Röder, Rösler, and Spence (2004) used a TOJ task in conditions with hands crossed or uncrossed. They investigated the effects of posture in blind people who were either congenitally blind (blind before birth) or late blind (blind after birth). The detrimental effect of crossing the hands was present in the sighted participants (control group) but also in the group which developed visual impairment onset after birth. However, the congenitally blind participants were not affected by crossing the hands. This suggested vision in childhood development is important in establishing the crossmodal link between vision and touch and the integration of external and somatotopic reference frames.

Röder, Föcker, Hötting, & Spence (2008) demonstrated similar effects of crossing the hands when also recording event-related potentials (ERPs) in an endogenous attention paradigm. Congenital blind and sighted people were instructed to detect infrequent tactile stimuli whilst attending to one hand and ignoring stimuli presented to the unattended hand. The behavioural data replicated previous findings with response times (RTs) not being affected by arm posture in the congenitally blind participants, whilst sighted people showed a detrimental effect of crossing their hands. The ERP results demonstrated an attention modulation (difference between valid and invalid trials) at the P100 component only in the sighted and not the blind participants. The following negativity (N140 and Negative difference (Nd)) was present in both groups. Sighted participants showed earlier attention modulations compared to blind patients. This later attention negativity effect was reduced in the crossed condition compared to uncrossed for sighted participants, whilst posture had no effect for the blind group. However, an earlier attention effect for sighted compared to blind participants is at odds with the findings reported by Forster, Eardley, and Eimer (2007). Forster and colleagues instead found earlier ERP attention effects in blind

compared to sighted people. Moreover, Eardley & van Velzen (2011) investigated the effects of crossing the hands on tactile attention in sighted and early blind. They found that attention modulations of ERPs elicited by the tactile stimuli (post-target time window) were delayed when hands were crossed compared to an uncrossed posture, and this difference did not differ between sighted and early blind. The precise relationship between different frames of reference and attention modulations in the post-target time window remains to be established.

Investigating the ERP components in the interval between cue and target has led to more consistent findings relating to external and somatotopic reference frames. Two successive lateralized ERP waveforms have been proposed to reflect attention processing during the cue-target time window. An anterior directed attention negativity (ADAN) is a component starting at around 350 - 400 ms post cue onset and reflects more negative waveforms over the hemisphere which is contralateral compared to ipsilateral to the attended side. This component originates over frontal areas. Following the ADAN, at about 600 ms, a more posterior late directing attention positivity (LDAP), with enhanced positivity for contralateral compared to ipsilateral electrode sites, has been demonstrated in attention studies using ERPs (e.g., Hopf & Mangun, 2000; Nobre, Sebestyen, & Miniussi, 2000). As outlined in the previous paragraph, Eardley and van Velzen (2011) compared crossed versus uncrossed posture effects in groups of sighted and early blind participants. They found the polarity of the ADAN to be reversed and also delayed when crossing the hands, and these effects were similar for both groups. They concluded that as well as sighted people, participants without sight, but not congenitally blind, automatically evoke an external spatial reference frame, and vision *per se* is not needed for this system to be used. The reversal of the ADAN polarity in the crossed hands posture is in line with the suggestion that the ADAN largely reflects a somatotopic reference frame with enhanced negativity contralateral to the anatomically stimulated hand rather than contralateral to the externally attended space which was stimulated (see also Eimer, van Velzen, et al., 2003). However, Eardley and van Velzen (2011) argue that the delayed onset of this component when hands are crossed indicates the conflict between somatotopic and external reference frames. Moreover, the lack of LDAP is consistent with the view suggesting this posterior component is mediated and driven by the presence of visual information about the external space around us (participants were blind or blindfolded and the cues were auditory in the study by Eardley and van Velzen (2011)).

ERP and behavioural studies have consistently reported that TOJ (e.g., Shore et al., 2002; Yamamoto & Kitazawa, 2001) and attention effects (e.g., Azañón & Soto-Faraco, 2008; Kennett, Eimer, Spence, & Driver, 2001; Spence, Pavani, et al., 2000) are negatively affected by crossing the hands compared to the more typical uncrossed posture. However, is it not necessarily required to directly conflict the somatotopic and external reference frames to illustrate postural effects of tactile processing. Behaviour and ERP effects have demonstrated to be attenuated when hands are held close together compared to far apart, whilst not adopting a crossed hand posture (Eimer et al., 2004; Shore, Gray, Spry, & Spence, 2005). Moreover, Heed and Röder (2010) have proposed "... that hand crossing may induce qualitatively different processing requirements rather than indicating a pure influence of nonaligned spatial reference frames" (p. 198). In an endogenous attention task using a visual symbolic cue to direct attention, Eimer et al. (2004) found that in the condition in which the hands were close together attenuated the LDAP component as compared to hands far apart. However, the ADAN was unaffected. This adds further support to the hypothesis that the ADAN is somatotopically based and the LDAP anchored in external spatial coordinates. In the time window following the tactile stimuli, Eimer and colleagues also showed an attention modulation at the N140 component to be more pronounced when hands were held far apart. The precise origin of the N140 component is not entirely known but has been suggested to originate from in particular from SII and frontal areas (Allison et al., 1992; Hari et al., 1993, 1984; Kakigi et al., 2000; Mima et al., 1998). That posture may affect processing in the SII is in line with research from animal studies suggesting this area is modulated by posture in monkeys (Graziano & Cooke, 2006). Moreover, Heed (2010) comments that; "Interestingly, VIP projects to SII (Lewis & Van Essen, 2000); postural influences may therefore be relayed to SII after having been remapped in VIP." (p. 605). Thus, there is evidence to suggest the SII – by modulations of the N140 and later components - may be influenced by posture.

Much of the evidence from behavioural and ERP studies, in particular when crossing the hands, suggest the integration of somatotopic and external reference frames is an automatic mechanisms. A similar distinction between automatic (exogenous) and voluntary (endogenous) mechanisms is found in attention. The majority of studies investigating the effects of posture on tactile attention have employed endogenous paradigms. Attention is typically deployed to one hand and comparisons between unattended and attended stimuli

are compared in conditions of different postures (e.g., Eardley & van Velzen, 2011; Eimer, Forster, et al., 2003; Eimer et al., 2004; Röder et al., 2008). A dissociation between exogenous and endogenous orienting has been shown in behavioural studies whereby endogenous attention leads to facilitation of cued targets and exogenous attention may result in inhibition of return (IOR) (e.g., Lloyd et al., 1999). IOR has been demonstrated cross-modally (Ferris et al., 2008; Spence, Lloyd, et al., 2000). This may indicate that this exogenous phenomenon is part of a system which can be accessed by all modalities and therefore needs to be anchored in external space. It could be reasonable to speculate that IOR operates in an external frame of reference. In other words, if a visual exogenous cue can induce IOR for a tactile target then, at least, the visual stimuli must have been anchored in an external frame of reference. This may suggest also tactile IOR makes use of an external frame of reference. Röder et al. (2002) aimed to investigate how exogenous attention is affected by posture. They presented tactile cues and targets to the middle and index fingers of both hands using a detection paradigm. Röder et al. used long cue-target intervals (300-1000 ms) to elicit IOR. They found IOR to be largest for cue and target presented to the same finger but also IOR when stimuli were presented to the adjacent finger of the same hand. Moreover, this effect was not influenced if the participants had their hands interwoven or not. They concluded that IOR is typically a process which relies on a somatotopic frame of reference rather than external.

The findings from Röder and colleagues (2002) suggested that IOR uses a somatotopic frame of reference. Their results (and the majority of research involving touch), are based upon findings in studies in which tactile stimuli were delivered to the fingers. There is some empirical evidence suggesting that the reference frame for fingers are particularly somatotopically anchored whilst the hands are affected by external space. Haggard, Kitadono, Press, & Taylor-Clarke (2006) asked participants' to identify which finger had been touch or which hand had been touched in a series of experiments were fingers were interwoven or not. They found the position of the hands and fingers in space influenced hand identification but not finger identification. Haggard and colleagues concluded that hand identification uses an external frame of reference whilst finger identification uses a somatotopic frame of reference and therefore, that remapping into external coordinates occurs only for hand identification.

In summary, when localizing tactile stimuli we can use a somatotopic and/or an external frame of reference. Dissociations between these two reference frames have particularly been established comparing tactile processing when hands are in an uncrossed to crossed posture. Behavioural results demonstrate reduced performance in a crossed hand posture as the two reference frames are in conflict. The most consistent ERP effects corresponding to difference frames of reference have been shown in the cue-target interval. The ADAN has been found to relate to the somatotopic reference frame whilst the LDAP largely reflects an external reference frame (Eimer, van Velzen, et al., 2003). These findings have however only been based upon studies investigating endogenous attention. It has been proposed that the fingers (which the vast majority of tactile studies have used as the stimulus location), are different in terms of reference frames compared to the hands. That is, the fingers use a somatotopic reference frame whilst the hands are mapped into external space (Haggard et al., 2006).

The present study aimed to investigate whether processing of tactile stimuli on fingers and hands is relative to different frames of references, and how this affects exogenous tactile orienting. Tactile stimuli were delivered to the fingers or the palms of each hand in separate blocks. The posture was manipulated by having hands either close together or far apart. The study adopted an exogenous Posner (1978) cue-target paradigm to investigate the effect of exogenous cueing. Based on the findings by Röder et al. (2002), who showed IOR to the fingers was somatotopically coded, we predicted posture would not affect IOR when stimuli was presented to the fingers. However, based upon Haggard et al.'s (2006) conclusion that the hands use an external frame of reference we hypothesised that the distance between the hands would affect tactile processing when the stimuli was delivered to the palms. Moreover, we aimed to investigate the neural correlates of IOR and how these are affected by posture, exploring both ERPs in the cue-target interval (presence of ADAN and LDAP) and somatosensory ERPs elicited by the tactile target. Generally, the ADAN has been suggested to relate to the orientation of somatically coded space whilst the LDAP is anchored in external space (e.g., Eimer et al., 2004). We aimed to establish whether any of these two cue-target waveforms, previously only reported in endogenous attention studies were also present during exogenous orienting (although see Chapters III, V, & VI in this thesis for the results demonstrating an ADAN together with IOR). In the post-target time window, modulations of attention at the N140 component have been linked to change in posture in an endogenous attention paradigm (Eimer et al., 2004). If endogenous and

exogenous tactile attention are similarly affected by posture then we hypothesised to also see modulations in the post-target time interval, possibly at components suggested to originate from SII (P100 and N140). Again, we proposed this modulation to be stronger for stimuli to the palms compared to the fingers. This is based on the theory that stimuli to the hands are re-coded into an external frame of reference whilst the fingers may not be. In turn, stimuli to the palms will be more affected by varying posture.

Finally, we will consider tactile processing in different areas of peripersonal space. The vast majority of research investigating how tactile perception is influenced by external space has explored the area in front of the participant, an area typically mediated by vision. As described earlier, people who do not have a visual representation of external space do not show the same influence of external reference frames in tactile perception (e.g., Röder et al., 2008). This further leads to the question whether the space behind us, which rarely relies on visual input, is processed similarly to the space in front which has detailed visual representations. Kóbor, Füredi, Kovács, Spence, & Vidnyánszky (2006) investigated this in a TOJ task when participants had their arms crossed or uncrossed in front and rear space. Although participants had their eyes closed they showed the detrimental effect of crossing the hands was reduced when hands were behind the back as compared to in front. They concluded the two spatial areas are different in that the space behind does not rely on an externally defined reference frame as much as the space in front. In addition, a growing body of evidence is forming suggesting the space behind us is processed differently compared to the space in front when integrating audiotactile information (see Ocelli, Spence, & Zampini, 2011, for a recent review). Following scarce but interesting finding of the space behind us, the present study included a condition where tactile stimuli were delivered to the hands when participants held them behind their back. This condition aimed to investigate whether exogenous tactile attention is affected differently if the hands are in a spatial location not usually available to vision (i.e. behind the back), compared to when the hands were in front of the participant.

4.2 Methods

4.2.1 Participants

Fifteen paid participants (9 female and 6 males) took part in the study and all gave written informed consent prior to their participation. All but one participant were right handed. The

mean age was 24.1 years old (range: 20-27 years). One participant was excluded from analysis due to excessive ERP artifacts.

4.2.2 Stimuli and materials

Stimuli and apparatus were identical in all conditions. Participants sat in a dimly lit, soundproofed chamber. Tactile stimuli were presented using two 12-V solenoids (5 mm in diameter), driving a metal rod with a blunt conical tip. The two tactors were fixed (using medical tape) to the left and right index finger or in the middle of the left and right palms. In the far condition the hands were 1 m apart and in the near condition the hands were as close together as possible but without touching. In both conditions the hands were placed so that the palms were facing each other and the little fingers were in contact with the table. Similarly, in the condition when participants had their hands behind their back they were as close together as possible without touching (see Figure 4.1 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 (when 1 m apart), 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.

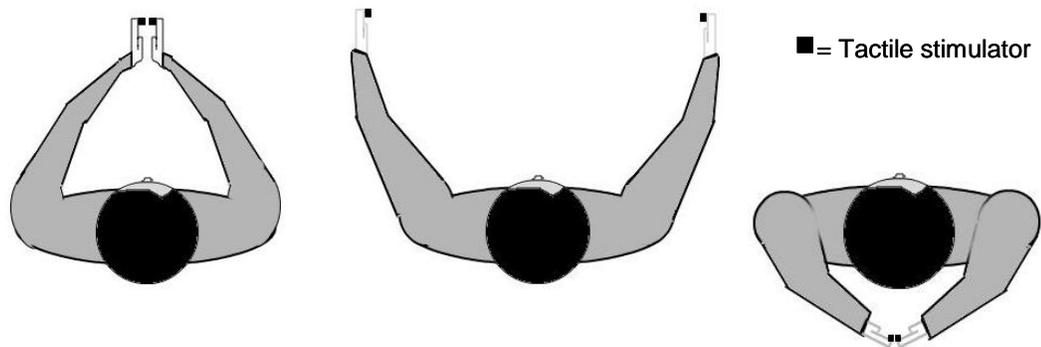


Figure 4.1 Schematic view over the different postures adopted by the participant; *left* - hands were near, *middle* - hands were far apart, *right* - hands behind participants back. Tactile stimuli were presented to either the fingers or in separate blocks, to the palms of the left and right hand.

4.2.3 Design and Procedure

We manipulated distance (near, far apart, & behind the back), shown in Figure 4.1 and stimulus location (fingers, hands). The experiment consisted of 15 blocks, 3 blocks for each of the 6 condition (hands far apart and stimuli on fingers, hands near and stimuli on fingers, hands far and stimuli on palms, hands near and stimuli on palms, hands behind the back and stimuli on fingers or palms). The postures were alternated across participants on a rolling basis to minimize any order effects, and similarly, starting with the presentation of stimuli to the palms and fingers were alternated for every other participant. The participants also completed two practice blocks each.

The trial procedure was identical in all blocks and differed only in the location of the stimuli (fingers or palms) and where the hands were placed in external space. Each block consisted of a total of 68 trials out of which 30, the cue and target were presented to the same location (valid), and in 30 trials were the cue and target were presented to opposite locations (invalid trials). In addition, each block consisted of 4 catch trials with no target, and 4 fast filler trials where the cue-target interval was 250 ms for two trials and 400 ms for two, rather than 750 ms as in all other trials. These trials served to reduce participant's expectation of the target appearing at exactly 750 ms after cue presentation. All trials were counterbalanced so half of the cues appeared to the left and half to the right. Each of the two practice blocks consisted of 18 trials, 6 valid, 6 invalid, 2 catch, and 4 fast filler trials. The trials were randomly presented within each block.

Each trial started with a 50 ms cue. This was followed by a 750 ms stimulus onset asynchrony (SOA) 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 2000-2800 ms. If no response was made within 1500 ms the trial terminated and the next trial began after the ITI. The participant was informed that the cue would not predict the target location and therefore to ignore the cue completely.

4.2.4 Behavioural analysis

For *Analysis 1*, to investigate the effects of stimulus location and stimulus distance upon IOR the behavioural data were submitted to a 2x2x2 repeated-measures ANOVA with the factors Distance (hands near, hands far apart), Location (stimuli to fingers, stimuli to

palms), Cue (valid, invalid). For *Analysis 2*, to compare the effects of having the hands in front compared to behind the participant's back the data were analysed with a 3x2 repeated-measures ANOVA. The factors were; Space (near and in front, far apart and in front, behind the back), and Cue (valid, invalid trials). Trials with response times less than 100 ms were excluded from analysis, resulting in removal of less than 2.3% of all valid trials and less than 2% of invalid trials, averaged across all five conditions. Moreover, on average there were 7% errors made for the catch trials, that is, participants incorrectly responded when there was no target.

4.2.5 EEG recording and data 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 and 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. 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 (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 in the post-target interval) were removed prior to EEG averaging. This artifact rejection resulted in removal of an average of less than 19% of all trials. 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).

4.2.5.1 Cue-target analysis

Investigating the effects of stimulus location and distance upon attention (*Analysis 1*), ERPs were average separately for each condition (finger far, finger near, palm far, palm near), and Cue (cue left and cue right) and analyzed 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).

The selection of electrodes was based upon sites commonly used to investigate the waveforms (e.g. ADAN and LDAP) that have been suggested to reflect the fronto-parietal attention network (see e.g., Gherri & Martin Eimer, 2008). Mean amplitude values were computed for two post-cue time windows, that is 400–600 ms , and 600–800 ms. These were subjected to separate repeated-measures ANOVAs with factors Distance (hands near, hands far apart), Location (stimuli on fingers, stimuli on palms), Cue (cued left, cued right), Hemisphere (left, right) 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 *Analysis 2* - investigating the effects of the external spatial hand location upon attention modulation - ERPs were averaged separately for Space (front near, front far apart, and back) and Cue (cue left and cue right). The cue-target interval was separated into the same two time windows as *Analysis 1* and a repeated-measures ANOVA was used with the factors Space (front near, front far apart, and back), Cue (cue left, cue right), Hemisphere (left, right) 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). The main aim was to investigate whether there were differences in attention modulations depending on whether the hands were located in a external space usually mediated by vision (i.e. in front of the participant) compared to space which rarely relies upon visual input (i.e. behind the back). In the condition with the hands behind the back, the hands were held close together. By including also a condition when hands were far apart in front of the participant, it was aimed to establish whether any differences in front and behind the back were also related to the proximity of the hands in external space.

4.2.5.2 *Post-target time window*

For post-target ERP analysis - investigating the effects of stimulus location and stimuli distance upon IOR (*Analysis 1*) - epochs were averaged separately for Condition (finger far, finger near, palm far, palm near) and Cue type (valid, invalid). ERP mean amplitudes were computed for measurement windows centred on the peak latencies of the somatosensory P45, N80, P100 and N140 components (40-50 ms, 66-86 ms, 98–122 ms and 122-146 ms post-stimulus, respectively). To investigate mid to longer-latency effects of spatial attention, mean amplitudes were also computed between 150-200 ms (Nd1) after tactile stimulus onset. A repeated-measures ANOVA was conducted to compare attentional

modulations with the factors Location (fingers, palms), Distance (near, far), Cue (valid, invalid), Electrode Site (CP1/2, CP5/6, C3/4, FC1/2, FC5/6, T7/8) and Hemisphere (ipsilateral, contralateral).

Analysis 2, investigating the effects of having the hands in front compared to behind the participant's back, used the same electrodes and time windows as in *Analysis 1*. A repeated-measures ANOVA was conducted with the factors Space (near, far apart, back), Cue (valid, invalid), Electrode Site (CP1/2, CP5/6, C3/4, FC1/2, FC5/6, T7/8) and Hemisphere (ipsilateral, contralateral).

Trivial effects such as main effects of Electrode site, or Hemisphere, or the interaction between the two are not reported throughout.

4.3 Results

Behavioural results demonstrated IOR. This effect was no different depending on whether stimuli were presented to the fingers or hands, and nor whether they were near and far apart (see Figure 4.2). Similarly, the IOR effect did not differentiate whether the hands were placed in front or behind the participant (see Figure 4.5). The ERP analyses also showed very similar results across all conditions. In the cue-target interval there was a significant enhanced negativity (ADAN) for contralateral compared to ipsilateral electrodes. The only difference between conditions was found in the cue-target interval were for anterior electrodes, the ADAN effect was larger in the condition when the palms were close together compared to far apart (see Figure 4.3). In the time window following the target there was an early attention modulation at the N80 with enhanced negative amplitude for invalid over valid trials. Following the N80 there were also attention modulations at the P100, N140 and Nd1. These attention effects did not differ across conditions suggesting hand location in space, nor varying stimuli locations (fingers or palms), influenced the post-target ERP pattern (see Figures 4.4 & 4.7).

4.3.1 Analysis 1- Near versus far in frontal space

4.3.1.1 Behavioural results

For *Analysis 1*, RT data was analysed to investigate any effects upon distance and location upon IOR (see Figure 4.2). There was a main effect of Cue ($F(1,13)=20.63$, $p=.001$, $\eta^2_p=.61$) demonstrating significant IOR with faster RTs for invalid (280.76 ms. SD=76.65)

compared to valid trials (302.69 ms, SD=77.32). However, Cue did not interact with Distance nor Location indicating stimuli presented near or far apart and to the fingers or palms did not affect IOR.

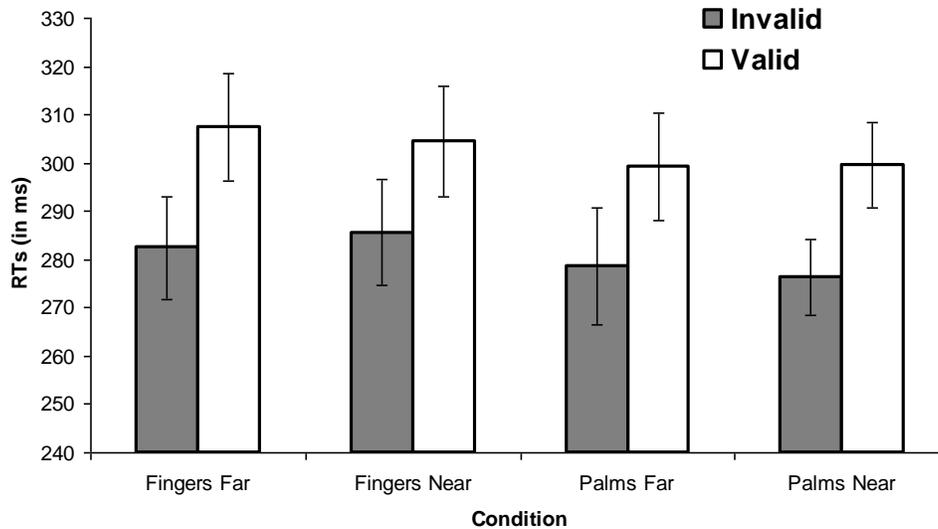


Figure 4.2 Behavioural results for stimuli to fingers and palms, near and far. Average response times (RTs in milliseconds) and standard error bars displayed for each of the four conditions; hands were near or far apart and tactile stimuli were presented to the fingers or palms of each hand. Overall there was significant IOR in all conditions. This demonstrated as invalid trials (grey bars) were significantly faster compared to valid trials (white bars). There was no difference in overall RTs or IOR effect between conditions.

4.3.1.2 ERP effects of stimulus location and distance

4.3.1.2.1 Cue-target ERP analysis

400-600 ms time interval

Anterior electrodes

There was a significant ADAN in the 400-600 ms time window in all conditions except when stimuli were presented to the palms and they were far apart (see Figure 4.3). The lateralized cueing effects in the cue-target interval (ADAN and LDAP) are denoted by a significant Cue*Hemisphere interaction. Analysis of the 400-600 ms time interval post cue onset showed a significant Location*Distance*Cue*Hemisphere interaction ($F(1,13)=10.58$, $p=.006$, $\eta^2_p=.45$, as well as Cue*Hemisphere ($F(1,13)=12.44$, $p=.004$, $\eta^2_p=.49$), Cue*Electrode site*Hemisphere ($F(2,26)=8.75$, $p=.001$, $\eta^2_p=.40$) interactions). The 4-way interaction was broken down further by separate analysis for fingers and palms.

Analysis of the finger condition showed a Cue*Hemisphere interaction ($F(1,13)=7.78$, $p=.015$, $\eta^2_p=.37$), and Cue*Electrode site*Hemisphere interaction ($F(2,26)=4.58$, $p=.02$, $\eta^2_p=.26$). Stimuli presented to the palms also showed a Cue*Hemisphere interaction ($F(1,13)=11.56$, $p=.005$, $\eta^2_p=.47$), and Cue*Electrode site*Hemisphere interaction ($F(2,26)=8.71$, $p=.001$, $\eta^2_p=.40$), but importantly, also showed a Distance*Cue*Hemisphere interaction ($F(1,13)=7.28$, $p=.018$, $\eta^2_p=.36$) suggesting the Cue*Hemisphere interaction (the ADAN) was different when hands were near versus far apart. Separate analysis for palms near and far apart showed an approaching significant Cue*Hemisphere interaction ($F(1,13)=3.80$, $p=.073$, $\eta^2_p=.23$), and Cue*Electrode site*Hemisphere interaction ($F(2,26)=12.34$, $p<.001$, $\eta^2_p=.49$) when palms were far apart and a significant Cue*Hemisphere interaction ($F(1,13)=13.18$, $p=.003$, $\eta^2_p=.50$), and Cue*Electrode site*Hemisphere interaction ($F(2,26)=3.51$, $p=.045$, $\eta^2_p=.21$) when palms were near.

Central electrodes

Analysis of ERPs over central electrodes showed a significant Cue*Hemisphere interaction ($F(1,13)=6.91$, $p=.021$, $\eta^2_p=.35$), and Cue*Electrode site*Hemisphere interaction ($F(1.2,15.8)=16.08$, $p=.001$, $\eta^2_p=.55$). However, there were no other interactions with Cue*Hemisphere suggesting the enhanced negativity for contralateral hemisphere was the same in all conditions over central electrodes at the 400-600 ms time window.

Posterior electrodes

There were no lateralized cueing effects over posterior electrodes.

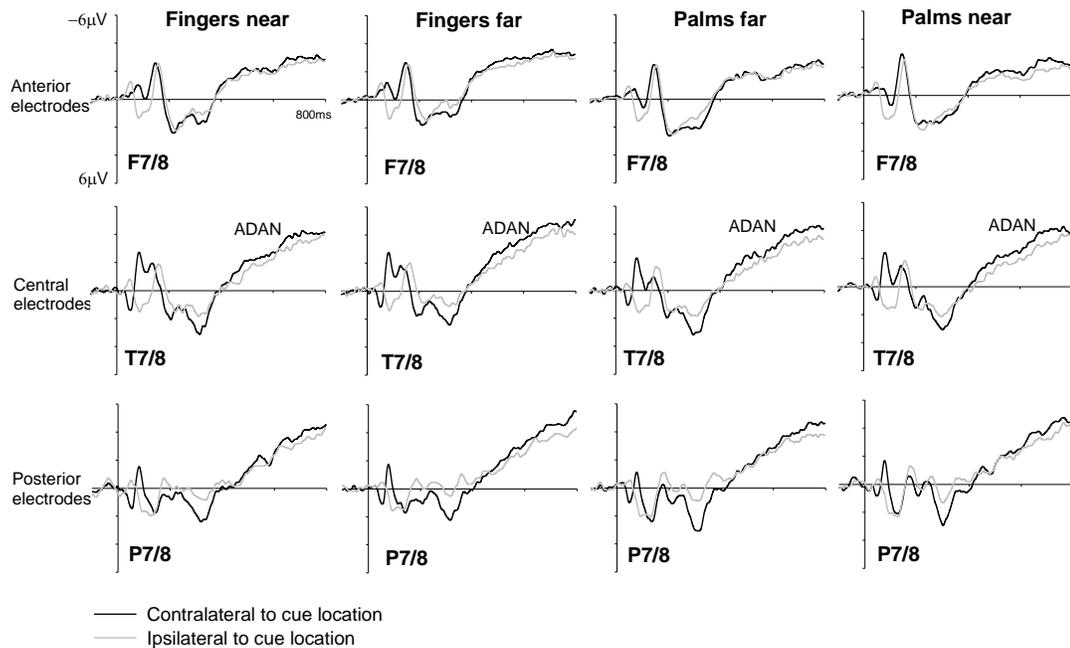


Figure 4.3 Cue-target ERPs. Grand average ERPs in the 800 ms cue-target interval at anterior (top), central (middle), and posterior electrodes (bottom row) for condition when stimuli were presented to the fingers or palms, and hands located near or far apart. Black lines represent ERPs contralateral to cue location and grey lines ERPs ipsilateral to cue location side. At anterior and central electrodes there is sustained enhanced negativity contralateral compared to ipsilateral to cue the location. This difference, starting at around 400 ms, reflects the presence of the anterior directed attention negativity (ADAN), also marked out on the figure at electrodes T7/8.

600-800 ms time interval

Anterior electrodes

In this time window the ADAN was significantly larger in the condition when hands were held close together compared to far apart (see Figure 4.3). Similar to the 400-600 ms time window, the 600-800 ms analysis over anterior electrodes demonstrated a significant Location*Distance*Cue*Hemisphere interaction ($F(1,13)=4.77$, $p=.048$, $\eta^2_p=.27$, as well as Cue*Hemisphere ($F(1,13)=3.04$, $p=.003$, $\eta^2_p=.50$), Cue*Electrode site*Hemisphere ($F(2,26)=6.50$, $p=.005$, $\eta^2_p=.33$), and Location*Cue*Hemisphere ($F(1,13)=5.75$, $p=.032$, $\eta^2_p=.31$) interactions). Follow-up analyses for finger and palms separately demonstrated no effect of distance on tactile stimuli to the fingers and the Cue*Hemisphere interaction for fingers only approached significance ($F(1,13)=3.53$, $p=.083$, $\eta^2_p=.21$). This suggesting that

there was no ADAN present when stimuli were presented to the fingers and they were held near or far apart at anterior electrodes at this time interval. However, the analysis of stimuli to the palms showed a Distance*Cue*Hemisphere interaction ($F(1,13)=5.65$, $p=.033$, $\eta^2_p=.30$, and Cue*Hemisphere interaction ($F(1,13)=29.59$, $p<.01$, $\eta^2_p=.70$). Separate analyses were conducted for palms near and far which demonstrated a Cue*Hemisphere interaction for palms far ($F(1,13)=9.39$, $p=.009$, $\eta^2_p=.42$, and Cue*Electrode site*Hemisphere interaction ($F(2,26)=7.48$, $p=.003$, $\eta^2_p=.37$)) and also a Cue*Hemisphere interaction for palms near condition ($F(1,13)=44.84$, $p<.001$, $\eta^2_p=.78$). Thus, there was no difference in the lateralized cue-target effects for fingers depending on distance apart, whilst for analysis of the stimuli presented to the palms, the ADAN was significantly larger in the condition when hands were held close together compared to far apart.

Central electrodes

The analysis showed an overall Cue*Hemisphere interaction ($F(1,13)=14.50$, $p=.002$, $\eta^2_p=.53$, and Cue*Electrode site*Hemisphere ($F(1.2,15.1)=21.23$, $p<.001$, $\eta^2_p=.62$), and Distance*Cue*Electrode site*Hemisphere ($F(1.3,16.6)=7.68$, $p=.009$, $\eta^2_p=.37$) interactions). However there was no Location*Distance*Cue*Hemisphere interaction

Posterior electrodes

Analysis over posterior electrodes showed a significant Cue*Hemisphere interaction ($F(1,13)=26.18$, $p<.001$, $\eta^2_p=.67$, and Cue*Electrode site*Hemisphere interaction ($F(2,26)=10.99$, $p<.001$, $\eta^2_p=.46$), demonstrating enhanced contralateral negativity for also posterior brain areas.

Table 4.1 Cue-target interval analysis of stimulus location and distance summary

	Condition	400-600 ms	600-800 ms
Lateralized Posterior electrodes P3/4, P7/8, O1/2	Fingers far apart	n.s.	p<.001
	Fingers near		
	Palms far apart		
	Palms near		
Lateralized Central Electrodes C3/4, CP5/6, T7/8	Fingers far apart	p=.021	p=.002
	Fingers near		
	Palms far apart		
	Palms near		
Lateralized Anterior electrodes F3/F4, F7/F8, FC5/Fc6	Fingers far apart	p=.015	p=.083
	Fingers near		
	Palms far apart	p=.073	p=.009
	Palms near	p=.003	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. For central and posterior electrodes the Cue*Hemisphere interaction was the same for all conditions whilst at anterior electrodes the lateralized effects interacted with stimulus location. In both time windows the Cue*Hemisphere interaction was significantly larger for stimuli to the palms when hands were near compared to far apart.

4.3.1.2.2 Summary of cue-target interval Analysis 1

There was a significant ADAN present from 400 ms until target onset over central electrodes. This effect did not differ depending on varied location or distance. For the posterior electrodes an enhanced contralateral negativity was found starting approximately 600 ms post cue onset, and similar to central areas, this effect did not differ depending on conditions. For anterior electrode areas, in both time windows, the ADAN was significantly larger for stimuli to the palms when hands were near compared to far apart. Distance did not affect the ADAN when stimuli were presented to the fingers.

4.3.1.2.3 Post-target ERP analysis

In the post-target time window any effects of Cue indicated a difference between valid and invalid conditions, that is, an attention effect.

P45

Analysis of the P45 revealed a significant Cue*Hemisphere interaction ($F(1,13)=6.2$, $p=.027$, $\eta^2_p=.32$), however, separate follow-up analysis demonstrated no significant effect of Cue for ipsilateral or contralateral hemisphere.

N80⁶

Analysis of the N80 demonstrated a significant Cue*Hemisphere interaction ($F(1,13)=40.92$, $p<.001$, $\eta^2_p=.76$, and Cue*Electrode site*Hemisphere interaction ($F(2.4,31.0)=14.50$, $p<.001$, $\eta^2_p=.53$)). Separate follow-up analyses for each hemisphere showed an effect of Cue over ipsilateral ($F(1,13)=20.18$, $p=.001$, $\eta^2_p=.61$) and contralateral hemisphere ($F(1,13)=8.73$, $p=.011$, $\eta^2_p=.40$, and also Cue*Electrode site interaction ($F(1.9,24.3)=10.77$, $p=.001$, $\eta^2_p=.45$)).

P100

The P100 analysis showed a significant Cue*Hemisphere interaction ($F(1,13)=24.07$, $p<.001$, $\eta^2_p=.65$, and also borderline main effect of Cue ($F(1,13)=4.56$, $p=.052$, $\eta^2_p=.26$), and Cue*Electrode site*Hemisphere interaction ($F(2.7,35.6)=6.64$, $p=.001$, $\eta^2_p=.34$)). Separate follow-up analysis for each hemisphere showed a main effect of Cue over ipsilateral hemisphere only ($F(1,13)=18.72$, $p=.001$, $\eta^2_p=.59$). Thus, there was an attention effect over ipsilateral hemisphere for the P100 time window, however, this attention effect did not interact with neither distance nor stimulus location.

N140

Analysis of the N140 time window demonstrated a Cue*Hemisphere interaction ($F(1,13)=10.78$, $p=.006$, $\eta^2_p=.45$, as well as main effect of Cue ($F(1,13)=13.22$, $p=.003$,

⁶ Analysis of the N80 time window showed an attention modulation over both ipsilateral and contralateral hemisphere. However, the N80 component is suggested to only stem from the primary somatosensory cortex contralateral to the stimulated side (Allison et al., 1992, 1989; Forss & Jousmäki, 1998; Hari et al., 1984; Inui et al., 2004; Mima et al., 1998). Descriptively, examining the ERPs for contralateral and ipsilateral hemisphere it suggests that the somatosensory component is only over contralateral hemisphere and this enhanced negative peak is absent over ipsilateral hemisphere. It may be reasonable to conclude that the attention modulation of the N80 *component* was only over contralateral hemisphere whilst the ipsilateral hemisphere effect should not be denoted as a modulation of the component but rather, an attention effect in the 66-86 ms time window following the stimuli.

$\eta^2_p=.50$) and Cue*Electrode site ($F(1.8,23.6)=5.55$, $p=.012$, $\eta^2_p=.30$), and Cue*Electrode site*Hemisphere ($F(2.5,33.0)=7.81$, $p=.001$, $\eta^2_p=.38$) interactions. Separate follow-up analyses for each hemisphere showed an effect of Cue for ipsilateral hemisphere ($F(1,13)=22.74$, $p<.001$, $\eta^2_p=.64$, and also a Cue*Electrode site ($F(1.8,23.8)=7.69$, $p=.003$, $\eta^2_p=.37$)) and contralateral hemisphere ($F(1,13)=5.89$, $p=.03$, $\eta^2_p=.31$, and also Cue*Electrode ($F(2.4,31.5)=4.73$, $p=.012$, $\eta^2_p=.27$) and Cue*Location ($F(1,13)=9.10$, $p=.01$, $\eta^2_p=.41$) interaction. There was an attention modulation over both contralateral and ipsilateral hemispheres in the N140 time window. This attention effect was the same regardless of distance between the hands.

Nd1

Analysis of the Nd1 showed a significant main effect of Cue ($F(1,13)=8.08$, $p=.014$, $\eta^2_p=.38$), with enhanced negativity for valid over invalid trials (see Figure 4.4). Importantly there were no Cue*Distance, Cue*Location, or Cue*Distance*Location interactions suggesting the attention modulation was not affected whether the hands were near or far and whether the stimuli was presented to the palms or fingers.

Table 4.2 Post-target ERP attention effects for analysis of stimulus location and distance

Component	N80		P100		N140		Nd1
	Contra.	Ipsi.	Contra	Ipsi	Contra.	Ipsi.	
Fingers Far	p=.011	p=.001	n.s.	p=.001	p=.030	p<.001	p=.014
Fingers Near							
Palm Far							
Palm Near							

Note: Summary of statistical results (probability levels (p) and non-significance (n.s.) stated) of post-target ERP attention effects (valid vs. invalid trials). The attention modulations did not differ between the four conditions. Probability levels reported as bilateral effects refer to attention modulations present over both hemispheres. For components where there was a significant Cue*Hemisphere interaction separate analysis of Cue was conducted for each hemisphere (contralateral & ipsilateral to target side).

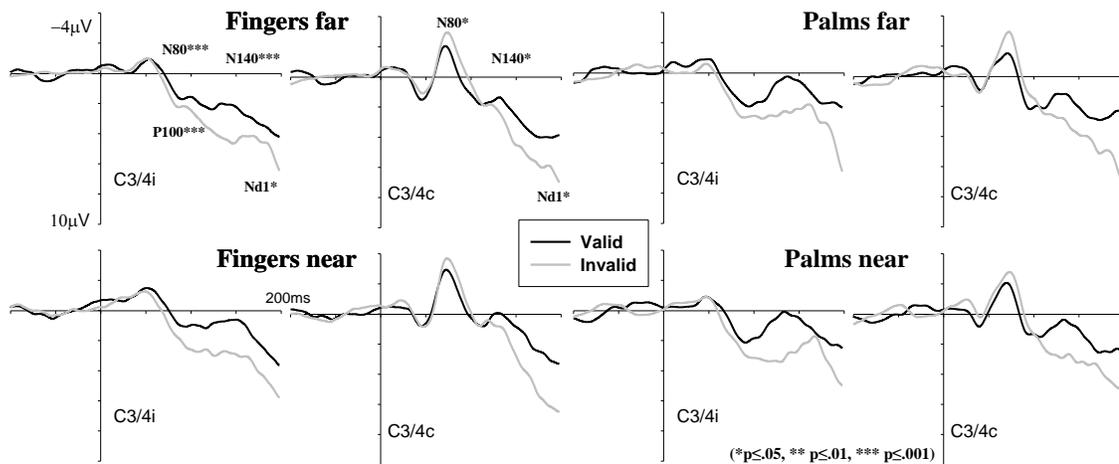


Figure 4.4 Post-target ERPs. Grand average ERP waveforms in the 200 ms time window following tactile targets on valid (black line) and invalid (grey line) trials. Attention modulations (difference between valid versus invalid trials) were found on the N80, P100, N140, and Nd1 components and were the same across all four conditions and are highlighted on the top left ‘Fingers far’ conditions panel. The left graph of each condition refers to ERPs ipsilateral to target location (C3/4i) and right refers to contralateral ERPs (C3/4c).

Summary

There were exogenous attention modulations at the N80, P100, N140 and Nd1 components. However, these effects were the same regardless of whether hands were close or far apart and whether the tactile stimuli were presented to the fingers or palms.

4.3.2 Analysis 2 –effects of front versus back space on attention

4.3.2.1 Behavioural results

Analysis 2 investigated the effect of external space upon IOR (see Figure 4.5) and similarly found a main effect of Cue ($F(1,13)=21.78$, $p<.001$, $\eta^2_p=.63$) with faster RTs for invalid (271.91 ms, SD-69.49) compared to valid (294.02 ms, SD-72.52), and a main effect of Space ($F(2,26)=6.44$, $p=.005$, $\eta^2_p=.33$) and pairwise post-hoc t-tests (Bonferroni corrected) indicated RTs to stimuli presented behind the participant’s (265.43 ms, SD- 72.75) were significantly faster ($p=.006$) compared to when hands were in front and far apart (291.95 ms, SD-71.19), and approaching significance ($p=.085$) in the condition when hands were in front and close together (291.51 ms, SD-69.06) versus behind. However no Cue*Space interaction ($F<0.2$) was observed, suggesting having the hands in front (near or far apart) or behind participants did not affect IOR (see Figure 4.5).

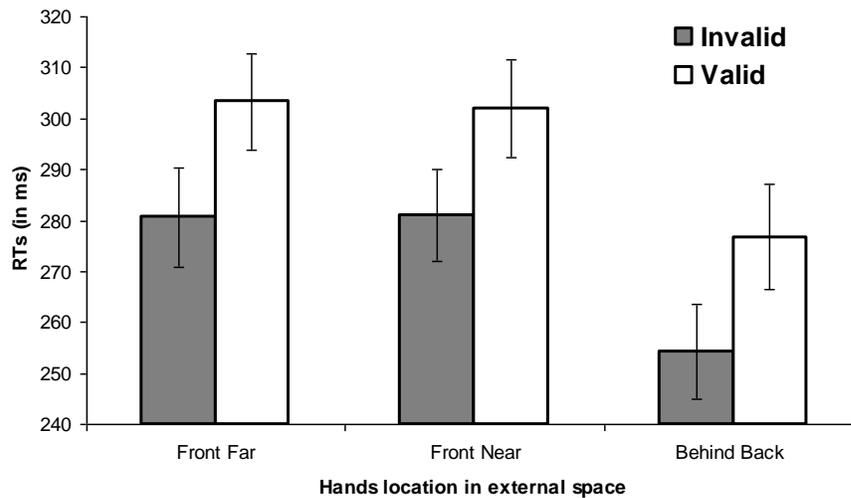


Figure 4.5 Behavioural results when hands in front and behind the participant. Average response times (RTs in milliseconds) and standard error bars for hands held in front of the participant either hands near of far apart, or when participants held their hands behind their back. There was significant IOR in all three conditions with faster RTs for invalid (grey bars) compared to valid trials (white bars). On average, having the hands behind the back was significantly faster compared to when presenting stimuli in front of the participant.

4.3.2.2 ERP results

4.3.2.2.1 Cue-target ERP analysis

400-600 ms interval

Anterior electrodes

Analysis of anterior electrode sites in the 400-600 ms time window demonstrated a significant Cue*Hemisphere interaction ($F(1,13)=18.24$, $p=.001$, $\eta^2_p=.58$, and also Cue*Electrode site*Hemisphere interaction ($F(1.6,21.3)=10.81$, $p=.001$, $\eta^2_p=.45$)), with enhanced contralateral negativity for electrodes contralateral compared to ipsilateral to cue location. There was an ADAN at anterior electrodes in this time window.

Central electrodes

Similar to anterior electrodes, there was a Cue*Hemisphere interaction over central electrodes ($F(1,13)=9.15$, $p=.01$, $\eta^2_p=.41$, and a Cue*Electrode site*Hemisphere interaction ($F(1.3,16.4)=20.34$, $p<.001$, $\eta^2_p=.61$)).

Posterior electrodes

There were no significant effects over the posterior area.

600-800 ms

Anterior electrodes

For the anterior areas there was a Cue*Hemisphere interaction ($F(1,13)=14.16$, $p=.001$, $\eta^2_p=.58$, and also Cue*Electrode site*Hemisphere interaction ($F(2,26)=9.98$, $p=.001$, $\eta^2_p=.43$)), with enhanced negativity for contralateral over ipsilateral to target location, however, no Space*Cue*Hemisphere interaction ($F<0.15$).

Central electrodes

Analysis showed a Cue*Hemisphere interaction ($F(1,13)=17.35$, $p=.001$, $\eta^2_p=.57$, and also Cue*Electrode site*Hemisphere interaction ($F(1.2,15.4)=28.74$, $p<.001$, $\eta^2_p=.69$)).

Posterior electrodes

Posterior electrodes analysis demonstrated Cue*Hemisphere interaction ($F(1,13)=29.00$, $p<.001$, $\eta^2_p=.69$, and also Cue*Electrode site*Hemisphere interaction ($F(2,26)=9.75$, $p=.001$, $\eta^2_p=.43$)), with enhanced negativity for contralateral side.

In both time window and all three areas analysed, the Space*Cue*Hemisphere interaction was not significant (All $F_s<1.1$) suggesting the cue-target waveforms and ADAN effect were similar in all three hand locations.

Table 4.3 Summary of ERP analysis effects of front and back space on attention

	Hand location	400-600 ms	600-800 ms
Lateralized Posterior electrodes P3/4, P7/8, O1/2	Hands near in front	n.s.	p<.001
	Hands far in front		
	Hands behind the back		
Lateralized Central Electrodes C3/4, CP5/6, T7/8	Hands near in front	p=.01	p=.001
	Hands far in front		
	Hands behind the back		
Lateralized Anterior electrodes F3/F4, F7/F8, FC5/Fc6	Hands near in front	p=.001	p=.001
	Hands far in front		
	Hands behind the back		

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. The lateralized cueing effects at each separate scalp area did not differ between hand locations.

4.3.2.2.2 Summary CT interval for Analysis 2

There was a significant ADAN starting at around 400 ms post cue onset and continuing until target onset at 800 ms. The clear lack of Space*Cue*Hemisphere interaction suggested this enhanced negativity for the contralateral over ipsilateral to target side hemisphere was the same in all three conditions. Thus, the ADAN was not demonstrated to be affected by the location of the hands in external space, whether in front or behind the participant (see Figure 4.6).

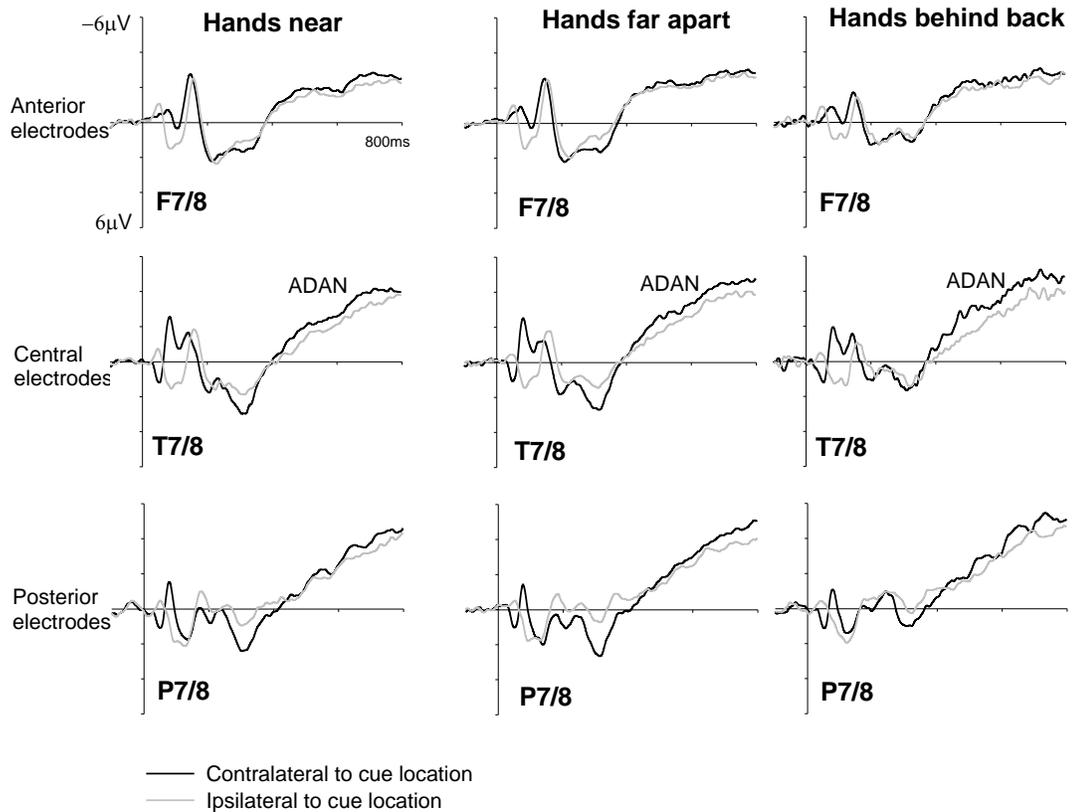


Figure 4.6 Cue-target ERPs when hands in front and behind the participant. Grand average ERPs in the 800 ms cue-target interval at anterior (top), central (middle), and posterior electrodes (bottom row) for when hands were held in front of the participant, either near or far apart (left and middle panel), or hands held behind their back (right panel). Black lines represent ERPs contralateral to cued hand and grey lines represent ERPs ipsilateral to the cued hand. At anterior and central electrodes there is sustained enhanced negativity contralateral compared to ipsilateral to the cue location. This difference, which starts at around 400 ms, reflects the presence of the anterior directed attention negativity (ADAN), (also marked out on the figure at electrodes T7/8), and there was no significant difference of these waveforms between the three hand locations.

4.3.2.2.3 Post-target ERP analysis

P45

There was a Cue*Hemisphere interaction ($F(1,13)=9.90$, $p=.008$, $\eta^2_p=.43$), however, follow-up analysis demonstrated no significant effect of Cue at either hemisphere (both F 's < 1.5).

N80

Analysis demonstrated a significant Cue*Hemisphere interaction ($F(1,13)=55.71$, $p<.001$, $\eta^2_p=.81$, and also a Cue*Electrode site*Hemisphere interaction ($F(2.6,34.3)=14.32$, $p<.001$, $\eta^2_p=.52$). Separate follow-up analyses for each hemisphere showed a significant effect of Cue for ipsilateral hemisphere ($F(1,13)=7.56$, $p=.017$, $\eta^2_p=.37$) with enhanced negative amplitude for valid over invalid trials. Contralateral hemisphere also showed a main effect of Cue ($F(1,13)=17.07$, $p=.001$, $\eta^2_p=.57$, and Cue*Electrode ($F(2.8,36.6)=10.49$, $p<.001$, $\eta^2_p=.45$) with enhanced negativity for invalid over valid trials. There was an attention effect in the N80 time window over both hemispheres, however, no interaction with Space suggesting where the hands were located in external space did not affect this attention modulation.

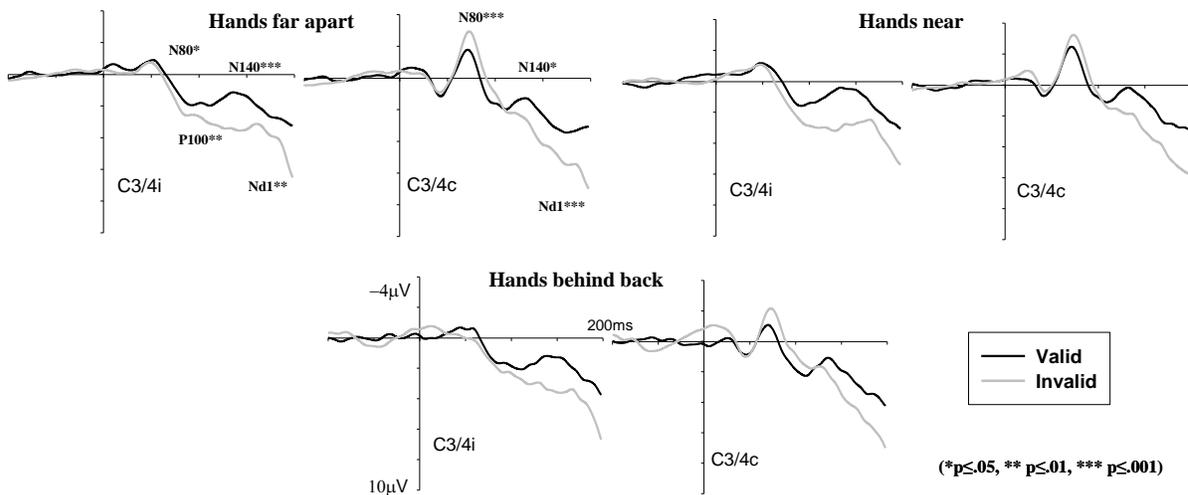


Figure 4.7 Post-target ERPs when hands in front and behind the participant. Grand average ERPs in the 200 ms time window following targets for valid (black line) and invalid trials (grey line). Attention modulations (valid versus invalid trials) did not differ depending upon whether the hands were located in front (either hands near or far apart) or behind the participants back. The significant attention modulated time windows (N80, P100, N140, & Nd1) for all three hand locations are highlighted in the top left graphs. For all three hand postures, the graph on the left (C3/4i) indicates ERPs ipsilateral and graphs on the right (C3/4c) contralateral to target location

P100

Analysis showed a Cue*Hemisphere interaction ($F(1,13)=27.92$, $p<.001$, $\eta^2_p=.68$, and also a Cue*Electrode site*Hemisphere interaction ($F(2.6,33.3)=8.23$, $p=.001$, $\eta^2_p=.39$).

Following the significant interaction separate follow-up analyses for each hemisphere revealed the attention effect to be over ipsilateral hemisphere only (Cue: $F(1,13)=16.94$, $p=.001$, $\eta^2_p=.57$).

N140

There was a significant Cue*Hemisphere interaction ($F(1,13)=12.97$, $p=.003$, $\eta^2_p=.50$, and also a main effect of Cue ($F(1,13)=12.82$, $p=.003$, $\eta^2_p=.50$), and Cue*Electrode site ($F(2.0,26.3)=4.30$, $p=.024$, $\eta^2_p=.25$), and Cue*Electrode site*Hemisphere ($F(2.7,35.5)=8.88$, $p<.001$, $\eta^2_p=.41$) interactions). Separate follow-up analyses for each hemisphere showed an effect of Cue over ipsilateral hemisphere ($F(1,13)=22.27$, $p<.001$, $\eta^2_p=.63$, and Cue*Electrode interaction ($F(2.0,25.5)=7.01$, $p=.004$, $\eta^2_p=.35$), and contralateral hemisphere ($F(1,13)=5.30$, $p=.039$, $\eta^2_p=.29$, and Cue*Electrode interaction ($F(2.4,30.7)=3.51$, $p=.036$, $\eta^2_p=.21$). Over both hemispheres the attention effect was driven by enhanced negative amplitude for valid over invalid trials.

Nd1

The analysis resulted in a significant main effect of Cue ($F(1,13)=9.02$, $p=.01$, $\eta^2_p=.41$, as well as Cue*Electrode site ($F(1.7,21.5)=5.14$, $p=.019$, $\eta^2_p=.28$), and cue*Electrode site*Hemisphere ($F(2.7,34.6)=3.32$, $p=.036$, $\eta^2_p=.20$) interactions. There was no Cue*Hemisphere interaction ($F<1$), nor any interactions of Cue with Space.

Table 4.4 *Post-target ERP attention effect of hands in front and back space*

Component	N80		P100		N140		Nd1
Laterality	Contra.	Ipsi.	Contra.	Ipsi.	Contra.	Ipsi.	Bilateral
Front far	p=.001	p=.017	n.s.	p=.001	p=.039	p<.001	p=.01
Front near							
Back							

Note: Summary of statistical results (probability levels (p) and non-significance (n.s.) stated) of post-target ERP attention effects (valid vs. invalid trials). The attention modulations did not differ between the four conditions.

4.3.2.2.4. Summary of post-target ERPs

The ERP analysis of somatosensory components in the post-target time window demonstrated significant attention modulations of the N80, P100, N140, and Nd1

components. However, no attention modulations interacted with hand position suggesting the post-target attention effects did not vary according to whether the hands are located in front or behind the participant.

4.4 Discussion

This study aimed to investigate how exogenous tactile attention is affected by posture. More specifically, to investigate whether the proximity of hands in external space (hands near or far apart) affected the processing differently if the tactile stimuli were presented to the palms versus the fingers. Moreover, we investigated whether exogenous attention to tactile stimuli differed depending on whether the hands were located in the space in front - which is typically mediated by vision - or behind or the participant's back. We used a cue-target paradigm eliciting IOR as a measure of exogenous tactile attention. The behavioural results demonstrated significant IOR (with faster RTs for invalid compared to valid trials) in all conditions. This exogenous effect did not differ depending on whether stimuli was presented to the fingers or palms. Further, no difference was found whether hands were placed close or far apart, and, the IOR effect was not affected by having the hands in the space in front or behind the participant. In other words, the behavioural data from this study suggests IOR is anchored in a somatotopic reference frame and different postures do not influence this effect. Analysis of the ERP data demonstrated an ADAN in the cue-target interval beginning at about 400 ms post cue onset for all conditions. From around 600 ms to target onset, analysis of the ADAN showed that when the distance between the hands was near or far apart there were no attention modulations for finger processing whilst having hands near or far apart influenced the attention effects for stimuli presented to the palms. More specifically, the ADAN was significantly larger in the condition when the hands were close together compared to far apart when stimuli were presented to the palms. However, this effect was only apparent at frontal electrodes and any difference in ADAN magnitude was absent at more central electrodes (this is discussed in more detail below). In the post-target interval there was an attention modulation with enhanced negativity for invalid over valid trials at the N80 component, possibly suggesting exogenous attention affects SI (see also studies presented in Chapters III, V, & VI, for similar results). Following this early effect there were attention modulations at the P100, N140 and Nd1 components as well. However, these attention effects did not differ whether the stimuli were presented to the fingers or palms, near or far, or hands in front or behind the participant.

All conditions in this study elicited IOR. These results support the view proposed by Röder et al. (2002) that IOR evokes a somatotopic frame of reference. Therefore, IOR is not affected where fingers, and this case also hands, are in space. It may be that the detection task, typically employed to elicit IOR, is not a complex enough task to require remapping of touch to external coordinates, as an external frame of reference is not necessarily required for the task. In other words, it is also possible that the simplicity of the detection task resulted in the absence of any posture effects of attention. There is some evidence suggesting task difficulty is related to whether remapping touch to external reference frame occurs. For example, in a simultaneous judgement task, Axelrod, Thompson, and Cohen (1968) found having hands near or far apart, as in the present study, had no effect on tactile perception in terms of RTs. In contrast, Shore et al. (2005) used a very similar posture manipulation with hands near and far apart but used a TOJ paradigm. They found a significant advantage of TOJ in the condition when hands were far compared to close together. Shore and colleagues concluded that a likely reason that they found an effect of posture whilst Axelrod et al. (1968) did not in their simultaneous judgement task, was due to that TOJ task require more information processing (not only judge that there were two stimuli but also in what order they appeared), and that spatial attention is required in TOJ tasks. In other words, the location of stimuli plays a particular role in TOJ tasks which may contrast simple detection task. This may underlie why TOJ task reveal more subtle effects of posture.

As mentioned, the present task was relatively simple whereby the participants only detected a stimulus at one of two possible locations. This likely required very little information processing of the stimuli, and maybe no benefit of remapping touch into external space. Future ways of addressing the issue of whether specifically IOR or the simplicity of a detection task underlies the lack of postural effect could be to employ a more complex discrimination task which may require more in depth processing of stimuli and require more attentional resources. This dissociation would be interesting to establish as IOR is a phenomena which is part of the exogenous orienting framework. If IOR is also not affected by posture in more demanding discrimination task, then it provides further empirical support that exogenous orienting and IOR employ a somatotopic reference frame whilst endogenous attention remaps touch into external space (e.g., Eimer et al., 2004). In tactile discrimination tasks, the timing of cue-target interval is of great importance as IOR occurs only at SOAs greater than approximately 1000 ms, as shorter SOAs lead to facilitation of

validly cued targets (Miles et al., 2008). By using a discrimination task with variable SOAs one could investigate whether the mechanisms of exogenous orienting as a whole uses only a somatotopic frame of reference or whether the remapping does not occur for IOR and particularly simple tasks.

An *a priori* hypothesis for this study was that holding hands close compared to far would affect tactile processing when stimuli was presented to the palms. This was based upon the findings from Haggard et al. (2006) who concluded that stimuli to the hands are remapped into external space whilst the fingers are not. The discrepancy of results in the present study may again be due to the different tasks used. Haggard and colleagues employed an identification task - judging which hand or finger had been touched - which likely requires a higher level of information processing leading to remapping effects in their study and not the present. Moreover, the present findings suggest that merely presenting stimuli to a location on the hand other than the fingers is not enough to evoke remapping of touch into external coordinates.

Evidence of any postural effects was not apparent from the behavioural data in the present study. Correspondingly, the ERP patterns were remarkably similar across all conditions suggesting remapping to external space did not occur differently across conditions. It would seem likely that if posture had an effect upon tactile processing, then this would be manifested to some degree in the ERP trace. The cue-target interval demonstrated an ADAN, enhanced negativity for the hemisphere contralateral to stimulated hand, in all different postures and regardless if the stimuli were presented to the palms or fingers. The only observable effect of posture in this cue-target interval in the present study was at frontal electrodes. There was no difference in the lateralized cue-target effects for fingers depending on distance apart. When the stimuli were presented to the palms, the ADAN was significantly larger when hands were held close together compared to far apart. This effect follows the opposite direction to what was initially predicted, as previous research has demonstrated larger lateralized differences to be coupled with having the hands far apart (Eimer et al., 2004). That is, the further away the hands are apart, the larger the lateralized ERP effect is. However, it should be noted that the ADAN waveform over more central electrodes in the same time windows were no different across any conditions (see Table 4.1 & Figure 4.3). Moreover, when hands were far apart and stimuli were presented to the palms, then there was an approaching significant ADAN ($p=.073$) in the 400-600 ms time

window, and highly significant ADAN in the later times window ($p=.009$). Based on previous research and the mix of results in the present study, any clear conclusions regarding the larger ADAN when palms were near compared to far are difficult to draw.

The LDAP is notably the component in the cue-target interval which has been reported to reflect an external frame of reference (although the exact functional significance is yet to be established) (e.g., Eimer, Forster, et al., 2003). In the present study no LDAP was observed. Previous studies have shown a lack of LDAP when studying postural changes but in conditions where the participant had no visual input of the surroundings (Eardley & van Velzen, 2011). In the present study participants' had their hands covered but there was sufficient light to provide information about the ambient space. This study did not set out to manipulate the LDAP. Therefore, it is not clear whether the absence of an LDAP was due to the posture manipulations used, and/or related to the lack of direct visual information of the hands and the surrounding space, and/or due to the exogenous nature of the present study. It is difficult to establish why there was no LDAP, however, the lack of this component and that the LDAP is suggested to reflect an external frame of reference is nonetheless consistent with the theory that IOR is anchored in a somatotopic frame of reference.

Posture has shown to affect attention modulations in previous endogenous attention studies. When investigating the effects of attention when hands were in a crossed versus uncrossed position, effects have been modulated by posture in the post-target time interval at the P100 component (Röder et al., 2008), and the N140 and following late negativity (Eardley & van Velzen, 2011; Röder et al., 2008). Moreover, in a more similar posture manipulation with hands near or far apart, Eimer et al. (2004) found N140 amplitudes to be enhanced for attended over unattended targets. This effect was more pronounced when hands were far apart. The present study demonstrated an attention effect at the N140 and also Nd1 components suggesting the secondary somatosensory cortex and frontal areas were involved in tactile processing (Hari et al., 1984; Mima et al., 1998). Crucially, these attention modulations were not affected by varying posture. An argument could be that the discrepancies between the present results and that of Eimer and colleagues for the N140 component may be due to a lack of power. However, the attention*posture effect seen in Eimer et al's (2004) study was relatively large ($F>12$). Large effects at the N140 were

shown in the present study which suggests a lack of power may not explain the non-significant results.

The present results also showed earlier effects of attention at the N80 component with enhanced negativity for invalid over valid trials. The effect at the N80 component, thought to originate from the SI (Allison et al., 1992, 1989; Forss & Jousmäki, 1998; Hari & Forss, 1999; Hari et al., 1984; Inui et al., 2004; Mima et al., 1998), indicated that exogenous attention modulated even this early stage of the tactile processing. Similarly to the P100 and N140 there was no difference in attention effect at the N80 time window as a function of posture. The ERP pattern elicited by targets demonstrates that several components were modulated by exogenous attention (N80, P100, N140 and Nd). Components previously reported to be affected by an external frame of reference (the P100, N140, and late negativity) were also observed in the present study. This suggests these components may be modulated by exogenous attention even though no external spatial reference is required.

Taken together, the present study demonstrated that posture does not affect behavioural or ERP effects of exogenous attention. This indicates that exogenous tactile attention and/or IOR uses a somatotopic frame of reference to localize tactile stimuli. It may be plausible that any effect of posture may have been too subtle to be observed in the behavioural results. However, it seems likely that if touch was remapped into external coordinates automatically, then this would be evident in the ERP pattern. A recent paper concluded that “A number of behavioural and electrophysiological studies in humans had previously suggested that touch is remapped not only when the context calls for it (as in crossmodal integration). Recoding from skin to space rather seems to be a default process, providing the brain with external spatial coordinates for any touch we perceive [9-13]” (p. 605, Heed, 2010). In contrast, the present study provides robust findings that re-mapping of touch does not occur automatically to external co-ordinates.

CHAPTER V

Disentangling neural correlates of endogenous and exogenous attention in touch

Three tasks were conducted in order to compare endogenous and exogenous ERP and behavioural effects. The exogenous task demonstrated IOR. The endogenous tasks resulted in facilitation of attended target. This was true when targets predicted the cue to appear at the same location (endogenous predictive task) as well as when the cue predicted the target to appear to the opposite location (endogenous counter-predictive task). Analysis of the cue-target interval showed lateralized cues induced an exogenous ADAN. This ADAN effect was further enhanced by endogenously orienting attention to the cued location in the endogenous predictive task. In the endogenous counter-predictive task, when the cue location and attended location were in conflict, no ADAN was present. Instead, an LDAP was found in the counter-predictive task suggesting an external frame of reference was used when shifting attention from one hand to the other. Analysis of the post-target interval demonstrated an N80 attention modulation in all three tasks. This effect likely reflecting exogenous attentional processing due to lateralized cues. The varying topography of the N80 modulation in the tasks demonstrated endogenous attention can modulate the N80 effect. The two endogenous orienting tasks showed attention modulation at the N140 and Nd components. Importantly, these were significantly correlated with endogenous behavioural effects indicating a direct link between behavioural and ERP attention effects.

5.1 Introduction

Attention mechanisms in our brain allow us to selectively process relevant information in our environment. Generally, research distinguishes between two ways in which attention is directed, namely, voluntary and automatic shifts of attention. Voluntary, or *endogenous* orienting are internally generated shifts of attention requiring effortful orienting processes, such as reading a book, or thinking about your left toe. Automatic, or *exogenous* attention, is when our attention is triggered by external stimuli, such as a flash of light or a tap on our shoulder (see e.g., Egeth & Yantis, 1997). The most common method of investigating these two types of orienting is using a cue-target paradigm first developed by Posner (1978). In an endogenous version of this paradigm a cue informs the participant of the most likely target location and after a variable stimulus onset asynchrony (SOA) a target appears at the expected location predicted by the cue (typically 70 or 80% likelihood) or at the unexpected location (30-20% likelihood). In an exogenous task the cue is presented peripherally and

does not indicate where the up-coming target will appear but only act as a distractor appearing at the same or different location to the target. Behaviourally there are differences between the two modes of orienting whereby facilitation of response times (RTs) in endogenous tasks occurs for targets appearing at expected/attended compared to unattended locations in vision (e.g., Müller & Rabbitt, 1989; Posner, Snyder, & Davidson, 1980), audition (e.g., Quinlan & Bailey, 1995; Robin & Rizzo, 1992), and tactile modality (e.g., Forster & Eimer, 2005). On the other hand, in exogenous orienting, responses to targets which appear at the same location as a cue are inhibited compared to RTs for targets at an un-cued location. This phenomena is known as inhibition of return and has been demonstrated within the visual (if cue-target interval is larger than approximately 250 ms; see Klein, 2000, for review), auditory (Schmidt, 1996; Tassinari & Campara, 1996), tactile modality (Cohen, Bolanowski, & Verrillo, 2005; Lloyd, Bolanowski, Howard, & McGlone, 1999; Röder, Spence, & Rösler, 2000; Röder, Spence, & Rösler, 2002) and between all modality pairings (Ferris, Sarter, & Arbor, 2008; Roggeveen, Prime, & Ward, 2005; Spence, Pavani, & Driver, 2000; Spence, Lloyd, McGlone, Nicholls, & Driver, 2000).

Neuroimaging studies have highlighted different networks related to endogenous and exogenous attention in vision. A set of areas around the posterior parietal cortex and precentral sulcus collectively known as the dorsal fronto-parietal (dFP) network has been associated with endogenously shifting and maintaining attention in the cue-target interval (e.g., Kelley et al., 2008). Visual attention studies have suggested unexpected targets to activate a ventral fronto- parietal network (vFP; such as inferior parietal cortex (temporal parietal junction; TPJ) and inferior pre-motor regions (inferior frontal gyrus (IFG) and frontal operculum) (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000). Although the vFP network is sometimes referred in relation to exogenous attention, it is only activated in response to unexpected (invalid) targets in an endogenous task whilst the more conventional exogenous cueing paradigm (explained above) where cues are non-informative do not activate the vFP system (Kincade, Abrams, Astafiev, Shulman, & Corbetta, 2005). However, Mayer, Dorflinger, Rao, and Seidenberg, (2004) demonstrated that although exogenous and endogenous attention activate separate neural networks, endogenous facilitation and IOR appear to use largely the same neural networks to mediate the two processes.

Electro-encephalogram (EEG) and event related potentials (ERPs) have also been used to investigate the neural basis of the two modes of orienting and studies of endogenous orienting have further supported the conclusion that the activity in fronto-parietal regions are part of an attention network. In the cue-target interval, lateralized ERP differences between waveforms contralateral and ipsilateral to the attended side are thought to reflect the fronto-parietal attention network. An anterior directing attention negativity (ADAN), starting at around 300-500 ms after cue onset, with enhanced negativity over frontal electrodes contralateral to the attended side has been demonstrated in a number of visual (e.g., Hopfinger & Mangun, 2000), auditory (e.g., Green & McDonald, 2006) and tactile studies (Forster et al., 2009) and suggested to reflect supramodal attention mechanism in the frontal areas (Eimer, van Velzen, & Driver, 2002; Seiss, Gherri, Eardley, & Eimer, 2007). Following the ADAN, the so called late directing attention positivity (LDAP) originating from occipitotemporal cortex (Mathews, Dean, & Sterr, 2006), has been suggested to reflect attentional orienting mediated by external visual space (van Velzen, Eardley, Forster, & Eimer, 2006). However, no studies (other than the studies presented in this thesis), to my knowledge, have investigated the ERP effects during the cue-target in exogenous attention and/or in response to IOR.

More commonly reported attention modulation in ERP studies are those present in the time window post-target onset and a handful of these studies have investigated endogenous *tactile* attention using ERPs. Studies employing sustained attention paradigms, where the subject attends to a particular location (e.g. the hand) throughout an experimental block, have shown attention directed to or away from the attended hand modulates early and mid-latency somatosensory ERPs with enhanced amplitude for attended compared to unattended waveforms. The early N80 component (a negative peak at around 80 ms post-target onset), has been suggested to originate from primary somatosensory cortex contralateral to the stimuli (Hari et al., 1984; Inui et al., 2004; Mima et al., 1998) and only a few studies have demonstrated an attention modulation at this components with enhanced negativity for attended compared to unattended stimuli (Eimer & Forster, 2003a; Michie et al., 1987; Schubert, Ritter, Wu, & Franklin, 2008). Following on from the N80 the P100 component has also been modulated by attention in sustained (Zopf, Giabbiconi, Gruber, & Müller, 2004) also transient paradigms (Eimer & Forster, 2003; Zopf, Giabbiconi, Gruber, & Müller, 2004) with enhanced positivity for attended compared to unattended locations. Moreover, the mid latency N140 component has also shown to be affected by endogenous

attention with enhanced negativity for attended versus unattended targets (Eimer & Forster, 2003a; Forster & Eimer, 2004; Zopf et al., 2004). Importantly, enhanced amplitude for attended versus unattended targets and facilitation of RTs at attended compared to unattended locations in the aforementioned studies is consistent with the theory that behavioural speed and accuracy are, at least in part, caused by enhanced sensory processing (Luck et al., 2000). More specifically, Luck and colleagues, based on visual attention findings, suggested that the P1 amplitude is usually directly linked to behavioural performance. Moreover, the P1 and N1 have been suggested to reflect mechanisms of selective attention, whereby the ERPs show enhanced amplitude for attended compared to unattended stimuli (see Hillyard, Vogel, and Luck, 1998, for a review). That is, attending to a spatial location increases the neuronal sensitivity for stimuli appearing at that location. Whilst the N1 has been proposed to reflect enhancement for attended stimuli, the P1 amplitude has been suggested to reflect suppression of irrelevant stimuli (Talsma et al., 2005). Although the conclusions drawn from visual research should only with caution be extended to tactile ERP findings, the likely tactile ERP component linked to behaviour, and IOR, would be the P100.

Exogenous attention has been far less researched, especially in touch where no previous study has investigated at the neural correlates of IOR. Within visual attention research, ERP studies have investigated the time course of IOR but painted a slightly inconsistent picture. The main component which has been linked to IOR in vision is the P1 with a smaller positive amplitude for valid compared to invalid trials (McDonald et al., 1999; Prime & Ward, 2004, 2006; Tian & Yao, 2008; Wascher & Tipper, 2004). As IOR shows the opposite behavioural effect to endogenous facilitation, whereby a previously cued location is inhibited rather than facilitated, these studies are in line with Luck et al.'s (2000) suggestion that enhanced amplitude at the P1 is related to behavioural effects. However, other studies have demonstrated a reduction in amplitude on validly cued trials without a behavioural IOR effect (Chica & Lupiáñez, 2009; Doallo et al., 2004; Hopfinger & Mangun, 1998) or a significant IOR effect but no P1 modulation (Prime & Ward, 2006).

In a cue-target paradigm, endogenous attention in vision is typically induced by a central symbolic cue (e.g. an arrow) and exogenous attention employ non-predictive peripheral cues. Whilst non-informative peripheral cues in exogenous tactile attention are easily applied, central cues in touch pose a more practical problem as where on the body midline

to attach stimulators without inducing bone conductance (although see Forster & Gillmeister, 2011, for tactile cues on the neck). Peripheral tactile cues which are informative (where the cue predicts target most likely to appear at the same side as the cue) have been used and shown to facilitate RTs for expected compared to unexpected locations (Cohen et al., 2005; Lloyd et al., 1999). However, a problem of using predictive peripheral cues is that they may elicit both endogenous and exogenous shifts of spatial attention, and the contribution of each orienting mechanism is hard to separate and pin to any observed behavioural effects. However, isolating the orienting processes may be achieved by using also a counter-predictive condition where the cue indicates most likely target location to be at the opposite side (Chica & Lupiáñez, 2009; Chica, Sanabria, Lupiáñez, & Spence, 2007; Posner, Cohen, & Rafal, 1982). Chica et al. (2007) used such a paradigm with tactile cues and targets (experiment 1) and found RTs to expected targets were faster compared to unexpected target. Moreover they found no differences between attention effects between the predictive and counter-predictive tasks suggesting IOR did not influence response times in their endogenous tasks. In a more recent ERP study, Chica and Lupiáñez (2009) used a similar paradigm. However, in this study the authors used visual cues and targets and found an attention effect in only the counter-predictive detection tasks whilst not in the predictive detection task. They concluded that the lack of behavioural endogenous attention effect in the predictive task was due to the influence of IOR acting as an inhibitory mechanism for the endogenous predictive targets. Although they did not behaviourally demonstrate IOR, they concluded that their P1 attention modulation was an indication of IOR.

In the present study we aimed to investigate the neural correlates of IOR and endogenous spatial attention in touch. We employed two endogenous tasks, similar to the above mentioned studies by Chica and colleagues, with expected targets at the same location as the cue (endogenous predictive task) and the expected target at the opposite side to the cue (endogenous counter-predictive task). In addition to previous studies (Chica & Lupiáñez, 2009; Chica, Sanabria, Lupiáñez, & Spence, 2007) we included an exogenous task with non-predictive cues to also incorporate a condition which behaviourally elicited IOR. Behaviourally we predicted IOR in the exogenous task whilst facilitation of RTs at expected compared to unexpected locations in the two endogenous tasks. Moreover, if IOR has an effect upon RTs in the endogenous tasks then we would predict RTs for stimuli at expected locations in the counter-predictive task to be faster compared to the RTs for

stimuli at expected locations in the predictive condition. That is, in the endogenous predictive condition the cue and target are presented to the same location which may result in IOR influences, even though the task is endogenous (see Chica & Lupiáñez, 2009, for such effect). Put differently, endogenous facilitation and exogenous IOR may be in conflict for validly cued targets. In the endogenous counter-predictive condition facilitation is expected due to the endogenous orienting. In addition, no IOR would be present for expected targets as the cue and target would appear at opposite locations.

ERPs were concurrently recorded and we predicted the endogenous predictive task would demonstrate an ADAN in the cue-target interval. This would be demonstrated as enhanced negativity for electrodes contralateral to attended side, indicating activation of the fronto-parietal attention network. As attention needed to be shifted from one side to the other in the endogenous counter-predictive tasks we made no prediction regarding the ERP waveforms in the cue-target interval. In other words, we had no prediction regarding a presence of an ADAN or LDAP component in the endogenous counter-predictive task. The exogenous task in the present study was a replication of the simple detection task presented in Chapter III. We therefore predicted an ADAN waveform in this task with enhanced negativity for the hemisphere contralateral compared to ipsilateral to the stimulated hand.

After target onset we aimed to investigate a series of early- and mid-latency (N80, P100, & N140) somatosensory ERPs as well as later stages of processing (Nd) which have been shown to be modulated by attention to tactile targets. In the endogenous tasks we predicted the P100, N140, and Nd to show enhanced waveforms for attended stimuli reflecting areas, such as secondary somatosensory cortex, involvement in attention. By comparing ERP attention effects between the endogenous predictive task and the exogenous task we aimed to separate attention modulations related to two behaviourally opposite effects. Moreover, comparing the endogenous predictive and counter-predictive tasks we aimed to disentangle endogenous attention effects from the stimulus driven modulations. Furthermore, we aimed to correlate any ERP attention modulations with behavioural effects in order to better understand the relationship between brain and behaviour.

5.2 Methods

5.2.1 Participants

12 paid participants (10 right-handed) took part in this study and all gave written informed consent prior to their participation. There were seven males and five females with a mean age of 25.6 years (range: 20-37 years).

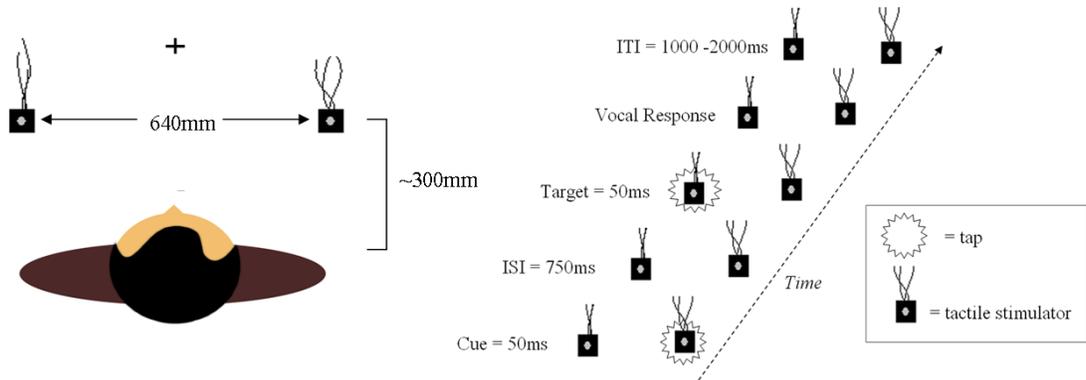


Figure 5.1 Experimental set-up and stimuli presentation. *Left:* Schematic view of the experimental set-up. The two boxes in front of subject represent two tactile stimulators attached to the index finger of each hand. *Right.* Schematic representation of events in a trial where cue and target are presented at opposite sides. In the exogenous task the schematic view represents an invalid trial, in the endogenous predictive task an unexpected trial, and in the endogenous counter-predictive the trial would be expected.

5.2.2 Stimuli and apparatus

Stimuli and apparatus were identical in the exogenous, endogenous predictive and endogenous counter-predictive tasks. Participants sat in a dimly lit, soundproofed chamber. 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 5.1 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.

5.2.3 Design and Procedure

The experiment consisted of 13 blocks, 5 for each of the two endogenous tasks and 3 blocks in the exogenous task and the 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. Thus, disregarding filler and catch trials, the weighting between expected and unexpected trials was 80% vs. 20%. The trials were randomly presented within each block. 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 valid (cue and target appeared at the same location) and invalid trials (cue and target appeared at opposite location) were equally weighted, 50 valid and 50 invalid trials in each block. As in the other two tasks there were 8 catch trials and 4 'fast filler trials'.

The stimuli presentation procedure for each trial was the same for all three tasks (see Figure 5. 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 response times. In the exogenous task the participant was informed that the cue would not predict the target location and therefore to ignore the cue completely.

5.2.4 Behavioural analysis

Behavioural data were submitted to a 2x3 repeated-measures ANOVA with the factors Task (endogenous predictive, exogenous, endogenous counter-predictive), and Cue (valid/expected, invalid/unexpected). A Task*Cue interaction was followed up by separate analysis for each task. To compare facilitation and inhibition in the different tasks the three condition hypothesized to be fastest were subjected to an ANOVA with factor Cue (endogenous predictive expected, exogenous invalid, endogenous counter-predictive expected). Similarly the hypothesised three slowest conditions were subjected to a repeated-measures ANOVA with factor Cue (endogenous predictive unexpected, exogenous valid, endogenous counter-predictive unexpected). Wherever the ANOVA assumption of Sphericity was violated, Greenhouse-Geisser adjusted degrees of freedom and probability levels were reported. The same adjustments were also made for the subsequent ERP analysis. Trials with response times less than 100 ms were excluded from analysis, resulting in removal of 5% of trials in the endogenous predictive, 3.7% exogenous, 6.0% in the endogenous counter-predictive task.

5.2.5 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 and 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. 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 (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 except O1/2 in post-target interval) were removed prior to EEG averaging. Additionally, the residual HEOG deflections were analysed to make sure no individual had a difference

which exceeded 4 μ 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 valid and 128 invalid trials per participants.

For cue-target interval analysis ERPs were averaged separately for Task (endogenous predictive, exogenous, and endogenous counter-predictive) and Cue (cued left and cued right) and analyzed 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). The selection of electrode in the analysis was based on sites commonly used to investigate lateralized cue activity associated with the fronto-parietal attention network (see e.g. Gherri & 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), and these were subjected to separate repeated-measures ANOVAs with factors Task (endogenous predictive, exogenous, endogenous counter-predictive), Cue (cued left, cued right), Hemisphere (left, right) 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). To clarify the factor Cue; in the endogenous predictive task the ‘cued left’ refers to attention directed to the left side, which is analogous with cue location at the left. In the exogenous task the cued left would refer to cue location at the left hand. Importantly, in the endogenous counter-predictive task cued left refers to physical stimulation to the right but attention directed to the left side.

For post-target ERP analysis epochs were averaged separately for task (endogenous predictive, exogenous, and endogenous counter-predictive) and cue type (valid/expected, invalid/unexpected). ERP mean amplitudes were computed for measurement windows centred on the peak latencies 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. A repeated-measures ANOVA was

conducted to compare attentional modulations with the factors Task (endogenous predictive, exogenous, endogenous counter-predictive), Cue (valid/expected, invalid/unexpected), Electrode Site (CP1/2, CP5/6, C3/4, FC1/2, FC5/6, T7/8) and Hemisphere (ipsilateral, contralateral). To clarify the levels and terminology of the factor Cue; in the exogenous task valid refers to cue and target appearing at the same side (and invalid; cue and target appearing at opposite sides). In the endogenous predictive task the expected refers to attention directed to the same side as the cue (e.g., a left cue indicated attention expected to the left) and unexpected refers to attention directed to the opposite side to the cue. In the endogenous counter-predictive task the expected refers to cue and target at opposite sides (e.g., a left cue indicated attention directed to the right). The electrode selection for post-target analysis was based on electrodes close to and around somatosensory cortex where tactile ERPs are found and attention effects on tactile processing were expected.

Any significant attention modulations in the post-target interval were correlated with behavioural RT effects to further investigate any relationship between the two measures. The ERP effect was the average amplitude difference between valid versus invalid trials at each component. The RT effect was similarly calculated as a difference in ms between valid and invalid 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.

5.3 Results

5.3.1 Behavioural performance

Analysis of participants' RTs to target stimuli showed there was a significant Task*Cue interaction ($F(2,22)=15.00$, $p<.001$, $\eta^2_p=.58$) indicating RTs for expected and unexpected trials were not the same across the three tasks (there was also a significant effect of Cue ($F(1,11)=46.51$, $p<.001$, $\eta^2_p=.81$) with overall faster RTs for expected compared to unexpected trials). Follow-up paired samples t-test analyses for the factor Cue was conducted for each task separately. For the endogenous predictive task, RTs to expected targets (315.32 ms) were significantly faster compared to unexpected (439.17ms) targets showing endogenous orienting facilitated RTs at the attended location ($t(11)= 4.26$, $p=.001$, $\eta^2_p=.62$). Analysis of the exogenous task demonstrated IOR as RTs for valid trials

(338.71ms) were significantly slower compared to invalid trial (319.06 ms) ($t(11) = -2.37$, $p = .037$, $\eta^2_p = .34$). Analysis of the endogenous counter-predictive task showed that RTs to expected targets (285.78 ms) were significantly faster compared to unexpected targets (450.93 ms) ($t(11) = 5.64$, $p < .001$, $\eta^2_p = .74$) (see Figure 5.2).

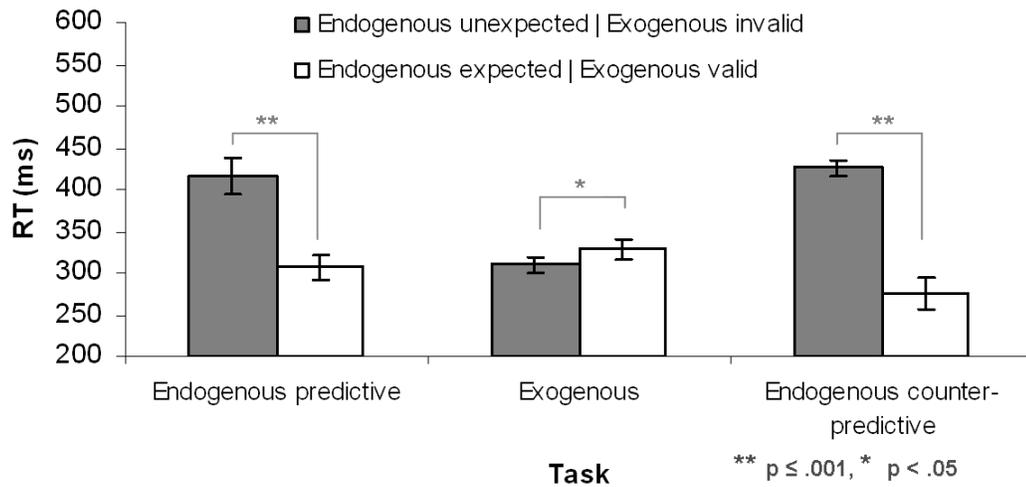


Figure 5.2 Behavioural results. Average response times (RTs in ms) and standard error bars displayed for each task. In the endogenous tasks the grey bars represent RTs for unexpected trials and white bars represent trials where targets appeared at the expected location. In both endogenous tasks, attention significantly facilitated RTs at expected locations. In the exogenous task the grey bar represents average RTs on invalid trials where cue and target appeared at different sides and the white bar represents valid trials (cue and target appeared at the same location). The exogenous task showed IOR as valid trials were significant slower compared to invalid trials.

To explore the nature of facilitation and inhibition, and if these are separate or competing mechanisms, further analyses of the RTs were conducted. To compare the hypothesized different forms of inhibition the three conditions (see introduction) to show the slowest RTs in each task were compared (i.e. exogenous valid, endogenous predictive unexpected, and endogenous counter-predictive unexpected condition). Overall the three conditions were significantly different ($F(1.3,14.4) = 4.34$, $p = .047$, $\eta^2_p = .28$). More specifically, exogenous valid trials (338.71ms) were significantly faster ($p < .001$) compared to unexpected endogenous counter-predictive trials (450.93ms) and close to significantly faster ($p = .075$) compared to unexpected endogenous predictive trials (439.17ms). It can be concluded that automatic inhibition does not inhibit RTs as much as in voluntary inhibition. Comparison of the three conditions hypothesised to show fastest RTs within their respective tasks were

compared to explore the effects facilitation showed no significant difference⁷. In particular, the planned comparison between expected trials in the two endogenous tasks showed no significant difference ($p=.40$). This suggested IOR may not affect and inhibit endogenous facilitation, even when informative cues are presented laterally. See also Figure 5.9 for ERP waveforms contrasted in this way.

5.3.2 ERP results

5.3.2.1 Effects of attentional orienting on cue-target interval ERPs

400-600 ms cue-target interval analyses

The cue-target interval was initially analysed with all three tasks together to explore task differences and to further see the effects of cue-target orienting, each task was also analysed separately. Cue*Hemisphere interactions represented differences between cue-target ERPs contralateral and ipsilateral to the cued location/side. To conclude what component (e.g., ADAN or LDAP) a Cue*Hemisphere interaction represented, the ERP waveforms (Figure 5.3) and topographical maps (Figure 5.4) were considered. ADAN waveforms were expected to be present over fronto-parietal areas with enhanced negativity for cues at contralateral compared to ipsilateral side. An LDAP would be expected over posterior areas with enhanced positivity for cues at contralateral compared to ipsilateral hemisphere.

In the 400-600 ms time window there was a significant Task*Cue*Hemisphere ($F(2,22)=11.40$, $p<.001$, $\eta^2_p=.51$) for central electrodes (as well as Cue*Hemisphere $F(1,11)=13.42$, $p=.004$, $\eta^2_p=.55$, Cue*Site*Hemisphere, $F(2,22)=11.70$, $p<.001$, $\eta^2_p=.52$, and Task*Cue*Site*Hemisphere, $F(4,44)=4.74$, $p=.003$, $\eta^2_p=.30$ interactions) and anterior electrodes ($F(2,22)=15.32$, $p<.001$, $\eta^2_p=.58$) indicating the difference between cue-target ERPs contralateral and ipsilateral to the cued location/side were different in the three tasks, thus differences of the ADAN between tasks. At the posterior electrodes there were no significant Task*Cue*Hemisphere or Cue*Hemisphere interactions suggesting no attention modulation at posterior electrodes in the 400-600 ms cue-target interval. Therefore, only central and anterior electrode sites were analysed separately for each task.

⁷ The overall ANOVA comparing three fastest conditions showed no significant difference ($F(1.2,13.5)=0.71$, $p=.41$, $\eta^2_p=.28$), however, the post hoc analysis suggested endogenous counter-predictive expected trials (285.78ms, $SD=20.13$) were significantly faster ($p=.027$) compared to exogenous invalid trials.

Analysis of endogenous predictive tasks showed a significant Cue*Hemisphere interaction ($F(1,11)=16.942, p=.002, \eta^2_p=.61$; as well as a Electrode site*Cue*Hemisphere $F(2,22)=13.67, p<.001, \eta^2_p=.55$ interaction) at central electrodes and also anterior electrodes (Cue*Hemisphere $F(1,11)=50.769, p<.001, \eta^2_p=.82$; as well as a Electrode site*Cue*Hemisphere $F(2,22)=6.736, p<.001, \eta^2_p=.38$ interaction) suggesting a central and anterior ADAN starting at 400 ms in the endogenous predictive task.

Analysis of the 400-600 ms time window of the endogenous counter-predictive task showed no significant interactions at any electrodes including Cue and Hemisphere.

For the exogenous task there was (similarly to the endogenous predictive task) a Cue*Hemisphere interaction at central ($F(1,11)=9.364, p=.011, \eta^2_p=.46$) and anterior electrodes (Cue*Hemisphere $F(1,11)=8.951, p=.012, \eta^2_p=.46$) indicating an ADAN at the 400-600 ms cue-target interval.

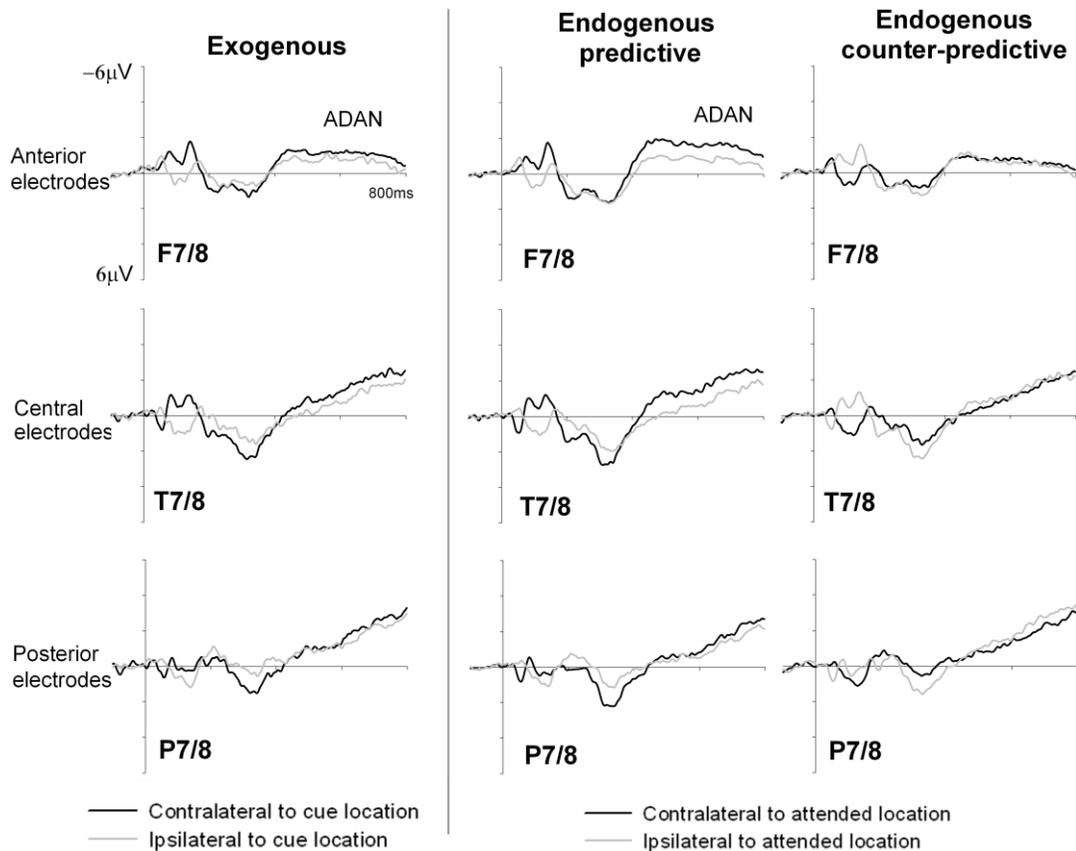


Figure 5.3 Cue-target ERP waveforms. Grand averaged ERPs in the 800 ms cue-target interval at anterior, central, and posterior electrodes for the exogenous, endogenous predictive, and endogenous counter-predictive tasks. In the exogenous task (left panel) black lines represents ERPs contralateral to cue location and grey lines represent ERPs ipsilateral to cue location side. At anterior and central electrodes there is sustained enhanced negativity contralateral compared to ipsilateral to cue the location. This difference, which starts at around 400 ms, reflects the presence of the anterior directed attention negativity (ADAN), also marked out on the figure and topographically represented in Figure 5.4. For the two endogenous tasks (middle and right panel) black lines represent ERPs contralateral to the side attention directed towards (as indicated by the cue) and grey lines represent cue-target interval ERPs ipsilateral to the attended side. In the endogenous predictive task the attended side and cue location were the same and similarly to the exogenous task, an ADAN is present over anterior and central electrodes⁸. In the endogenous counter-predictive task no ADAN is present. However, at posterior electrodes

⁸ The cue-target ERP waveforms in the exogenous and endogenous predictive tasks were also compared against each other which showed the ADAN was significantly larger (represented by a significant Task*Cue*Hemisphere interaction) in the endogenous compared to the exogenous task at anterior electrodes for both 400-600 ms ($F(1,11)=10.768, p=.007$) and 600-800 ms time windows ($F(1,11)=8.017, p=.016$).

there was enhanced positivity for trials contralateral to attended side at the later 600-800 ms time window also known as late directing attention positivity (LDAP). The absence of an ADAN and presence of posterior activity in the endogenous counter-predictive task is also shown in the topographical maps in Figure 5.4.

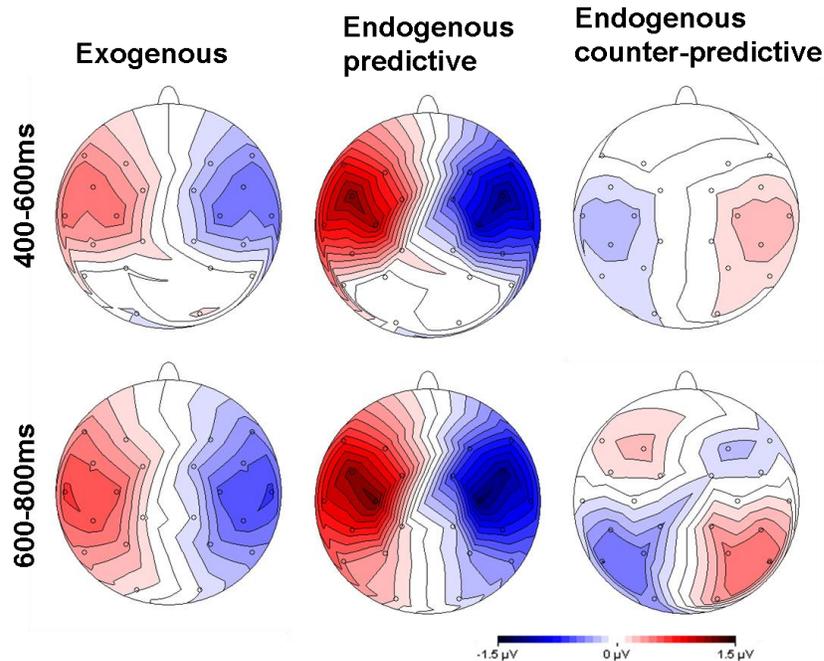


Figure 5.4 Scalp distribution of cue-target interval data for the exogenous (left), endogenous predictive (middle), and endogenous counter-predictive task (right) in the 400-600 ms (top) and 600-800 ms (bottom) time window post cue onset. Maps represent differences between brain activity observed over hemispheres ipsilateral and contralateral to the cued side. The obtained difference waveforms were mirrored to obtain symmetrical but inverse amplitude values for both hemispheres. That is, the same effect is presented over both left and right hemispheres in the figure. Each contour line represents 0.05µV changes (amplitude range between -1.0 and 1.0 µV). The exogenous and endogenous predictive tasks demonstrated an ADAN waveform at central and anterior electrodes. The endogenous counter-predictive task demonstrated an LDAP with reversed polarity of the effect at posterior electrodes.

600-800 ms cue-target interval analyses

Overall analysis of the 600-800ms interval showed a significant Task*Cue*Hemisphere ($F(2,22)=12.13$, $p<.001$, $\eta^2_p=.52$) interaction for posterior electrodes (and also a Task*Cue*Electrode site*Hemisphere interaction $F(4,44)=3.70$, $p=.011$, $\eta^2_p=.25$) as well as at central electrodes (Task*Cue*Hemisphere $F(2,22)=16.56$, $p<.001$, $\eta^2_p=.60$; as well as

Cue*Hemisphere $F(1,11)=27.67$, $p<.001$, $\eta^2_p=.72$, Cue* Electrode site*Hemisphere $F(2,22)=10.79$, $p=.001$, $\eta^2_p=.50$, and Task*Cue* Electrode site*Hemisphere $F(4,44)=4.80$, $p=.003$, $\eta^2_p=.30$ interactions) and also at anterior electrodes (Task*Cue*Hemisphere $F(2,22)=8.06$, $p=.002$, $\eta^2_p=.42$, Cue*Hemisphere $F(1,11)=54.53$, $p<.001$, $\eta^2_p=.83$, Task*Cue* Electrode site*Hemisphere $F(4,44)=3.83$, $p=.009$, $\eta^2_p=.26$). These interactions were followed up by separate analyses for each task.

The endogenous predictive tasks showed a Cue*Hemisphere interaction at posterior ($F(1,11)= 5.411$, $p=.040$, $\eta^2_p=.33$), central (Cue*Hemisphere $F(1,11)=36.873$, $p<.001$, $\eta^2_p=.77$); as well as Electrode site*Cue*Hemisphere $F(2,22)=12.192$, $p<.001$, $\eta^2_p=.53$) and anterior electrodes (Cue*Hemisphere $F(1,11)=79.989$, $p<.001$, $\eta^2_p=.88$; as well as Electrode site*Cue*Hemisphere $F(2,22)=9.31$, $p=.001$, $\eta^2_p=.46$). Thus, confirming a widespread ADAN also at the later time window for the endogenous predictive task.

The endogenous counter-predictive task demonstrated a significant Cue*Hemisphere interaction ($F(1,11)=10.069$, $p=.009$, $\eta^2_p=.48$) at only posterior electrodes (although there was an Electrode site*Cue*Hemisphere $F(2,22)=9.00$, $p=.001$, $\eta^2_p=.45$ interaction at central electrodes which was broken down further and revealed a Cue*Hemisphere interaction for electrode CP5/6 only ($F(1,11)=8.19$, $p=.015$, $\eta^2_p=.43$)). The lack of Cue*Hemisphere interaction for central and anterior electrodes suggested there was no ADAN in the endogenous counter-predictive task. However, the posterior effect confirms an LDAP with enhanced positivity contralateral to the attended side compared to ipsilateral to the attended side. The effect at central CP5/6 is likely part of the LDAP present over posterior electrodes as seen by the topographical maps in Figure 5.4.

Analysis of the exogenous task at the 600-800 ms time interval revealed (similar to the endogenous predictive task) a Cue*Hemisphere interaction at posterior ($F(1,11)=8.19$, $p=.015$, $\eta^2_p=.43$, as well as Electrode site*Cue*Hemisphere $F(2,22)=8.532$, $p=.002$, $\eta^2_p=.44$), central (Cue*Hemisphere $F(1,11)=25.332$, $p<.001$, $\eta^2_p=.70$), and anterior electrodes (Cue*Hemisphere $F(1,11)=8.866$, $p=.013$, $\eta^2_p=.47$). Thus, confirming ADAN like waveforms also in the exogenous task.

Table 5.1 Cue-target interval analysis summary

	Task	400-600 ms	600-800 ms	Polarity
Lateralized Posterior electrodes P3/4, P7/8, O1/2	Endogenous	n.s.	p= .040	Neg.
	Exogenous	n.s.	p= .018	Neg.
	Counter-Predictive	n.s.	p=.009	Pos.
Lateralized Central Electrodes C3/4, CP5/6, T7/8	Endogenous	p=.002	p <.001	Neg.
	Exogenous	p=.011	p<.001	Neg.
	Counter-Predictive	n.s.	n.s.	-
Lateralized Anterior electrodes F3/F4, F7/F8, FC5/Fc6	Endogenous	p<.001	p <.001	Neg.
	Exogenous	p=.012	p=.013	Neg.
	Counter-Predictive	n.s.	n.s.	-

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. The Polarity column refers to whether the contralateral enhancement was positive (Pos.) or negative (Neg.). This column therefore depicts whether the Cue*Hemisphere interaction represented an ADAN (contralateral negativity) or LDAP (contralateral positivity).

5.3.2.2 Effects of attentional orienting on post-target ERPs

Figure 5.6 shows ERP waveforms elicited by tactile target stimuli on valid (black line) and invalid (grey line) trials in the exogenous task. The attention effect in the exogenous task was present at the N80 component with enhanced amplitude for invalid compared to valid trials at electrodes contralateral (right panel) to target location (marked out on the C3/4c electrode). Figure 5.5 and 5.7 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 5.5), the N80 effect was similar to that in the exogenous task with larger negativity for unexpected compared to expected 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 5.7), the earliest attention effect was seen also at the N80 component. However, this effect was, contrary to the other two tasks, only present at electrodes ipsilateral to target location (marked out on electrode C3/4i, left pane in Figure 5.7). Following early somatosensory attention effects, both endogenous tasks showed modulations at N140 and Nd with larger negativity for expected compared to unexpected trials. The N140 effect was bilateral in both endogenous tasks whilst the Nd

was bilateral in the endogenous predictive tasks but only present at ipsilateral electrodes in the endogenous counter-predictive task (see Table 5.2 for main post-target attention effects). In the subsequent analyses the attention effect is represented by an effect of Cue.

Table 5.2 *Post-target ERP attention effects*

Component	N80		P100		N140	Nd1		
	Ipsi.	Contra.	Ipsi.	Contra.	Bilat.	Bilat.	Ipsi.	Contra.
Endogenous predictive	n.s.	p=.044	n.s.	p=.03	p=.002	p=.002	*	*
Exogenous	n.s.	p=.009	n.s.	n.s.	n.s.	n.s.	*	*
Endogenous Counter-predictive	p=.023	n.s.	n.s.	n.s.	p=.044	n.s.	p=.039	n.s.

Note. Summary of statistical results (probability levels or non-significant (n.s.) stated) of post-target attention effects for each task separately. For the endogenous tasks the probability level reflects a difference in mean amplitude between expected and unexpected trials. In the exogenous task the effects reflect a difference in mean amplitude between valid versus invalid trials. Probability levels reported as bilateral (Bilat.) effects refer to attention modulations present over both hemispheres. For components where there was a significant Cue*Hemisphere interaction separate analysis of Cue was conducted for each hemisphere. Thus, laterality refers to attention modulations present at electrodes contralateral (Contra.) or ipsilateral (Ipsi.) to target presentation side.

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 Cue*Hemisphere $F(1,11)=7.40$, $p=.02$, $\eta^2_p=.40$, and Task*Cue*Electrode Site*Hemisphere $F(4.0,44.4)=8.49$, $p<.001$, $\eta^2_p=.44$ interactions). This interaction was broken down further and each task was analysed separately.

Analysis of the **exogenous task** showed a significant Cue*Hemisphere ($F(1,11)=29.51$, $p<.001$, $\eta^2_p=.73$) effect (as well as Cue*Electrode site*Hemisphere $F(5,55)=7.46$, $p<.001$, $\eta^2_p=.40$) which was followed up by separate analyses for each hemisphere. This 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 attention 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 (as well as; Cue*Electrode site*Hemisphere $F(2.4,26.9)=9.71$, $p<.001$, $\eta^2_p=.47$) and separate follow up analyses for each hemisphere showed that the attention effect was present over electrodes contralateral to target presentation (Cue: $F(1,11)=5.19$, $p=.044$, $\eta^2_p=.32$) only. 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 ($F(1,11)=12.97$, $p=.004$, $\eta^2_p=.54$; as well as Cue*Electrode site*Hemisphere $F(1.9,20.5)=3.93$, $p=.039$, $\eta^2_p=.26$ interaction) 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.).

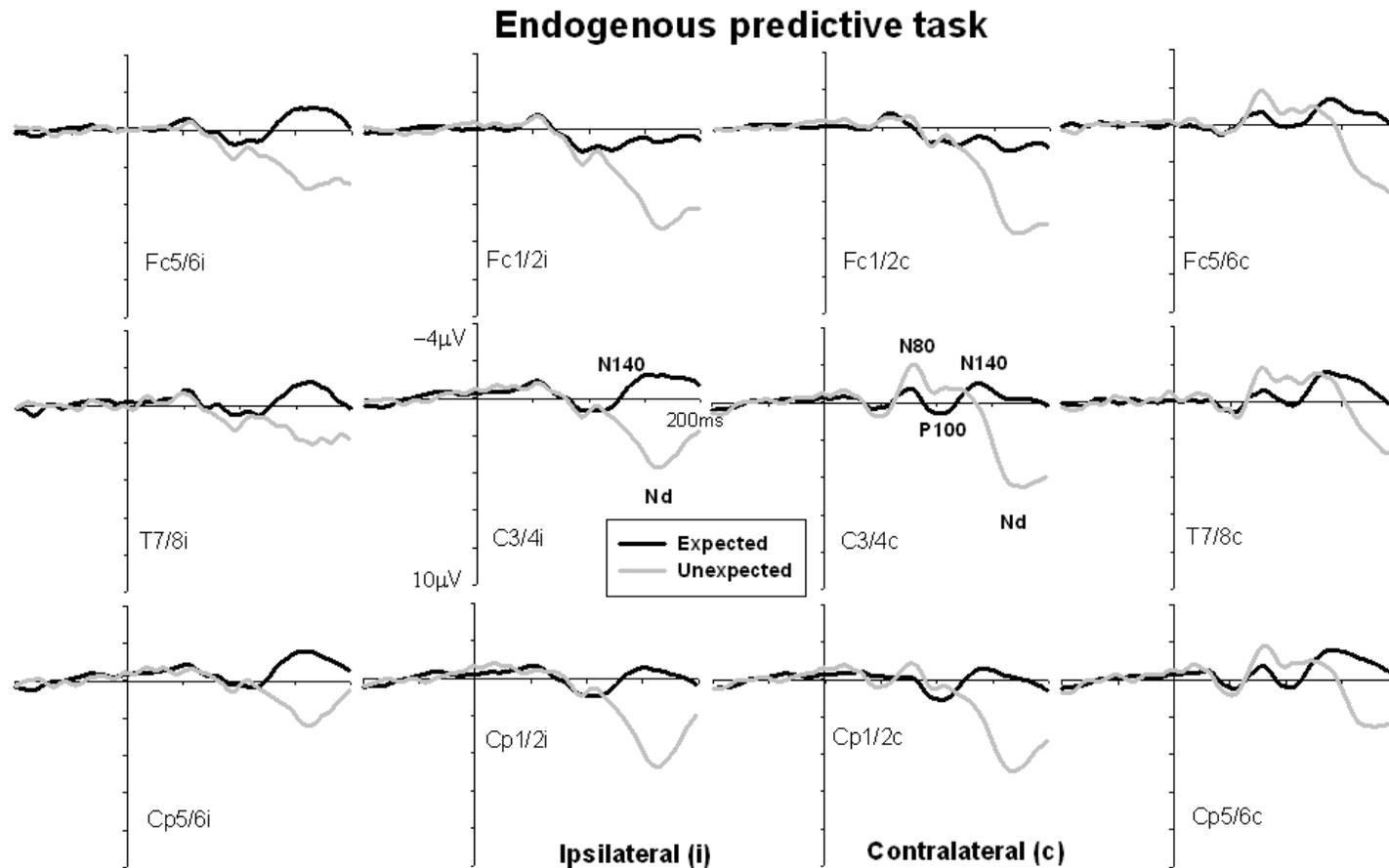


Figure 5.5 Post-target ERPs in the endogenous predictive task. Endogenous predictive task grand averaged somatosensory ERPs elicited on expected (black lines), and unexpected (grey lines) trials in the 200 ms following target onset. The left side shows ERPs over ipsilateral hemisphere and right are ERPs contralateral to target side. The marked out components on C3/4 electrodes denotes if the component was modulated by attention (significant difference between expected and unexpected trials).

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 $F(1,11)=15.95$, $p=.002$, $\eta^2_p=.59$, Cue*Electrode site*Hemisphere $F(3.3,36.2)=7.21$, $p<.001$, $\eta^2_p=.40$, Task*Cue*Electrode site*Hemisphere $F(3.3,36.2)=5.06$, $p=.004$, $\eta^2_p=.32$). Thus, follow up analyses were conducted for each task separately.

The **exogenous task** showed a significant Cue*Hemisphere ($F(1,11)=12.25$, $p=.005$, $\eta^2_p=.53$); as well as Cue*Electrode site*Hemisphere $F(5,55)=5.90$, $p<.001$, $\eta^2_p=.35$) interaction. However, separate follow-up analysis revealed no significant effect of attention at either hemisphere⁹.

In the **endogenous predictive task** there was a Cue*Hemisphere $F(1,11)=14.54$, $p=.003$, $\eta^2_p=.57$ interaction (as well as; Cue*Electrode site $F(2.5,27.5)= 3.68$, $p=.03$, $\eta^2_p=.25$, and Cue*Electrode site*Hemisphere $F(2.6,28.4)=12.25$, $p<.001$, $\eta^2_p=.53$) and separate follow-up analyses for each hemisphere showed a Cue*Electrode site interaction at contralateral electrodes ($F(2.9,32.2)=7.07$, $p=.001$, $\eta^2_p=.39$). 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.

⁹ At contralateral electrodes in the exogenous task there was a close to significant Cue*Electrode site effect ($F(2.1,23.3)=3.02$, $p=.066$, $\eta^2_p=.22$). Based on previous findings (detection task in Chapter III) suggesting the contralateral P100 may be linked to behavioural IOR in touch the close to significant interaction was further broken down and separate attention analysis for each electrode pair was conducted. Paired sample t-tests showed a borderline significant attention effect (valid vs. invalid) at contralateral T7/8 ($t(11)=-2.18$, $p=.052$). The correlation between attention modulation and RT effect across participants did not yield significant results ($r=.02$, $p=.98$).

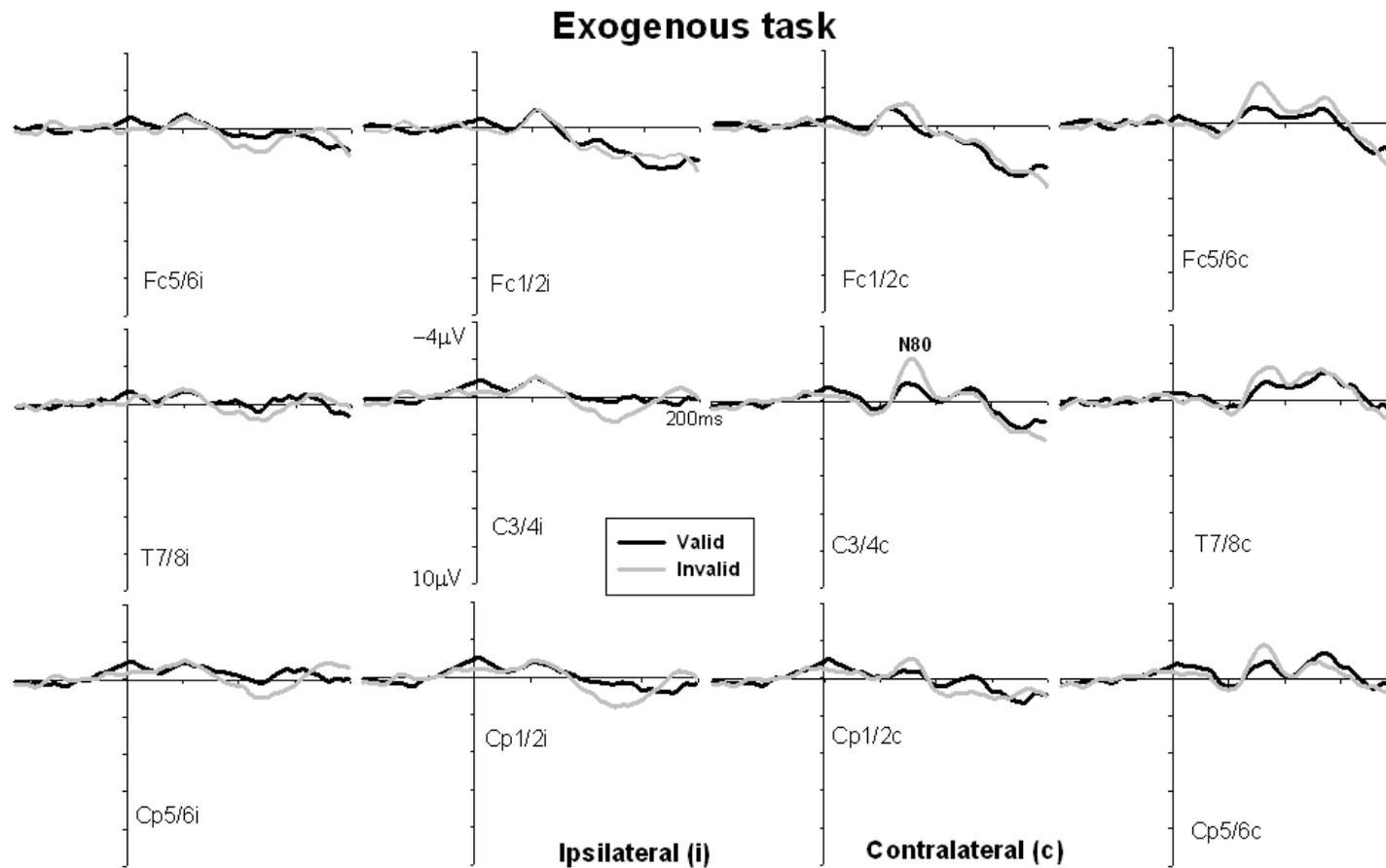


Figure 5.6 Post-target ERPs in the exogenous task. Exogenous task grand averaged somatosensory ERPs elicited on valid (black line), and invalid (grey lines) trials in the 200 ms following target onset. The left side shows ERPs over ipsilateral hemisphere and right are ERPs contralateral to target side. The marked out N80 component on C3/4 electrodes demonstrates that this component was modulated by attention (significant difference between valid and invalid trials). No other components were significantly modulated by exogenous attention.

N140

Analysis including all three tasks showed a significant Task*Cue*Hemisphere interaction ($F(2,22)=7.05$, $p=.004$, $\eta^2_p=.39$), as well as a Cue $F(1,11)=20.87$, $p=.001$, $\eta^2_p=.66$ main effect and Cue*Electrode site $F(2.2,24.5)=9.09$, $p=.001$, $\eta^2_p=.45$, Cue*Hemisphere $F(1,11)=16.27$, $p=.002$, $\eta^2_p=.60$, Task*Cue*Electrode site $F(2.3,25.8)=4.31$, $p=.020$, $\eta^2_p=.28$, Cue*Electrode site*Hemisphere $F(2.2,24.2)=4.18$, $p=.025$, $\eta^2_p=.28$, Task*Cue*Electrode site*Hemisphere $F(4.1,44.6)=3.35$, $p=.017$, $\eta^2_p=.23$ interactions). The significant task interactions were further broken down into separate analysis for each task.

Exogenous task analysis of the N140 showed a significant Cue*Electrode site*Hemisphere ($F(5,55)=3.34$, $p=.029$, $\eta^2_p=.23$) interaction 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 ($F(1,11)=21.53$, $p=.001$, $\eta^2_p=.66$) interaction. The Cue*Hemisphere interaction was broken down further and separate effects of Cue at each hemisphere were analysed. This revealed a significant effect of Cue both for ipsilateral ($F(1,11)=26.66$, $p<.001$, $\eta^2_p=.71$) and contralateral electrodes ($F(1,11)=8.77$, $p=.013$, $\eta^2_p=.44$); as well as Cue*Electrode site $F(2.2,24.3)=9.04$, $p=.001$, $\eta^2_p=.45$ interaction) 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 5.6). That is, the N140 attention effect in the endogenous predictive task was present over both hemispheres. Moreover, there was a significant correlation between the ERP attention modulation and the behavioural RT effect, with larger amplitude difference between valid and invalid conditions for each participant relating to larger RT attention effect ($r=.69$, $p=.013$).

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 ($F(1,11)=5.16$, $p=.044$, $\eta^2_p=.32$); and also; Cue*Electrode site $F(2.2,23.8)=7.39$, $p=.003$, $\eta^2_p=.40$). There was no significant correlation between ERP attention modulation and RT effect ($r=.32$, n.s.).

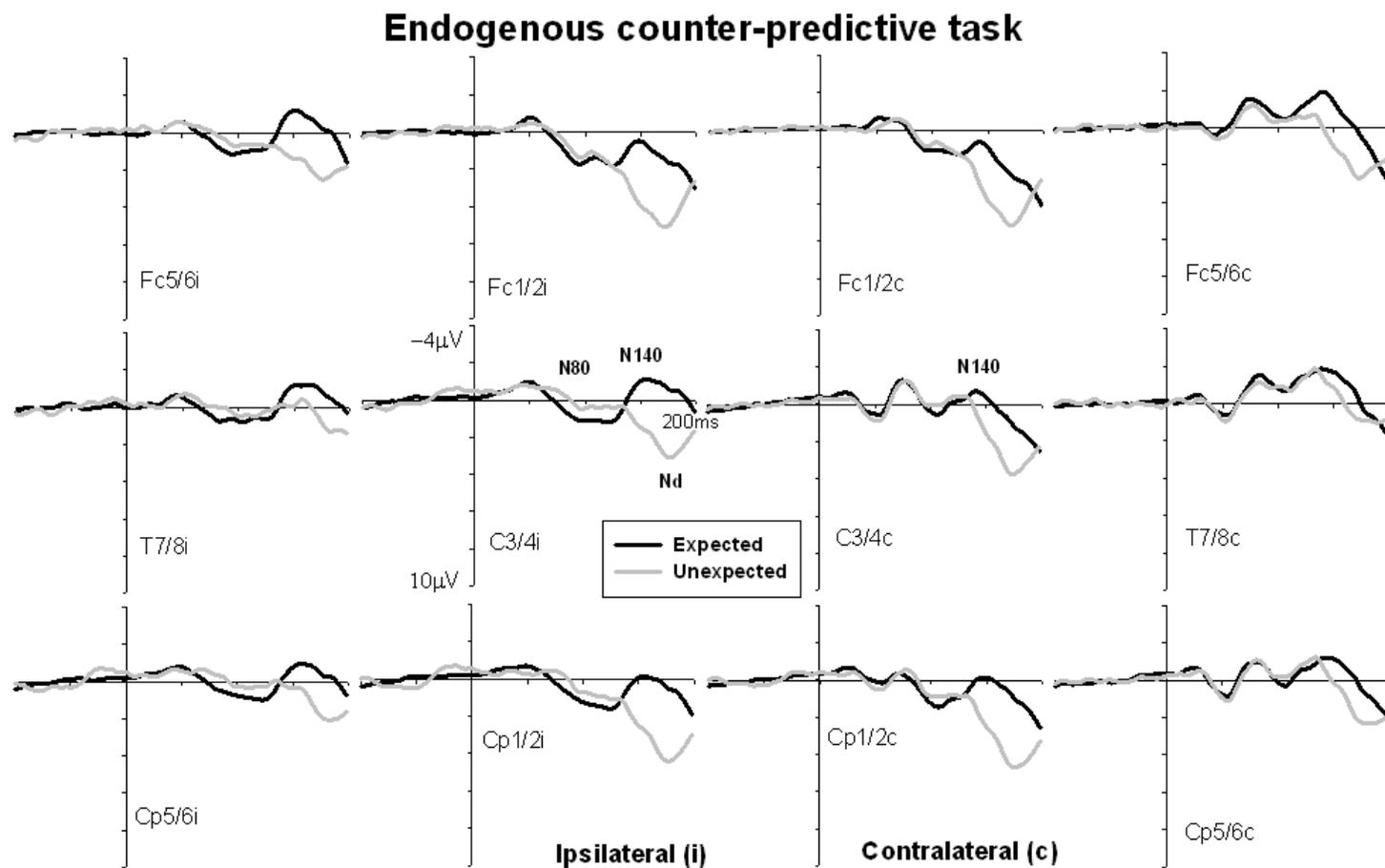


Figure 5.7 Post-target ERPs in the endogenous counter-predictive task. Endogenous counter-predictive task grand averaged somatosensory ERPs elicited on expected (black lines), and unexpected (grey lines) trials in the 200 ms following target onset. The left side shows ERPs over ipsilateral hemisphere and right are ERPs contralateral to target side. The marked out components on C3/4 electrodes denotes if the component was modulated by attention (significant difference between expected and unexpected trials). In the counter-predictive task the early (N80) effect is contralateral to the cue.

Nd

At this last analyzed 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 $F(1,11)=11.02$, $p=.007$, $\eta^2_p=.50$, Cue*Electrode site $F(1.8,19.6)=5.66$, $p=.014$, $\eta^2_p=.34$). The interaction was further broken down and the effects of attention were separately analysed for each task.

The **exogenous task** revealed a Cue*Hemisphere interaction ($F(1,11)=8.57$, $p=.014$, $\eta^2_p=.44$); as well as Cue*Electrode site*Hemisphere $F(2.6,29.0)=3.22$, $p=.043$, $\eta^2_p=.23$). However, separate follow-up analyses for contralateral and ipsilateral hemisphere demonstrated 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 ($r=.81$, $p=.001$).

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 ($r=.60$, $p=.041$).

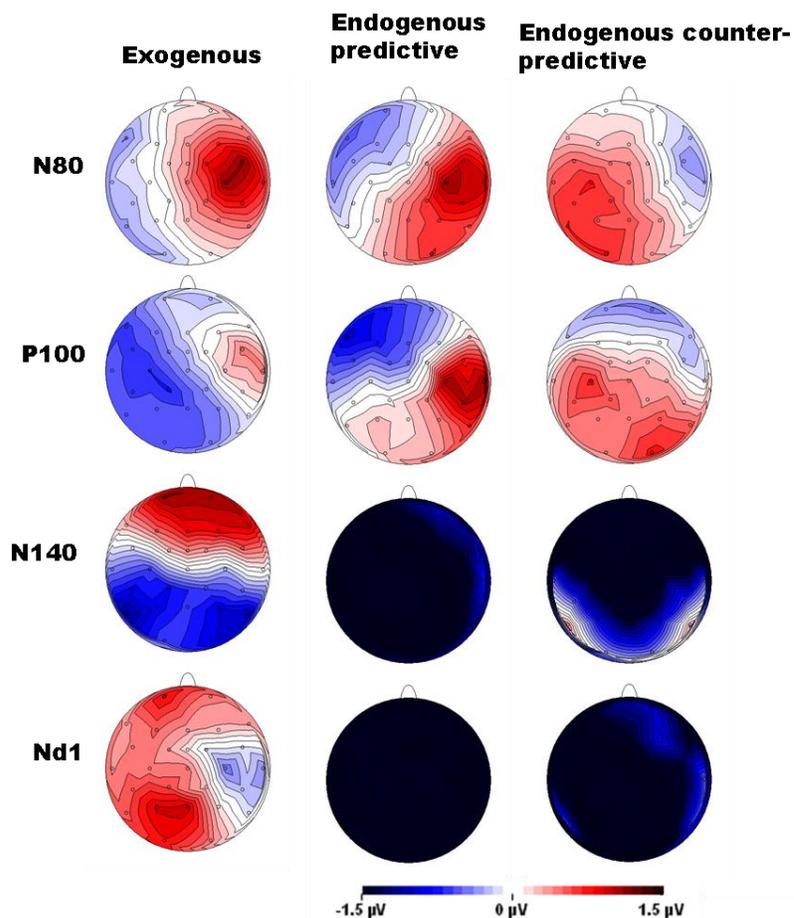


Figure 5.8 Topographic maps of the post-target attention effects. In the exogenous task (left panel) ERPs on invalid were subtracted from valid trials. In the endogenous tasks (right two panels) the ERPs on unexpected were subtracted from expected trials. The right hemisphere shows attention effect contralateral to the target side and the left hemisphere shows ipsilateral attention effects. At the N80 component, the attention effects are contralateral to the target in the exogenous and endogenous predictive task. In the endogenous counter-predictive task the attention modulation is over ipsilateral hemisphere. However, in all three tasks the attention effect is contralateral to the cued side. In the mid and later time windows (N140 and Nd) there are widespread attention effect over both hemispheres in the two endogenous tasks. These attention effects are further supported by significant correlations between endogenous behavioural effect and the magnitude of the ERP attention modulation.

The behavioural data across tasks was compared in terms of the three conditions which were hypothesized to demonstrate the fastest RTs in each condition. Similarly, the three conditions hypothesized to demonstrate the slowest RTs in each task were compared (see

section 5.3.1). In line with the behavioural analysis the post-target ERPs were also visually graphed in a similar way (Figure 5.9). The behavioural hypothesis suggested that if IOR influences processing of a valid cue, even when endogenous, then the expected condition in the counter-predictive task would be faster compared to the expected in the endogenous predictive task. The behavioural results suggested there was no difference between these two conditions. The ERP waveforms descriptively suggest differences between these conditions at several processing stages. However, without any clear *a priori* predictions regarding the processing stages which would differ in the three fastest and three slowest conditions this analysis was not taken further.

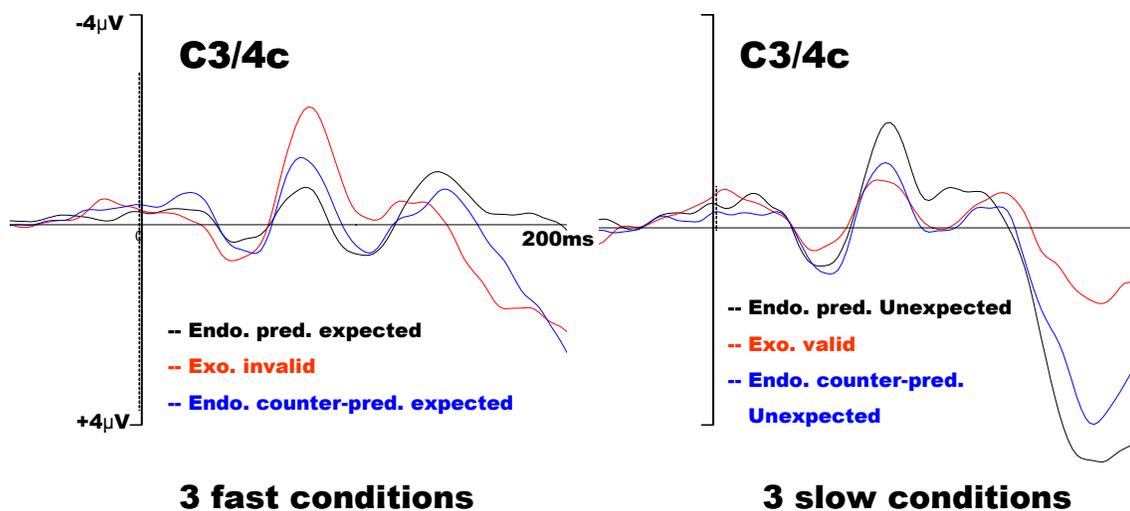


Figure 5.9. ERPs for three fastest and three slowest conditions contrasted, respectively. *Left:* Grand averaged ERPs for the three conditions hypothesized to behaviourally demonstrate the fastest RTs (the expected targets in endogenous predictive and counter-predictive tasks, and the invalid condition in the exogenous task). *Right:* Grand averaged ERPs for the three conditions which behaviourally were hypothesized to result in slowest RTs within each task (the unexpected targets in the endogenous tasks and valid targets in the exogenous task).

5.4 Discussion

This study was designed to investigate neural correlates of tactile attention, in particular to compare and map out attention modulations related to endogenous and exogenous orienting. As predicted, the behavioural data showed facilitation of RTs for expected compared to unexpected locations in both endogenous tasks whilst IOR in the exogenous task (see Figure 5.2). The ERP cue-target interval data showed the presence of attentional orienting. That is, an ADAN in the endogenous predictive task as well as in the exogenous

task whilst in the counter-predictive task an LDAP was present. Analysis of post-target ERPs showed a similar N80 attention modulation in all three tasks suggesting the N80 mainly reflects exogenous attentional processing due to lateralized cues. That is, the attention effect was present contralateral to the location of the cue in all three tasks. The later N140 and Nd components were only modulated by attention in the endogenous tasks suggesting these mid to late stages of somatosensory processing are not related to IOR. Moreover, in the endogenous predictive task the N140 and Nd attention modulations were positively correlated with the corresponding behavioural attention effect. In the endogenous counter-predictive task the Nd was also correlated with corresponding RT effect. This further confirms a direct link between behaviour and endogenous attention modulations at later stages of processing.

5.4.1 Behavioural effects of tactile attention

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), facilitation of attended targets in the endogenous predictive task (Cohen et al., 2005; Lloyd et al., 1999) and endogenous counter-predictive task (Chica, Sanabria, Lupiáñez, & Spence, 2007). An issue with the endogenous predictive task is that the observed effect is not clear whether it is influenced by IOR. As the cue appears to the same location as the target, although informative, the cue may result in both endogenous facilitation and IOR for validly cued targets. Such a conflict between facilitation and IOR has been demonstrated in visual attention. Chica and Lupiáñez (2009) found visual peripheral cues, although informative, also induced IOR. That is, when cue and target were presented to the same peripheral location then the facilitation effect expected from endogenous orienting was masked by IOR. This resulted in no observable difference between expected and unexpected targets in their endogenous predictive task. In contrast, the present endogenous predictive task demonstrated facilitation of attended stimuli. To further investigate whether IOR may still have influenced endogenous tactile orienting, the expected target conditions were compared for the two endogenous tasks. In the endogenous counter-predictive task there is no conflict between endogenous facilitation and exogenous inhibition. The comparison between the expected target conditions, where one potentially could be influenced by IOR whilst not the other, showed no difference (see also Chica, Sanabria, Lupiáñez, & Spence, 2007, for similar results). In other words, there were no signs that IOR was influencing the response times in the endogenous predictive task. Based upon these comparisons it could be concluded that

voluntary attention in touch has the ability to eliminate and/or mask IOR effects, possibly to a greater extent compared to vision.

5.4.2 ERP correlates of tactile attention

ERP waveforms in the cue-target interval are assumed to reflect neural processes underlying a fronto-parietal attention network. More specifically, these are commonly investigated by contrasting ERPs contralateral and ipsilateral to the attended side. Previous studies have, to our knowledge, only investigated the cue-target interval ERPs of endogenous attention (apart from the studies presented in this thesis). Two waveforms which have been linked to the attention network are the anterior directed attention negativity (ADAN), suggested to reflect supramodal attention mechanism in the frontal areas (Eimer, van Velzen, & Driver, 2002; Seiss, Gherri, Eardley, & Eimer, 2007), followed by a late directing attention positivity (LDAP), assumed to originate in the lateral occipital cortex (Praamstra, Boutsen, & Humphreys, 2005).

The exogenous task demonstrated an ADAN component, with enhanced negativity contralateral to the side stimulated by the cue. This demonstrating that an exogenous task can elicit the hemispheric waveform differences previously only shown in endogenous studies. It is however not clear whether this exogenous ADAN component is the result of unilateral physical stimulation or whether the exogenous cue results in activation of an exogenous attention system. It may be that the two are not mutually exclusive. It is not possible to activate an exogenous attention network without physical stimulation. The relative lateness (400 ms and onwards) of the ADAN in the exogenous task suggests activation of a topographically more widespread attention network rather than early stimulus processing.

In line with previous endogenous tactile attention studies (e.g., Forster et al., 2009) the endogenous predictive task showed an ADAN, with enhanced negativity for anterior electrodes contralateral compared to ipsilateral to attended side. Importantly, the ADAN effect in the endogenous predictive task was significantly larger in magnitude compared to the ADAN demonstrated in the exogenous task. This may suggest that the ADAN waveform can be made up of two parts. An exogenous ADAN effect due to unilateral cues, and further enhanced by directing endogenous attention to the stimulated site. The endogenous counter-predictive task further provides support for two types of ADAN. In

this task no ADAN component was present. This is likely the result of the exogenous and endogenous ADAN conflicting, resulting in no effect. For example; a cue presented to the left hand would evoke enhanced contralateral negativity in the right compared to the left hemisphere. The left cue also indicates to attend to the opposite side. Thus, the endogenously attended location is the right hand. The endogenous ADAN would therefore evoke enhanced contralateral negativity in the left hemisphere. As a result, the two processes cancel each other out.

Moreover, the endogenous counter-predictive task showed the more posterior LDAP waveform (see Figures 5.3 & 5.4). This enhanced posterior contralateral positivity has been suggested to reflect attentional orienting processes mediated by external visual space (van Velzen, Eardley, Forster, & Eimer, 2006). This may suggest that orienting attention from one side to the other in the counter-predictive task was mediated by external space rather than a somatotopic spatial frame of reference. In the endogenous predictive task, applying a visual frame of reference is less likely required as attention needs to be maintained at the cued location in the cue-target interval, and together with the hands being covered, this leading to an absence of an LDAP. However, it should be noted that there is an alternative explanation for the LDAP. The LDAP in the counter-predictive task is contralateral negativity to the location of the cue, similar to an ADAN. However, due to the posterior location and time window of the LDAP it seems most plausible that this cue-target waveform in the counter-predictive task is what previous research denotes an LDAP, rather than a posterior exogenous ADAN. .

The presence of the ADAN and LDAP is assumed to reflect the activation of the fronto-parietal attention network. The presence of the ADAN in the exogenous task may suggest similar brain areas are involved in both types of orienting. Neuroimaging studies have consistently highlighted endogenous orienting as part of a dorsal fronto-parietal (dFP) network (see Macaluso, 2010, for review). A more ventral fronto-parietal (vFP) network has been suggested to be activated in response to orienting to unexpected targets in an endogenous task (Corbetta et al., 2000). This condition is sometimes referred to as exogenous attention. In an event-related fMRI study Kincade et al. (2005) found that both the dFP and vFP was activated more for their endogenous predictive compared to exogenous non-predictive task suggesting salient but task irrelevant cues do not trigger

activation in the in fronto-parietal network to the same extent. Importantly though, their exogenous task elicited facilitation of RTs at validly cued locations rather than IOR. Furthermore, Mayer et al. (2004) found different brain regions activated in their endogenous vs. exogenous facilitation tasks, however, when they compared endogenous facilitation to exogenous IOR they found largely similar brain areas activated. Mayer and colleague proposed the similarity of neuronal areas involved in endogenous facilitation and IOR may suggest similar neuronal resources are employed to limit exogenous facilitation from dominating visual attention. They suggest, endogenous attention is employed to selectively attend to relevant information out of the stream of information bombarding our sensory system. Similarly, IOR is a mechanism used to save attention resources and reduce the influence of irrelevant stimuli. The similarity between endogenous facilitation and IOR found in Mayer et al.'s fMRI study may serve as a plausible explanation why the exogenous task in the present study also produced an ADAN. In other words, the present results are in line with fMRI data suggesting IOR and endogenous attention evoke the same dFP attention network. Future ERP studies may wish to compare exogenous facilitation (e.g., through a tactile discrimination task) and endogenous attention to investigate whether the waveforms such as the ADAN are directly related to the dFP network.

ERPs time locked to target presentation showed significant N80, P100, N140 and Nd attention modulations (see Table 5.2). The earliest component showing an attention effect was the N80 component. In the exogenous task N80 showed enhanced negativity for invalid over valid trials and enhanced amplitude for unexpected compared to expected trials in the endogenous tasks. This early attention modulation was very similar in the exogenous and endogenous predictive task and present contralateral to target side. The similarity of the attention modulations between the two tasks may suggest this early effect is stimuli driven, rather than top-down controlled by endogenous orienting. The endogenous counter-predictive task showed an N80 attention effect only at electrodes ipsilateral to target location. Importantly, this effect was contralateral to the cue. In other words, in all three tasks the N80 effect was contralateral to the side of the cue. However, the N80 component is proposed to originate from the primary somatosensory cortex contralateral to the stimuli (e.g., Mima et al., 1998). This suggests the effect in the counter-predictive task did not modulate the N80 *component per se* but rather, the ipsilateral effect was present in the time window where the contralateral N80 appears. This may be of importance as it can suggest the contralateral N80 component was modulated by endogenous attention. That is,

shifting endogenous away from the cued side as in the counter-predictive task, reduces the effect on the contralateral N80 component.

Attention modulation of the N80 has not previously been demonstrated in a transient paradigm but only in sustained endogenous attention in touch. Under sustained attention conditions enhanced negativity for attended over unattended stimuli has been reported (Eimer & Forster, 2003a; Michie et al., 1987). In contrast, in the present study enhanced negativity for unattended over attended was found. Taken together our data suggests that N80 attention modulation in a transient paradigm reflects mainly exogenous attentional processing due to lateralized cues which may be influenced by endogenous processing as seen in the counter-predictive task. Moreover, the N80 is suggested to originate from primary somatosensory cortex (Hari et al., 1984; Inui et al., 2004; Mima et al., 1998) demonstrating for the first time that transient attention paradigms can modulate such early somatosensory stages.

Following on from the N80 the P100 component was only modulated by attention in the endogenous predictive task with larger positive amplitude for attended compared to unattended stimuli. This is in line with previous tactile attention studies which have found similar P100 attention effects (Eimer & Forster, 2003a, 2003b; Zopf et al., 2004). Based upon past research associating the P1 to IOR in vision we speculated the P100, if anything, be modulated by IOR in touch. There was an attention effect approaching significance (see Footnote 7) in the exogenous task but the lack of any clear effect and correlation leads us to conclude the P100 is not directly or strongly linked to IOR in touch. This unclear result is mirrored in the visual attention literature of ERPs and IOR where studies have found a P1 attention modulation without IOR (Doallo et al., 2004; Hopfinger & Mangun, 1998) or IOR with no attention effect at the P1 (Prime & Ward, 2006).

The two latest components analysed - the N140 and Nd - were only modulated by attention in the endogenous tasks suggesting these mid to late stages of processing are not linked to IOR. Importantly, there was a significant correlation between the behavioural attention effect and the N140 and Nd attention effect in the endogenous predictive task. In the endogenous counter-predictive task there was a correlation between behavioural and Nd attention modulations. That is, participants with larger behavioural attention effects also demonstrated relatively larger ERP amplitude effect between valid and invalid trials. This

demonstrated that these two components are directly linked to observed endogenous behaviour. That the N140 was only correlated in the endogenous predictive task may suggest that orienting in the counter-predictive task occurs slightly later, possibly because it may take longer to shift attention from the cue location to the opposite side in the counter-predictive task compared to maintaining attention at the cued location as in the predictive task. The N140, assumed to originate from secondary somatosensory cortex (Frot, Rambaud, Guénot, & Mauguière, 1999), has been found in previous endogenous tactile attention studies (Eimer & Forster, 2003a; Forster & Eimer, 2004; Zopf et al., 2004), however, no previous studies of tactile attention have established a clear relationship between neural correlates and behaviour.

5.4.3 Summary and conclusion

The behavioural effects were in line with previous research demonstrating IOR in the exogenous task and facilitation of attended target in the endogenous task. Analysis of the cue-target interval showed lateralized cues induced an exogenous ADAN. This ADAN effect is further enhanced by endogenously orienting attention to the cued location in the endogenous predictive task. When the cue location and attended location are in conflict, as in the endogenous counter-predictive task, no ADAN is present. However, an LDAP was found in the counter-predictive task suggesting an external frame of reference was used when shifting attention from one hand to the other. The post-target interval demonstrated similar contralateral N80 effects in the exogenous and endogenous predictive tasks. This indicated the N80 mainly reflected exogenous attentional processing due to lateralized cues as the effect was present contralateral to the location of the cue. The attention modulation seen at the N140 and Nd components were significantly correlated with endogenous behavioural effects. This indicated a direct link between behavioural and ERP attention effects.

CHAPTER VI

Perceptual load influences perception and inhibition of return in touch. Evidence from ERPs and behaviour

The load theory of attention suggests increased load in a central task decreases the ability for irrelevant peripheral stimuli to capture our attention. Participants viewed a rapid serial visual presentation stream (RSVP) of letters on a central monitor. During the presentation of letters participants received a lateralized tactile exogenous cue to the left or right hand. In a single task participants responded to a tactile target to the same or opposite hand as the cue (low perceptual load). In a dual task, participants searched the RSVP stream for a number and responded also to this visual target (high perceptual load). Behavioural results demonstrated tactile IOR in the single whilst no exogenous attention in the dual task. ERPs immediately following the cue (cue-locked ERPs) demonstrated increased load resulting in decreased somatosensory processing at the P100. ERP analysis of attentional control processes (cue-target interval) demonstrated an ADAN in both tasks. The ADAN was significantly larger in the single compared to the dual task. That is, increased load led to a decreased ADAN. Analysis of post-target ERPs demonstrated earlier attention modulations (N80) when load was low compared to high. Taken together, this study demonstrates, through several analyses (behavioural and ERP), that increased visual load resulted in decreased processing of irrelevant tactile stimuli.

6.1 Introduction

The ability to prioritise certain information out of the stream of sensory input constantly bombarding our senses is known as selective attention. Directing our attention consciously towards a particular spatial location or focusing on particular stimuli is generally known as voluntary or *endogenous* attention. Attention can also be driven by external stimuli in our environment which grabs our attention, also known as automatic or exogenous attention. Much of the attention research has explored these attention mechanisms separately, in particular by using the well established *Posner* cueing paradigm (e.g., Posner, 1980). The typical structure of this paradigm is to first present a cue and after an interval (stimulus onset asynchrony (SOA)) a target appears to which the participants needs to make a response. In endogenous versions the cue will inform the participants of the likely target location. In exogenous versions, the cue does not indicate the location of an upcoming target. In exogenous versions of this paradigm it has commonly been observed that peripheral cues, although instructed to be ignored, automatically influence our behaviour. The peripheral exogenous cues, can facilitate response times to targets at the same

location¹⁰ but also inhibit target processing, known as inhibition of return (IOR) (see Klein, 2000, for a review).

In our everyday lives endogenous and exogenous attention constantly compete for our resources (e.g., Spalek, Falcon, & Di Lollo, 2006). A central topic in the relationship between endogenous and exogenous attention is whether exogenous attention is a truly automatic mechanism. For a process to be considered automatic, two main criteria have been put forward: Firstly, an automatic process may not be subject to any voluntary control. Secondly, an automatic process is not hindered when information load is increased (e.g., Yantis & Jonides, 1990). Much of the research into the automaticity of exogenous attention has looked at to what extent irrelevant stimuli can capture attention when it is otherwise engaged (see Santangelo & Spence, 2008, for a review). It is clear that irrelevant stimuli can attract our spatial attention. However, there is a large body of evidence suggesting exogenous peripheral cues are not a truly automatic process, and there are circumstances where the attentional capture does not take place (see Ruz & Lupiáñez, 2002; Santangelo & Spence, 2008, for reviews). It has in particular been demonstrated that varying the perceptual, attentional and cognitive load in a central task affects how well irrelevant peripheral stimuli captures our attention. The load theory of selective attention suggests perception has a limited capacity and that all stimuli are processed in an automatic fashion until the available capacity has been exhausted (Lavie, 1995; Lavie, Hirst, de Fockert, & Viding, 2004). Under a high perceptual load condition, where our attentional capacity is fully engaged in processing task relevant information, then there is no spare capacity to process irrelevant stimuli. On the contrary, when we engage in a task with low perceptual load, any capacity which has not been utilized in the relevant task is left over to process task irrelevant stimuli. In other words, by increasing the perceptual load in one task, the ability for task irrelevant stimuli to capture our attention decreases.

The load theory incorporates the longstanding and still ongoing debate regarding the locus of selective attention during perception - whether selection occurs early (Broadbent, 1958) or late (Deutsch & Deutsch, 1963). According to the load model, the bottleneck of attentional selection is an adaptive filtering mechanism and is not fixed at either early or

¹⁰ In vision, facilitation occurs when the SOA is smaller than approximately 250 ms. However, in the tactile modality no such early facilitation period seems to be present for detection of tactile targets but only inhibition of return. However, a biphasic response time pattern is evident for tactile discrimination (Miles et al., 2008).

late stages of processing. Instead, the filter varies according to the amount of concurrently presented information and attentional load. That is, the theory proposes that high perceptual load filters out irrelevant stimuli early in the selection process and low load conditions result in a late selection process (Lavie, 1995; Lavie et al., 2004).

Neuroimaging studies have provided support for the load theory. For example, Rees et al. (1997) demonstrated in an fMRI experiment that increasing perceptual load decreased the neural activity for irrelevant peripheral visual stimuli. Schwartz et al. (2005) presented participants with a central rapid serial visual presentation (RSVP) stream of letters. They found the activation in the primary visual cortex (V1) for task-irrelevant checkerboard stimuli in the periphery was decreased by higher perceptual load in the central RSVP task. Moreover, this latter study also suggested that higher perceptual load can modulate and affect early sensory visual processing. In terms of the debated locus of selective attention, Schwartz and colleagues' findings indicate that the selective filter occurs early during the perceptual process.

ERPs have been used to investigate how perceptual load influences processing of irrelevant stimuli. Due to the good temporal resolution, ERPs also provide a good method in addressing the debate of *when* attentional selection takes place during perceptual processing. Visual perceptual load studies have compared the ERP pattern elicited by irrelevant stimuli when the load in a central task is varied. Rauss, Pourtois, Vuilleumier and Schwartz (2009) presented peripheral task irrelevant visual stimuli during conditions when participants engaged in a centrally located task of high or low load. They found the C1 component (suggested to originate from primary visual cortex; Clark & Hillyard, 1996) for the irrelevant peripheral stimuli to be reduced when task difficulty was high compared to low. This suggests that engaging in high perceptual load conditions, affects and “filters out” irrelevant stimuli early during the perceptual process. Similarly, in a study by O’Connell et al. (2011) participants viewed a central RSVP stream whilst presented with peripheral task irrelevant targets. They found increased load in the central task led to diminished processing of peripheral visual stimuli as indicated by reduced amplitude of the P2 and P3 components. Taken together, neuroimaging (e.g., Schwartz et al., 2005) and now also electrophysiological studies (Fu, Fedota, Greenwood, & Parasuraman, 2010; Handy, Soltani, & Mangun, 2001; O’Connell et al., 2011; Rauss et al., 2009), have demonstrated

neural activity elicited by task irrelevant stimuli to be modulated by the amount of perceptual and attentional load.

The question of how perceptual load affects our spatial attention can also be investigated by comparing differences in attention effects during high and low load. In terms of ERPs this has been investigated by comparing post-target attention modulated ERP components and how these are affected by increasing load. In other words, to use the now well established attention effects seen in the post-target interval at particular ERP components, and how these attention modulations are affected by varying perceptual load. For example, in an exogenous cue-target paradigm Fu et al. (2009) showed the attention effect of the P1m (over midline electrodes, at around 100-140ms post-target onset) interacted with perceptual load. This suggests perceptual load impacts and interacts with exogenous attention effects.

A series of components (P100, N140, & 'Negative difference' – Nd) in the post-target time interval have consistently been reported to be modulated by tactile attention (see Sambo & Forster, 2011 for a review). Moreover, an early N80 component has been suggested to originate in primary somatosensory cortex contralateral to the tactile stimuli (Allison et al., 1992, 1989; Forss & Jousmäki, 1998; Hari & Forss, 1999; Hari et al., 1984; Inui et al., 2004; Mima et al., 1998) and a few studies have demonstrated an attention modulation for the N80 with enhanced negativity for attended compared to unattended stimuli (Eimer & Forster, 2003a; Michie et al., 1987; Schubert, Ritter, Wu, et al., 2008). It is not established whether these components are also modulated by exogenous attention. Moreover, it is unclear whether load influences post-target stages of tactile processing in a cue-target paradigm.

Taken together, ERP studies have investigated the effects of perceptual load in two ways. Firstly; by comparing the ERP amplitudes for irrelevant stimuli during high or low load conditions. Secondly; investigating the interaction of attention effects and load by looking at how attention modulations in the post-target time window are affected by varying perceptual load. These two methods focus on the effects of load upon early sensory processing of stimuli. That is, investigating the ERP effects of perceptual load immediately following a stimulus (e.g., the somatosensory evoked potentials in touch). Effects of attention have also been researched at later post perceptual stages of processing. Evidence from neuroimaging studies has suggested endogenous and exogenous attention activate a

fronto-parietal attention network (see Macaluso, 2010, for a review). In ERP studies this network is assumed to be manifested in the cue-target interval in terms of an anterior directed attention negativity (ADAN) and late directing attention positivity (LDAP). These late (starting after 300 ms post stimuli onset), attention modulated waveforms have been demonstrated in visual (e.g., Hopfinger & Mangun, 2000), auditory (e.g., Green & McDonald, 2006) and tactile studies (Forster et al., 2009). Other than the studies presented in previous chapters of this thesis (Chapters III-V) the cue-target interval components have only been explored during endogenous attention. Moreover, no previous studies known to the author have investigated the effects of perceptual load upon the ADAN and LDAP.

The vast majority of research into the effects of perceptual load using neuroimaging and ERPs has explored the visual modality. However, in a behavioural task, Santangelo and Spence (2007) showed that varying the visual perceptual load influenced processing of irrelevant tactile stimuli. In a low perceptual load task the participants focused their visual attention on a fixation cross whilst they received task-irrelevant tactile cues followed by a tactile target to the left or right. In a high perceptual load task participants viewed a RSVP stream instead of a fixation cross and had to also detect a visual target (a number) as well as respond to tactile targets. This demonstrated that the irrelevant tactile cues only had a facilitation effect on tactile targets at the cued side in the single task, whilst it was suppressed in the dual task (high load). In other words, the reasoning is that a high load condition requires our attentional resources for the central task. The cue, a task irrelevant stimulus, in this condition is then not fully processed leading to a lack of response time effect. Using an RSVP stream to manipulate perceptual load has also demonstrated similar effects where high perceptual load reduces the influence of how well irrelevant visual (Santangelo, Botta, Lupiáñez, & Spence, 2011) and auditor targets (Santangelo et al., 2008) capture attention.

Attending to a central task has thus shown to modulate neural activity and attention effects to task irrelevant visual stimuli. In the present study we aimed to investigate whether varying the visual central task load at fixation would affect the processing of tactile stimuli in terms of perception and attention. We employed a similar paradigm to that of Santangelo and Spence (2007) outlined above. However, instead of exploring facilitation of validly cued targets we aimed to investigate perceptual load effects upon tactile IOR. Participants ignored a tactile cue and detected a tactile target in a single task (low

perceptual load). In a dual task (high perceptual load) participants were also required to detect and respond to also a number within the RSVP stream¹¹.

Based upon previous exogenous tasks investigated in this thesis (presented in Chapters III-V) and previous research on tactile IOR (e.g., Lloyd et al., 1999), we predicted IOR in the single task. We made no prediction regarding behavioural effects in the dual task. The exogenous cue-target paradigm allowed us to investigate the neural correlates of exogenous tactile attention and perception during varying load in three ways. 1) *Cue-locked ERPs* - This analysis investigated somatosensory ERPs in the time window immediately following the cue. ERPs were compared for the task irrelevant tactile stimuli (i.e. the cue) in the high versus low perceptual load task. If tactile processing is in accordance with the load theory (Lavie, 1995; Lavie et al., 2004) and findings from visual attention research (e.g., Fu, Fedota, et al., 2010; Handy et al., 2001; Rauss et al., 2009; Schwartz et al., 2005), then there should be a difference in amplitude between the two tasks at sensory components following the cue. This would indicate somatosensory processing is affected by load. It is however possible that neural responses to irrelevant tactile stimuli may be different compared to those found in visual research, in particular as the tactile modality cannot be shut out and ignored as possible with auditory and visual information. 2) *Cue-target interval ERPs* – This analysis investigated the effects of perceptual load upon the attentional control processing during the later cue-target interval, from 400 – 800 ms post cue onset. We aimed to establish whether the ADAN and/or LDAP were present during exogenous orienting. Further, to explore whether these cue-target interval waveforms were affected by varying the perceptual load. 3) *Post-target ERP analysis* – This analysis investigated the post-target ERPs which allowed us to explore the interaction between perceptual load and attention modulations of sensory specific components.

¹¹ It should be noted that the manipulation between the two tasks may not be purely perceptual differences but also different types of load may have been varied. For example, the Dual task will likely, in addition to increased perceptual load, also involve higher task difficulty which may increase the demands of other cognitive processes. The distinction between attentional, cognitive, task, and perceptual load are not clear. In particular the distinction, if there is any, between attentional and perceptual load is unclear. Lavie's (1995) load theory proposes increased attentional/perceptual load in a central task decreases the influence of task irrelevant stimuli. However, increased memory and/or cognitive load have the opposite effect whereby increasing central load also increases the ability of irrelevant stimuli to capture attention. The terminology used in the present chapter and thesis is based on similar research in the area which has used high and low perceptual load terminology in relation to single and dual tasks using a central RSVP stream (e.g., Ho, Santangelo, & Spence, 2009; Santangelo et al., 2011).

6.2 Methods

6.2.1 Participants

Seventeen paid participants (15 right-handed) took part in this study and all gave written informed consent prior to their participation. There were seven males and ten females with a mean age of 26.5 years (range: 21-35 years). One participant (right handed female) was excluded from analysis due to excessive alpha waves during EEG recording.

6.2.2 Stimuli and apparatus

Stimuli and apparatus were identical in the single and dual tasks. 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. The two tactile stimulators were fixed (using medical tape) to the left and right index finger and the hands were 640 mm apart. 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 100 ms single tap, thus, the contact time between rod and skin was 100 ms. The RSVP stream consisted of black letters (C, D, K, M, S, D, Y, P, X, R, B, Z, L, E, F, T, J, N) on a white background presented in the centre of a 15 inch monitor (Courier New font, size 25) placed 60 cm directly in front of the participant. The numbers (2-9) embedded within the RSVP stream were of the same font and size as the letters. All letters and numbers were presented for 100 ms. Responses to both visual and tactile targets were made into a microphone, placed directly in front of the participant. A black cloth covered the participant's hands to avoid any visual information of the tactile stimulation.

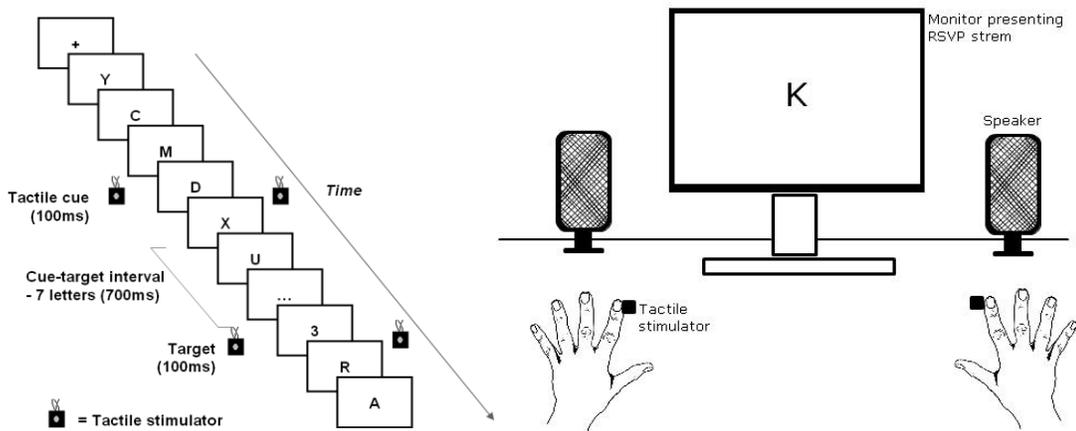


Figure 6.1 Stimuli presentation and experimental set-up. *Left:* The sequence and time course of events for a typical trial. In both the single and dual task a tactile cue was presented to either the left or right hand. Following a 700 ms inter-stimulus interval either a number or a tactile target appeared (together with a letter) for 100 ms. In the single task the participant responded as rapidly as possible to the tactile target only and in the dual task the participant responded also if a number appeared on the screen. Visual and tactile targets were never presented together in the same trial. The *cue-locked* ERP analysis was in the 350 ms window following the tactile cue. The *cue-target interval* analysis was in the interval between the tactile cue and target (400-800 ms post cue-onset). The *post-target* ERP analysis was in the 200 ms following the target. *Right:* Graphical representation of experimental set-up with monitor presenting the visual RSVP stream and visual targets. Tactile stimulators were attached to the left and right index fingers and hands were covered during the experiment.

6.2.3 Design and procedure

Each trial consisted of a stream of 15 or 16 letters. Within this RSVP stream a tactile cue appeared to the left or right, which the participant was instructed to ignore. In the single task, if the participant felt a second tap (i.e. the tactile target) then they responded by saying *tap*. In the dual task the participant also responded if a number was presented within the visual stream. Tactile and visual target were never presented together in the same trial.

Each task consisted of 6 blocks with 88 trials in each block. All trials included a tactile cue. Following this cue, on 40 trials there was a tactile target, on 40 trials a number was presented and the remaining 8 trials were catch trials where no number or tactile target was presented. The trials were randomly presented within each block. Out of the 40 trials with tactile targets, 20 trials were valid (cue and target presented to the same side) and 20 invalid

(cue and target at opposite sides), and this was balanced across left and right. In total there were 120 valid and 120 invalid trials. Each participant completed a practice block consisting of 28 trials for each task, 12 with visual targets and 12 trials with tactile targets (6 valid and 6 invalid) and 4 catch trials. As the visual targets were presented centrally and not laterally, these were not valid or invalid.

Each trial started with the presentation of 3 letters, each 100 ms in duration (see Figure 6.1 for graphical representation of a trial). This was followed by the tactile cue to either the left or right, and simultaneous presentation of a 4th letter, both 100 ms long. Following the 100 ms tactile cue (which participants were instructed to ignore), 7 letters were presented (ISI of 700 ms) prior to the presentation of either a number for 100 ms or a tactile target to either the left or right for 100 ms. The target (tap or number) was followed by 3 additional letters. The tactile target stimuli were always presented together with a letter to not create a break in the letter stream presentation. In the single task the participant only responded if there was a tactile target by saying *tap* as rapidly as possible. Following the response (or if no response was made within 1500 ms) there was a random inter-trial interval of 1700-2700 ms before the presentation of the next trial. A fixation cross was presented throughout the ITI. In the dual task the participants responded *tap* to the tactile targets and *screen* if presented with a number. The experimenter manually coded the response in the adjacent room as the voice key did not distinguish between the two responses.

To reduce the anticipation of when the cue would appear, half the trials had 4 instead of 3 letters prior to the cue presentation, however, the SOA was the same in all conditions. Each trial of 15 letters was randomly selected out of a set of 20 different letter streams. The reason for not completely randomizing the letter presentation was to avoid a letter being presented twice in one trial. In particular to avoid presenting the same letter one after the other and therefore appear over 200 ms, as this may result in that letter appearing to “pop-out” in the RSVP stream. The numbers were completely randomly generated from trial to trial. The numbers were also presented during the single task, even though they did not require a response.

6.2.4 Behavioural analysis

Behavioural data were submitted to a 2x2 repeated-measures ANOVA with the factors Task (single, dual) and Cue (valid, invalid). A Task*Cue interaction was followed up with

paired samples t-test for each task separately. To compare RTs between modalities a paired samples t-test was conducted comparing RTs to visual targets and tactile targets (averaged over valid and invalid trials) in the dual task. Trials with RTs less than 100 ms and greater than 1200 ms were excluded from subsequent analysis, and in the dual task discrimination errors were also excluded. This led to the exclusion of less than 3% of trials in the single task and 7% in the dual task. Moreover, out of the catch trials in the dual task there were on average 12.5% errors (incorrect responding to the catch trial).

6.2.5 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 . 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. For the interval between the cue and target (which encompassed the *cue-locked* and *cue-target interval* analysis) EEG was epoched offline into 900 ms periods starting 100 ms prior to cue onset and ending at target onset. For *post-target* ERP analysis EEG was epoched offline into 300 ms periods starting 100 ms before the target and 200 ms after cue onset. The time window was restricted to 200 ms post-target to diminish contamination of the ERPs by behavioural responses. Baseline correction was performed for both cue-target and post-target analysis time windows (100 ms period preceding onset of cue and target, respectively). Trials with eye movements or eye-blinks (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 in the analysed intervals) 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 and catch trials were excluded from EEG analysis. This resulted in subsequent ERP analysis being based on an average of 234 trials in the dual task (less than 5% of trials removed) and 228 trials in the single task (less than 3% of trials removed).

The interval between the cue and target was divided into two types of analysis; *cue-locked* ERPs and *cue-target interval* ERPs. The *cue-locked* analysis investigated the

somatosensory components in the time window immediately (350 ms) following the cue. The later *cue-target interval* (400 – 600 ms post cue onset) analysis investigated the lateralized effects of attention (e.g., presence of ADAN).

For *cue-locked* analysis of somatosensory components, ERPs were averaged separately for Task (single and dual) and 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, 70-90 ms, 90–120 ms and 120-150 ms post-stimulus, respectively). To investigate longer-latency effects of somatosensory processing differences between Tasks, mean amplitudes were also computed between 150-200 ms (Nd1) and 200-350 ms (Nd2) after cue onset. A repeated-measures ANOVA was conducted to compare perceptual load modulations with the factors Task (single, dual), 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 around somatosensory areas and where attention effects on tactile processing have previously been reported (e.g., Eimer & Forster, 2003a).

For later *cue-target interval* analysis, ERPs were averaged separately for Task (single and dual) and Cue (cue left and cue right) and analyzed 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). The selection of electrodes in the analysis was based on sites commonly used to investigate lateralized cue activity associated with the fronto-parietal attention network (see e.g., Gherri & Martin Eimer, 2008). Mean amplitude 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). These were subjected to separate repeated-measures ANOVAs with factors Cue (cue left, cue right), Hemisphere (left, right) 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 (single and dual) and cue type (valid, invalid). ERP mean amplitudes were computed for measurement windows centred on the peak latencies of the somatosensory P45, N80, P100 and N140 components (46-66 ms, 70-90 ms, 92–122 ms and 124-158 ms post-stimulus, respectively). To investigate mid to longer-latency effects of spatial attention, mean amplitudes were also computed between 160-200 ms (Nd1) after tactile stimulus onset. A repeated-measures

ANOVA was conducted to compare attentional modulations with the factors Task (single, dual), Cue (valid, invalid), Electrode Site (CP1/2, CP5/6, C3/4, FC1/2, FC5/6, T7/8) and Hemisphere (ipsilateral, contralateral). The electrode selection for *post-target* analysis was the same as for *cue-locked* analysis.

For all ANOVAs analysed in which the assumption of Sphericity was violated, Greenhouse-Geisser adjusted degrees of freedom and probability levels were reported.

Any significant attention modulations in the post-target interval were correlated with behavioural RT effects to further investigate any relationship between the two measures. An ERP attention effect was computed for electrodes demonstrating the significant modulation, thus, if the attention effect was over contralateral electrodes, then only effects over contralateral electrodes would be correlated with RT effect.

6.3 Results

Behavioural performance showed IOR in the single task whilst no difference in RTs in the dual task suggesting increased visual perceptual load affects exogenous tactile processing (see Figure 6.2). Analysis of *cue-locked* somatosensory ERPs showed a task modulation of the P100. Specifically, increased perceptual load resulted in decreased amplitude at the P100. ERP analysis in the later *cue-target interval* showed an ADAN at anterior and central electrodes starting at around 400 ms post cue onset and continuing until target onset at 800 ms in both tasks. Analysis of *post-target* ERP effects showed attention to modulate earlier somatosensory components (N80) in the single task whilst not in the dual task. Following the N80, both tasks demonstrated attention modulations at the P100, N140, and mid to late latency Nd1.

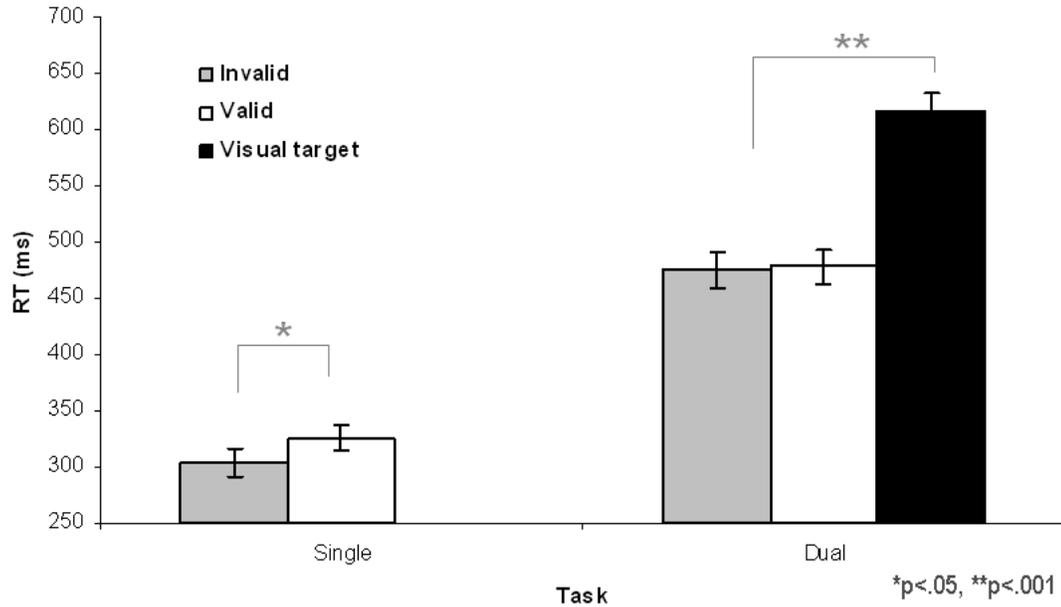


Figure 6.2 Behavioural results. Average response times (RTs in ms) and standard error bars displayed for each task. In the single task there was significant inhibition of return, whilst no difference between valid (white bars) and invalid trials (grey bars) in the dual task. Response times to visual targets (black bar) were significantly slower compared to tactile targets in the dual task.

6.3.1 Behavioural performance

There was a significant main effect of Task ($F(1,15)=69.21$, $p<.001$, $\eta^2_p= .82$) with faster RTs for single (M-314.21 ms, SD-97.41) compared to the dual task (M-476.62 ms, SD-123.89). There was also a main effect of Cue ($F(1,15)=20.07$, $p<.001$, $\eta^2_p= .57$) and importantly, a significant Task*Cue interaction ($F(1,15)=14.98$, $p=.002$, $\eta^2_p= .50$). Follow-up paired samples t-test for each task demonstrated significant IOR in the single task ($t(15)=-7.16$, $p<.001$) with faster RTs for invalid trials (M-302.84 ms, SD - 96.13) compared to valid trials (M-325.58 ms, SD - 100.47). There was no difference between invalid (M - 475.27, SD-1242.88) and valid trials (M-477.96 ms, SD - 126.97) in the dual task ($t<1$). Moreover, visual targets (M-616.07 ms, SD-123.15) were significantly slower ($t(15)=-5.04$, $p<.001$) compared to tactile targets in the dual task (M-476.62 ms, SD-125.62) (see Figure 6.2). To eliminate the possibility of order effects (although the task order was counterbalanced) a Task*Cue*Order analysis was carried out and showed no significant main effects or interaction with Order indicating that starting the experiment with the single or dual task did not affect the findings.

6.3.2 Cue-target ERP analysis

6.3.2.1 Cue-locked analysis of perceptual load effects on somatosensory processing

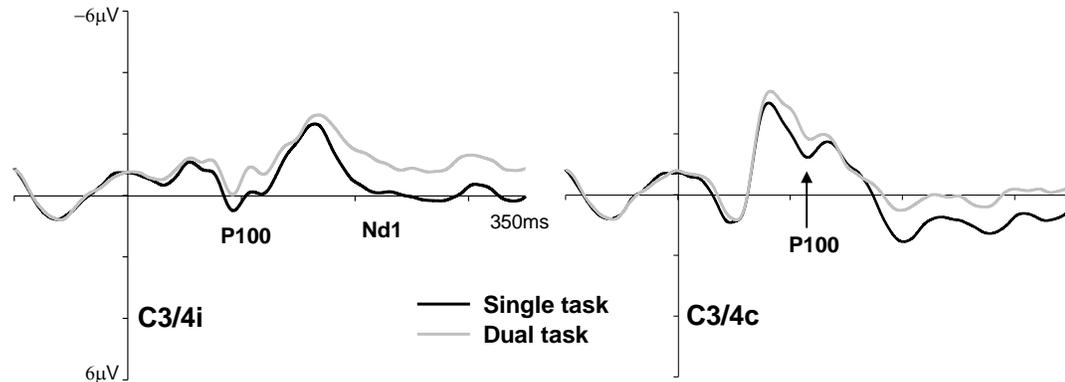


Figure 6.3 Grand average *cue-locked* ERPs in for single (black line) and dual task (grey line) over contralateral (right pane) and ipsilateral hemisphere (left pane) to cued side. There was a task difference at the P100 with enhanced positivity for the single over dual task as well as an amplitude difference for Nd1 (150-200 ms) over ipsilateral hemisphere.

In the Cue-locked ERP analysis, effects including the factor ‘Task’ represented a difference of somatosensory processing for the cue when load was high versus low.

Analysis of the **P45** and **N80** time windows showed no effect of Task, nor interactions including Task.

Analysis of the **P100** time window (90-120 ms) demonstrated a significant effect of Task ($F(1,15)=10.02$, $p=.006$, $\eta^2_p=.40$; and Task*Electrode Site interaction ($F(1.8,27.1)=6.03$, $p=.008$, $\eta^2_p=.29$)) with enhanced negativity for the single over dual task (see Figure 6.3).

Analysis of the **N140** (120-150 ms) effect showed no main effect of Task but a significant Task*Electrode site interaction ($F(2.1,30.9)=4.79$, $p=.015$, $\eta^2_p=.24$) Separate follow-up analysis showed a significant Task*Electrode interaction for both ipsilateral ($F(1.5,22.7)=18.36$, $p<.001$, $\eta^2_p=.55$) and contralateral hemisphere ($F(2.3,35.2)=5.20$, $p=.008$, $\eta^2_p=.26$), however, paired samples t-test revealed no significant effect of Task for any electrode pair. In other words, there was no effect of Task at for the N140 time window analysed.

The **Nd1** (150-200ms) analysis showed a borderline Task*Hemisphere interaction ($F(1,15)=4.43$, $p=.053$, $\eta^2_p=.23$; and also Task*Electrode site $F(1.5,23.1)=6.34$, $p=.01$, $\eta^2_p=.30$) and separate analysis for each hemisphere showed an ipsilateral effect of Task ($F(1,15)=4.95$, $p=.042$, $\eta^2_p=.25$) only. However, the **Nd2** (200-350 ms) was not significant ($F(1,15)=3.07$, $p=.10$, $\eta^2_p=.17$).

6.3.2.2.1 Cue-target interval analysis of late lateralized ERPs – ADAN and LDAP

Analysis of the cue-target interval showed ADAN effects, from 400 ms post cue onset to target onset at 800 ms, over anterior and central areas in both tasks (see Figure 6.5 for ERP waveforms and Figure 6.4 for topographical maps of ADAN distribution). Over Anterior electrodes, the ADAN was significantly larger in the single compared to the dual task. There was no LDAP in the single nor dual task. In the subsequent analyses the ADAN is represented by a Cue*Hemisphere interaction

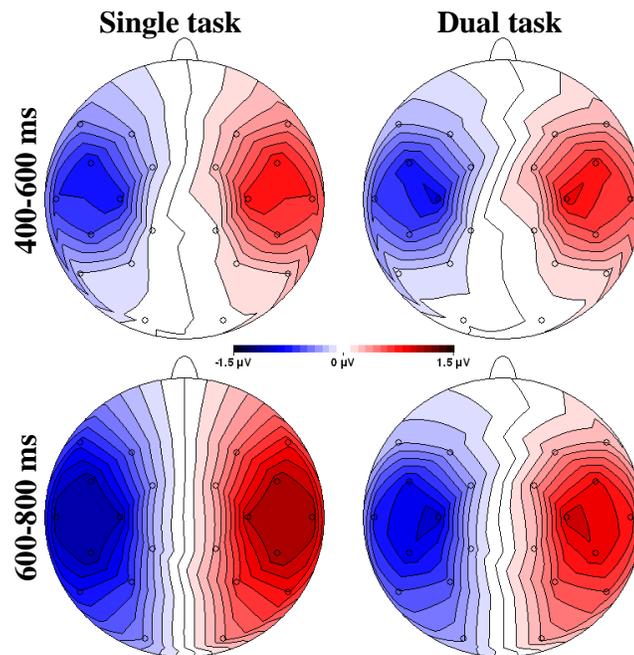


Figure 6.4 Scalp distribution of cue-target interval data for the single (left) and dual task (right), 400-600 ms (top) and 600-800 ms (bottom) post cue onset. Maps represent differences between brain activity observed over hemispheres ipsilateral and contralateral to the cued side. The obtained difference waveforms were mirrored to obtain symmetrical but inverse amplitude values for both

hemispheres. That is, the same effect is presented over both left and right hemispheres in the figure. Each contour line represents $0.05\mu\text{V}$ changes (amplitude range between -1.5 and $1.5\mu\text{V}$).

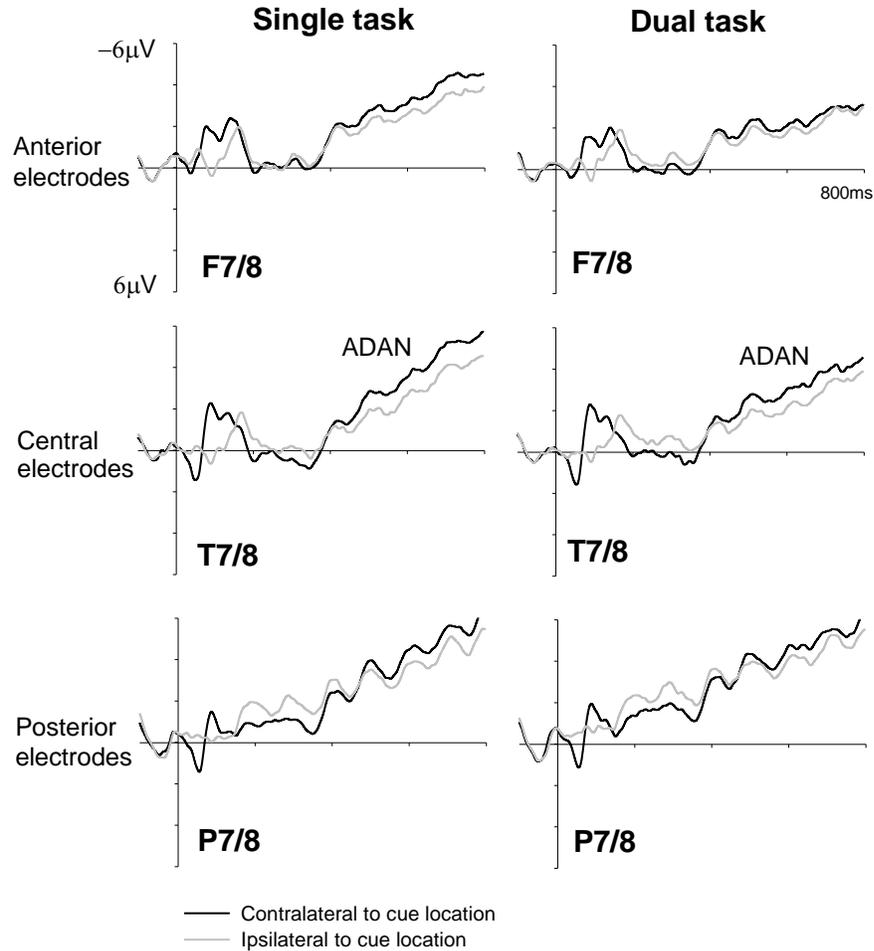


Figure 6.5 *Cue-target interval ERPs.* Grand-averaged ERP waveforms for the cue-target interval in single (left panel) and dual task (right panel). Black lines represent ERPs at electrodes contralateral and grey lines represent ERPs at electrodes ipsilateral to the cued side. Enhanced negativity (upward deflections) for contralateral compared to ipsilateral electrodes, indicating the presence of the ADAN. There was an ADAN demonstrated in both tasks. At anterior electrodes the ADAN effect was significantly larger in the single compared to dual tasks at the 600-800 ms window.

400-600 ms time window

In both single and dual tasks there was an ADAN like waveform at anterior and central electrode sites in the 400-600 ms time window.

Anterior electrodes

Analysis of anterior electrodes showed a significant Cue*Hemisphere interaction ($F(1,15)=33.72$, $p<.001$, $\eta^2_p=.69$), and also Cue*Electrode site*Hemisphere interaction ($F(2,30)=34.48$, $p<.001$, $\eta^2_p=.70$) with enhanced negativity for electrodes contralateral to Cue location. There was no Task*Cue*Hemisphere interaction

Central

There was a significant Cue*Hemisphere interaction ($F(1,15)=27.0$, $p<.001$, $\eta^2_p=.64$), and also Cue*Electrode site*Hemisphere interaction ($F(2,30)=9.56$, $p=.001$, $\eta^2_p=.40$).

Posterior

There were no Cue*Hemisphere, nor Task*Cue*Hemisphere interactions. There was a significant Cue*Electrode site*Hemisphere interaction ($F(2,30)=5.73$, $p=.008$, $\eta^2_p=.28$). However, follow-up analysis for each electrode (Bonferroni corrected) yielded no significant Cue*Hemisphere interaction.

Table 6.1 Summary of cue-target interval attention effects

	Task	400-600 ms	600-800 ms
Lateralized Posterior electrodes P3/4, P7/8, O1/2	Single	n.s.	p<.001
	Dual		
Lateralized Central Electrodes C3/4, CP5/6, T7/8	Single	p<.001	p<.001
	Dual		
Lateralized Anterior electrodes F3/F4, F7/F8, FC5/Fc6	Single	p<.001	p<.001
	Dual		p<.001

Note. Summary of statistical results (probability levels (p) and non-significance (n.s.) stated) of lateralized cueing effects (Cue*Hemisphere interaction stated) for the cue-target interval at three different scalp areas and at two time intervals during which the ADAN and LDAP are commonly observed. Where there was a significant Task*Cue*Hemisphere interaction the lateralized cueing effects are reported for each task separately.

600-800 ms time window

At this later time interval there was an ADAN in the 600-800 ms time interval over anterior, central and posterior electrodes. Over anterior electrodes, this ADAN effect was significantly larger in the single task compared to the dual task (see Figure 6.4 & 6.5). There was no LDAP at this time interval.

Anterior electrodes

Analysis of anterior electrodes showed a significant Task*Cue*Hemisphere interaction ($F(1,15)=15.02$, $p=.001$, $\eta^2_p=.50$, and also Cue*Hemisphere ($F(1,15)=43.50$, $p<.001$, $\eta^2_p=.74$) and Cue*Electrode site*Hemisphere ($F(2,30)=40.35$, $p<.001$, $\eta^2_p=.73$) interaction). Follow-up analysis for each task separately showed a Cue*Hemisphere interaction in the single task ($F(1,15)=45.09$, $p<.001$, $\eta^2_p=.75$, and also Cue*Electrode site*Hemisphere interaction ($F(2,30)=31.82$, $p<.001$, $\eta^2_p=.68$)) and analysis of the dual task also showed a Cue*Hemisphere interaction ($F(1,15)=28.69$, $p<.001$, $\eta^2_p=.66$, and also Cue*Electrode site*Hemisphere interaction ($F(2,30)=12.61$, $p<.001$, $\eta^2_p=.46$)). Thus, both tasks showed enhanced contralateral negativity and this ADAN effect was significantly larger in the single compared to the dual task.

Central electrodes

There was a Cue*Hemisphere interaction ($F(1,15)=53.46$, $p<.001$, $\eta^2_p=.78$) and close to significant Task*Cue*Hemisphere interaction ($F(1,15)=3.82$, $p=.070$, $\eta^2_p=.20$, and also Task*Cue*Electrode site*Hemisphere ($F(2,30)=2.96$, $p=.067$, $\eta^2_p=.17$) interaction). Separate analysis for each task showed a Cue*Hemisphere interaction ($F(1,15)=43.48$, $p<.001$, $\eta^2_p=.74$) in the single task, and also in the dual task (Cue*Hemisphere; ($F(1,15)=51.85$, $p<.001$, $\eta^2_p=.78$), and Cue*Electrode site*Hemisphere (($F(2,30)=4.65$, $p=.017$, $\eta^2_p=.24$) interaction).

Posterior electrodes

At posterior electrodes there was a Cue*Hemisphere interaction ($F(1,15)=34.75$, $p<.001$, $\eta^2_p=.70$, and also Cue*Electrode site*Hemisphere (($F(2,30)=12.86$, $p<.001$, $\eta^2_p=.46$) interaction).

6.3.2.2.2 Post-target ERP analysis

Analysis of the somatosensory processing in the 200 ms interval following the target demonstrated an attention modulation of the N80 component in the single whilst not in the dual task. The single task showed enhanced negativity for invalid over valid trials over contralateral hemisphere (see Figure 6.7). There was enhanced positivity at the P100 for valid over invalid trials in both tasks. The mid and late latency somatosensory ERPs (N140 and Nd1) showed enhanced negativity for valid over invalid trials in both tasks. In the subsequent analyses the attention effect is represented by an effect of Cue.

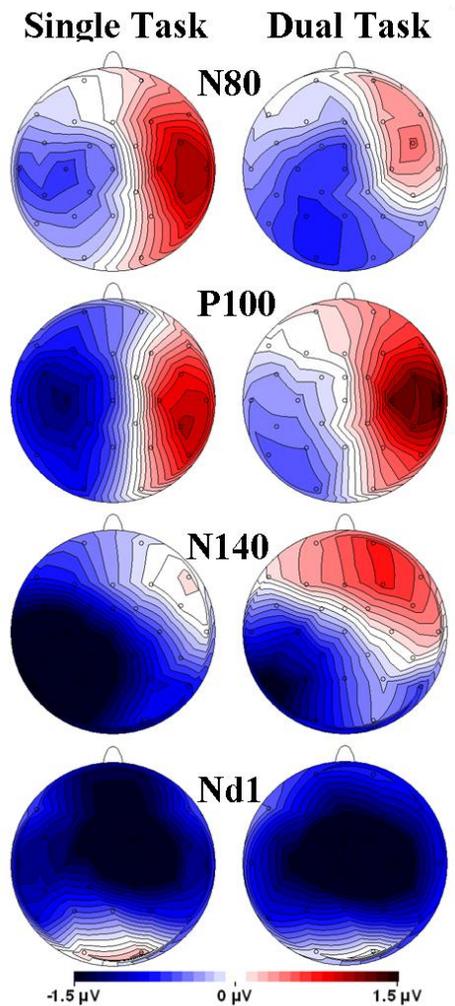


Figure 6.6 Topographic maps of the post-target attention effects (ERPs on invalid were subtracted from valid trials) at each time window analyzed presented for the single (left panel) and dual task (right panel). The right hemisphere shows attention effects contralateral to the target side and the left hemisphere shows ipsilateral attention effects in each task. The most prominent difference in attention effects between the two tasks is for the time range of the N80 component. Here the attention effect is present over contralateral hemisphere in the single task whilst not in the dual task. This difference was also supported by a significant Task*Cue*Hemisphere interaction for the N80.

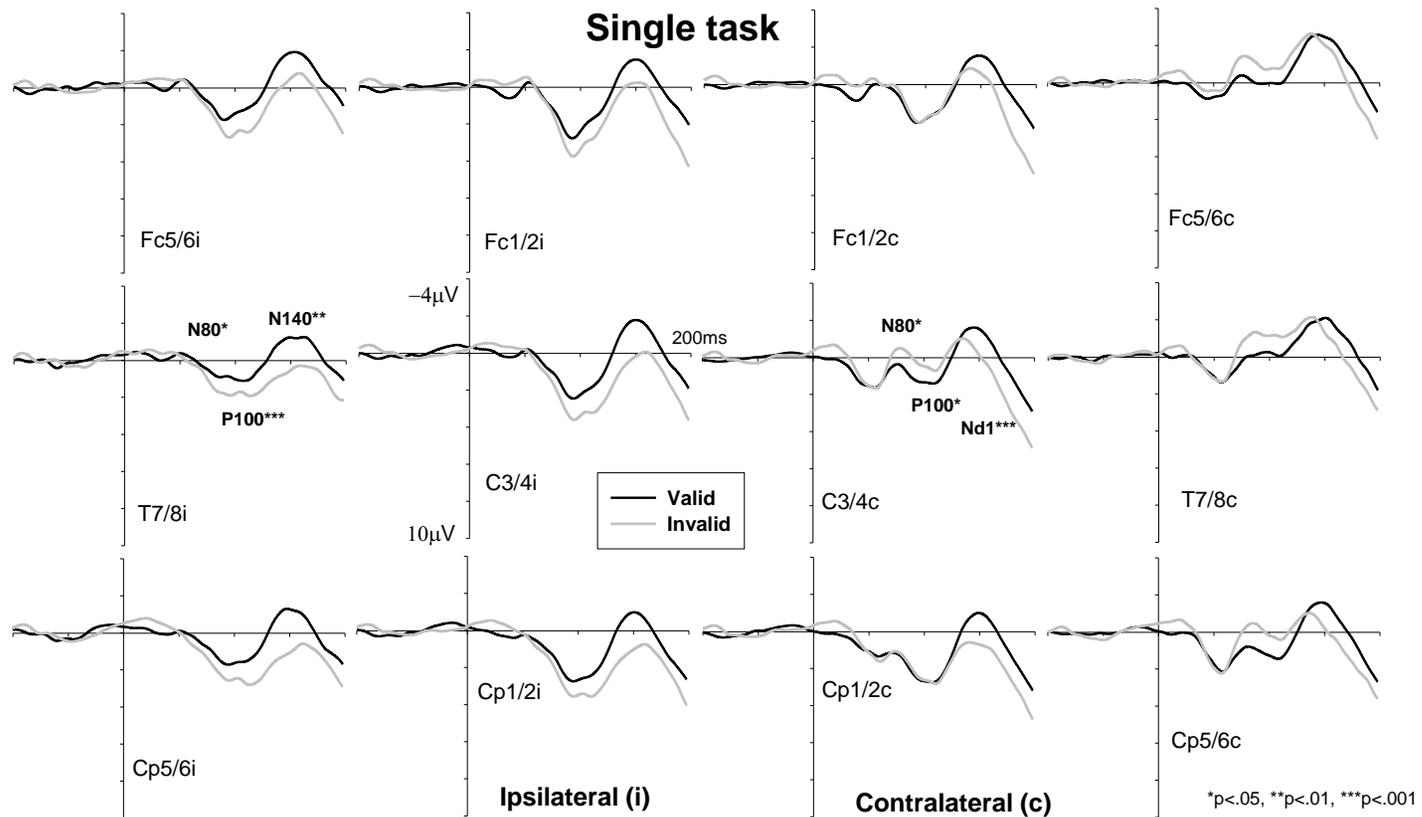


Figure 6.7 *Post-target ERPs in the single task.* Single task grand averaged somatosensory ERPs elicited on valid (black lines) and invalid (grey lines) trials in the 200 ms following target onset. The left side of the figure shows ERPs elicited over electrodes ipsilateral to target side and the right side shows contralateral electrodes. The components marked out on the graphs denote if the component was modulated by attention (significant difference between valid and invalid trials).

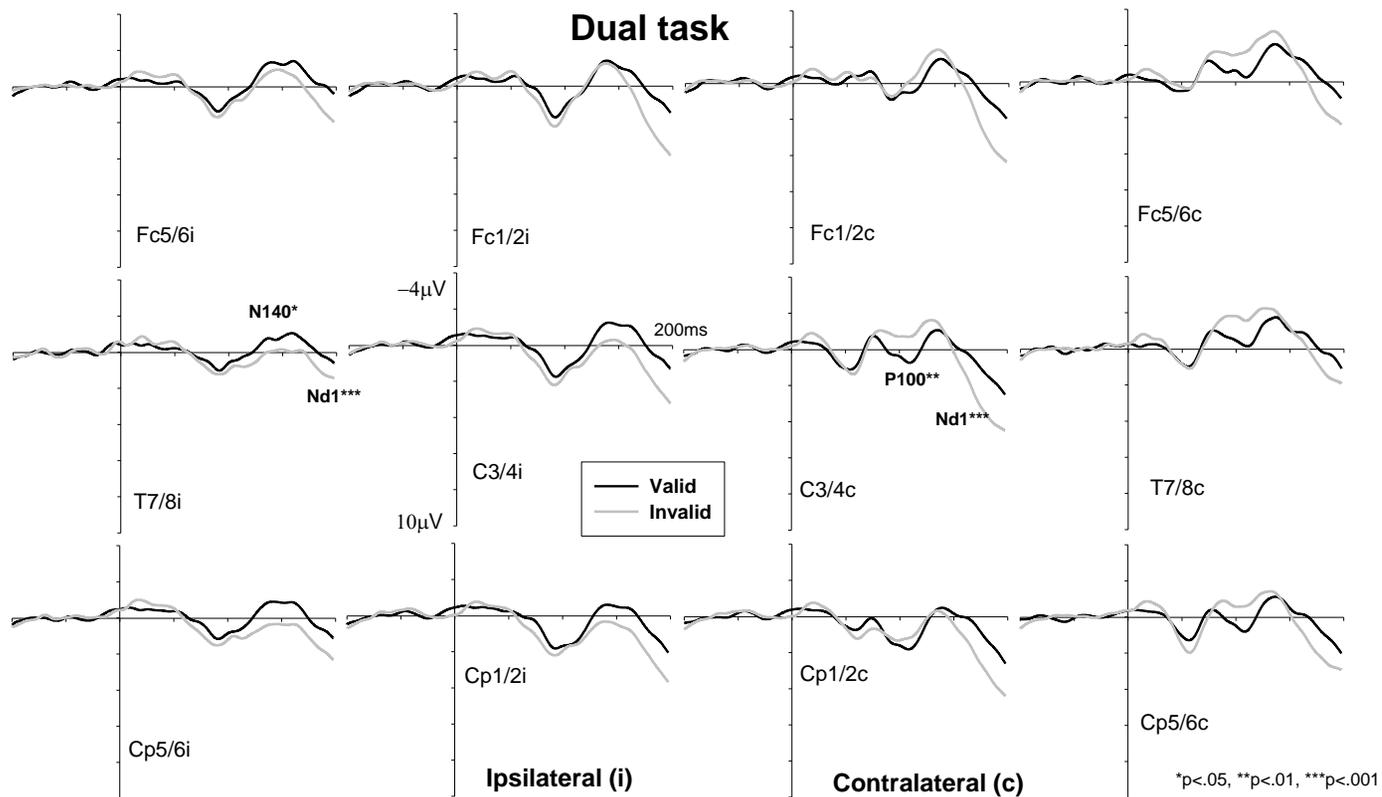


Figure 6.8 *Post-target ERPs in the dual task.* Dual task grand averaged somatosensory ERPs elicited on valid (black lines) and invalid (grey lines) trials in the 200 ms following target onset. The left side of the figure shows ERPs elicited over electrodes ipsilateral to target side and the right side shows contralateral electrodes. The components marked out on the graphs denote components modulated by attention (significant difference between valid versus invalid trials).

P45

Analysis of the P45 time window demonstrated a significant Cue*Electrode site interaction ($F(2.2,32.4)=5.43$, $p=.008$, $\eta^2_p=.27$). To break down the interaction further new variables for each electrode were created, with an average over both tasks and both hemispheres and paired samples t-tests for each electrode, comparing valid vs. invalid trials, showed no significant difference. That is, there was no overall P45 attention effect at any electrode.

N80

Analysis of the N80 time window showed a Task*Cue*Hemisphere interaction ($F(1,15)=14.27$, $p=.002$, $\eta^2_p=.49$; as well as; Task*Cue*Electrode Site*Hemisphere ($F(3.0,45.1)=8.81$, $p<.001$, $\eta^2_p=.37$), Cue*Electrode site*Hemisphere ($F(2.2,33.0)=8.01$, $p=.001$, $\eta^2_p=.35$), Cue*Hemisphere ($F(1,15)=29.64$, $p<.001$, $\eta^2_p=.66$), and Cue*Site ($F(1.8,27.4)=5.89$, $p=.009$, $\eta^2_p=.28$) interactions). This interaction was broken down further and each task was analysed separately.

Analysis of the **single tasks** showed a significant Cue*Hemisphere interaction ($F(1,15)=53.10$, $p<.001$, $\eta^2_p=.78$, and also Cue*Electrode site*Hemisphere interaction ($F(2.6,38.6)=13.74$, $p<.001$, $\eta^2_p=.48$)). Following the significant interaction, analysis of contralateral electrodes revealed a significant effect of Cue ($F(1,15)=7.86$, $p=.013$, $\eta^2_p=.34$, and Cue*Electrode interaction ($F(2.8,43.4)=10.81$, $p<.001$, $\eta^2_p=.42$)) demonstrating enhanced negativity for invalid over valid trials. The N80 attention modulation was also present over ipsilateral electrodes (Effect of Cue; $F(1,15)=4.58$, $p=.049$, $\eta^2_p=.23$) with enhanced negativity for valid over invalid trials. Thus, the N80 was modulated by attention over both hemispheres in the single task.

Analysis of the N80 time window for the **dual task** demonstrated a Cue*Hemisphere interaction ($F(1,15)=8.43$, $p=.011$, $\eta^2_p=.36$ and also Cue*Electrode site*Hemisphere interaction ($F(2.4,35.8)=3.17$, $p=.046$, $\eta^2_p=.17$)) Separate follow-up analyses showed no attention effect over ipsilateral hemisphere whilst a Cue*Electrode site interaction ($F(1.6,24.0)=4.23$, $p=.034$, $\eta^2_p=.22$) for the contralateral hemisphere analysis. This interaction was further broken down into paired samples t-tests which however revealed no significant effects. That is, there was no N80 attention modulation in the dual task.

P100

The overall analysis for the P100 showed no interactions including the factors Task and Cue together, however, there was a Cue*Hemisphere interaction ($F(1,15)=40.87$, $p<.001$, $\eta^2_p=.73$), and also Cue*Electrode site*Hemisphere interaction ($F(1.9,28.2)=14.17$, $p<.001$, $\eta^2_p=.49$), which was followed up with separate analysis for each hemisphere. Analysis of electrodes ipsilateral to target location showed a significant effect of Cue ($F(1,15)=8.67$, $p<.001$, $\eta^2_p=.37$) and a marginally significant Cue*Task interaction for ipsilateral electrodes ($F(1,15)=4.47$, $p=.052$, $\eta^2_p=.23$). Separate follow-up analysis for each task showed no effect of Cue over ipsilateral hemisphere in the dual task, whilst a significant P100 attention modulation over ipsilateral hemisphere in the single task (Cue; $F(1,15)=10.97$, $p=.005$, $\eta^2_p=.42$). Contralateral hemisphere analysis also demonstrated a significant effect of Cue ($F(1,15)=7.89$, $p=.013$, $\eta^2_p=.35$), and also Cue*Electrode ($F(2.0,30.0)=11.80$, $p<.001$, $\eta^2_p=.44$) with enhanced positivity for valid compared to invalid trials in both tasks. Concluding, the P100 attention modulation was present over both hemispheres in the single task whilst only over contralateral hemisphere in the dual task.

N140

There was a main effect of Cue ($F(1,15)=5.00$, $p=.041$, $\eta^2_p=.25$). There was a close to significant Task*Cue interaction ($F(1,15)=4.41$, $p=.053$, $\eta^2_p=.23$), and also significant Cue*Electrode site*Hemisphere ($F(2.0,29.4)=7.19$, $p=.003$, $\eta^2_p=.32$), Cue*Hemisphere ($F(1,15)=23.77$, $p<.001$, $\eta^2_p=.61$), and Cue*Electrode Site ($F(2.2,33.0)=7.66$, $p=.001$, $\eta^2_p=.34$). The interactions were followed up by separate analysis for each task.

Analysis of the **single task** showed a significant Cue*Hemisphere interaction at the N140 ($F(1,15)=25.70$, $p<.001$, $\eta^2_p=.63$), and also; Cue*Electrode site*Hemisphere ($F(2.0,29.7)=7.93$, $p=.002$, $\eta^2_p=.35$), Cue*Electrode site ($F(2.5,37.7)=11.23$, $p<.001$, $\eta^2_p=.43$) interactions and a main effect of Cue ($F(1,15)=7.84$, $p=.013$, $\eta^2_p=.34$). Follow-up analysis for each hemisphere showed no effect of attention at contralateral electrodes whilst for the ipsilateral hemisphere there was a main effect of Cue ($F(1,15)=16.30$, $p=.001$, $\eta^2_p=.52$), and also a Cue*Electrode Site interaction ($F(1.9,29.3)=8.50$, $p=.001$, $\eta^2_p=.36$). In other words, the N140 attention modulation in the single task was present over ipsilateral hemisphere with enhanced negativity for valid over invalid trials.

The **dual task** analysis showed a significant Cue*Hemisphere interaction ($F(1,15)=11.56$, $p<.001$, $\eta^2_p=.44$, and also; Cue*Electrode site*Hemisphere ($F(2.0,29.6)=3.51$, $p=.044$, $\eta^2_p=.19$) interaction) and follow-up analysis for each hemisphere separately showed, similar to the single task, a main effect of Cue ($F(1,15)=4.94$, $p=.042$, $\eta^2_p=.25$, and also Cue*Electrode interaction $F(2.2,33.6)=4.42$, $p=.017$, $\eta^2_p=.23$) only over the ipsilateral hemisphere.

Nd1

Analysis of the last time window showed a significant main effect of Cue ($F(1,15)=16.19$, $p=.001$, $\eta^2_p=.52$, and also Cue*Electrode interaction ($F(2.0,30.5)=5.86$, $p=.007$, $\eta^2_p=.28$)) with enhanced negativity for valid compared to invalid trials in both tasks

Table 6.2 *Post-target ERP attention effects*

Component	N80		P100		N140		Nd1
Laterality	Contra.	Ipsi.	Contra	Ipsi	Contra.	Ipsi.	Bilateral
Single task	p=.013	p=.049	p=.013	p=.005	n.s.	p=.001	p=.001
Dual task	n.s.	n.s.		n.s.	n.s.	p=.042	

Note. Summary of statistical results (probability levels (p) and non-significance (n.s.) stated) of post-target ERP attention effects (valid vs. invalid trials). For components where there was a significant Cue*Hemisphere interaction, separate analysis of Cue was conducted for each hemisphere (contra and ipsilateral to target location), otherwise stated as bilateral if attention effect present over both hemispheres. Where there was a Task*Cue interaction, further separate analysis for each task has been conducted (N80 & N140).

6.3.3 Behavioural and ERP performance correlations

Correlations between the ERP amplitude attention modulation in the post-target time window and the behavioural RT effect showed no significant relationship at any component analysed.

6.4 Discussion

This study was designed to investigate the effects of perceptual load on exogenous tactile orienting. The behavioural results showed IOR in the single task whilst this effect disappeared in the dual task. This suggested that increased perceptual load decreased the level of exogenous capture elicited by the tactile cues, which is in line with the load theory of selective attention (Lavie, 1995; Lavie et al., 2004). Moreover, the lack of exogenous

effect in the dual task adds to the now more widely accepted view that exogenous attention is not truly automatic (Santangelo & Spence, 2008). The behavioural results were similar to those of Santangelo and Spence (2007) who also used an RSVP stream with tactile cues and visual and tactile targets. In their dual task they found no effect of exogenous attention. When participants simply viewed a fixation cross, then tactile cues influenced behaviour in that valid trials were significantly faster compared to invalid trials (facilitation). In other words, low perceptual load led to exogenous cueing effects but not during high perceptual load. Santangelo and Spence (2007) also included a third condition whereby participants simply viewed the RSVP stream whilst only responding to tactile targets (as in the single task in the present study). In this condition they found no attention effect. They concluded that merely the presence of an RSVP stream was perceptually demanding. In turn, the attentional resources were exhausted and this led to abolished effects of exogenous tactile attention. This contrasts the present single task results which demonstrated an exogenous attention effect (IOR) in the condition where the RSVP stream was viewed but required no response. This may, if anything, suggest that tactile IOR is more resilient to the increase of perceptual load as compared to exogenous tactile facilitation effects. Although, a direct comparison would be required in order to establish this speculation.

The results are, as mentioned, in line with the load theory of selective attention (Lavie, 1995). However, exactly what the load manipulation was in this study may not be clear or easily distinguishable. The difference between the single and the dual task may have manipulated more than purely perceptual load. Attentional and task load may likely also have differed between the two tasks. Importantly, the results suggest that perceptual and not cognitive load was manipulated as the latter is proposed to show the opposite behavioural effect (Lavie et al., 2004). That is, increased cognitive load leads to increased capture of irrelevant peripheral stimuli. The results clearly indicated that load was manipulated, whether this load consisted of perceptual, attentional, and task load may not be possible to distinguish. In the literature these terms are used relatively interchangeably suggesting attentional and perceptual load refer to the same or similar underlying processes.

The ERP data was divided into three types of analyses, relating to three different time windows; *cue-locked*, *cue-target interval*, and *post-target* ERPs. Analysis of the *cue-locked* somatosensory evoked ERPs following the cue showed reduced P100 amplitude in the single compared to the dual task. That is, the somatosensory processing for task-irrelevant

stimuli was reduced with increased perceptual load. Similar conclusions can be drawn from analysis of the *cue-target interval*. The results showed an anterior directed attention negativity (ADAN) in both tasks starting at around 400 ms until target onset at 800 ms. Importantly, the ADAN effect was significantly smaller in the dual compared to single task at anterior electrodes. This indicated that increased perceptual load in a central task influences the ADAN effect following exogenous lateralized cues.

The behavioural findings, suggesting increased perceptual load decreased the attention capture by irrelevant tactile stimuli, were also supported by ERP findings. The *cue-locked* somatosensory ERPs showed significantly smaller amplitude in the dual compared to the single task at the P100 (see Figure 6.3). These findings are in line with research on the effects of visual processing and perceptual load. Studies using neuroimaging (Rees et al., 1997; Schwartz et al., 2005) and electrophysiology (Fu, Fedota, et al., 2010; Handy et al., 2001; Rauss et al., 2009) have shown decreased sensory processing for irrelevant peripheral stimuli when increasing a central load. In particular, an ERP study by Handy et al. (2001) showed a reduced P1 with increased perceptual load suggesting similar ERP modulations were affected in vision and touch. Moreover, O'Connell et al. (2011) presented participants with a central RSVP stream as well as flashing irrelevant visual stimuli in the periphery. O'Connell et al found the amplitude for the P2 and P3 components elicited by the irrelevant stimuli decreased as a function of increasing load. The present study is therefore consistent with findings resulting from research of visual processing, that processing of irrelevant stimuli is diminished with increasing central load.

The *cue-locked* ERP analysis also provided insight into the locus of selective attention in touch - whether attentional selection occurs early or late during sensory processing. The present study showed a task modulation in the *cue-locked* analysis at the P100. This early to mid latency component is suggested to originate bilaterally from the secondary somatosensory cortex (Frot et al., 2001; Mauguière et al., 1997; Zhu et al., 2007). Recent studies of visual attention have suggested V1 to be modulated by perceptual load. Rauss et al. (2009) found increased amplitude for the C1 component in their low compared to high load, suggesting high load filters out task irrelevant information at an early stage of processing. The *cue-locked* ERPs in the present study suggested attentional selection occurs relatively early, possibly in the SII. However, filtering irrelevant stimuli did not appear to affect primary sensory areas in touch as has been suggested in vision (Rauss et al., 2009).

The effects of varying perceptual load upon ERP effects were also demonstrated in the cue-target interval analysis investigating the presence of the ADAN and LDAP components. An LDAP was not found in either the single nor dual task. This is in line with previous studies in this thesis (in Chapter III-V) suggesting an LDAP to be absent during exogenous orienting. The presence of an ADAN in both tasks was in line with the results from studies using lateralized tactile cues in this thesis (Chapter III-V). The novelty of the ADAN in this study was that it was influenced by perceptual load. When perceptual load was low, there was a larger ADAN effect compared to during high perceptual load. The ADAN has been suggested to reflect supramodal endogenous attention mechanisms in the frontal areas (Eimer, van Velzen, & Driver, 2002; Seiss, Gherri, Eardley, & Eimer, 2007). In line with this hypothesis the present results demonstrated cross-modal effects of the ADAN. That is, increased *visual* perceptual load demonstrated decreased ADAN effect in *touch*. Importantly, the ADAN modulation was demonstrated following exogenous cue and not endogenous cues as previously reported (Eimer et al., 2002). In turn, indicating that perceptual load can influence cross-modal exogenous attention components possibly reflecting the fronto-parietal network.

The more commonly investigated ERP components modulated by attention are those in the *post-target* time window. The main difference between the two tasks in terms of post-target ERPs was the presence of an attention modulation for the N80 in the single but not dual task. In other words, this difference demonstrated that exogenous attention and perceptual load interacted at early somatosensory processes, likely primary somatosensory cortex (Allison et al., 1992, 1989; Forss & Jousmäki, 1998; Hari & Forss, 1999; Hari et al., 1984; Inui et al., 2004; Mima et al., 1998). The N80 component has, in a couple of studies, been shown to be modulated by endogenous tactile attention with enhanced negativity for attended over unattended stimuli (Eimer & Forster, 2003a; Michie et al., 1987). These endogenous studies demonstrated enhanced negativity for valid over invalid stimuli which was the opposite pattern to the present N80 (see Figure 6.7). The N80 has consistently been modulated by exogenous attention in previous studies presented in this thesis (Chapters III-V). It is likely that the N80 reflects an exogenous component driven by lateralized cues. Interesting is that the N80 is abolished when increasing perceptual load. The earliest exogenous attention modulation for the dual task was at the P100. Thus, the post-target ERP effects indicate that high perceptual load also delays the exogenous spatial attention

effects. In vision, perceptual load has shown to affect spatial based selection within extrastriate areas, through interactions of attention and perceptual load at the P1 (Handy & Mangun, 2000) and P1m (peak latency at around 100-140 ms over midline electrodes; Fu, J. Fedota, et al., 2010). The present *post-target* ERP results may therefore indicate that increased load can delay tactile attention modulations originating from the primary somatosensory cortex (the N80) whilst in vision, perceptual load interacts with attentional selection at a slightly later stage of processing, namely in extrastriate cortical areas...

Following the N80, the P100, N140 and Nd1 were modulated by attention in both tasks. The P100 is suggested to be a bilateral component originating in the secondary somatosensory cortex (Frot et al., 2001; Mauguière et al., 1997; Zhu et al., 2007) and the N140 is less clear as to a precise origin with multiple areas suggested (Garcia-Larrea et al., 1995), in particular the secondary somatosensory cortex and frontal areas (Allison et al., 1992; Hari et al., 1993, 1984; R Kakigi et al., 2000; Mima et al., 1998). These two components have repeatedly been demonstrated to be modulated by endogenous tactile attention (P100; Adler, Giabbiconi, & Müller, 2009; Eimer & Forster, 2003a, 2003b; Zopf et al., 2004), N140; (Adler et al., 2009; Eimer & Forster, 2003a; Forster & Eimer, 2004; Zopf et al., 2004). The similarity of attention modulations of the P100, N140 and Nd1 in both tasks suggests the attention effects at these components are less affected by varying load.

Taken together, this study demonstrated the effects of varying perceptual load in several different ways. Behavioural results showed increased perceptual load diminished exogenous attention effects (IOR). The load theory of attention suggests increased load reduces the ability for irrelevant stimuli to capture our attention. The behavioural results were consistent with this hypothesis as the “irrelevant” cue failed to have an effect in the high but not low load condition. The ERPs were compared between the single and the dual task for the cue – which participants were instructed to ignore. Analysis of these *cue-locked* ERPs demonstrated that higher load in a visual task reduced the somatosensory processing of the P100. A longstanding debate is the locus of selective attention, whether attention filters out irrelevant stimuli early (Broadbent, 1958) or late (Deutsch & Deutsch, 1963) during the perceptual process. The *cue-locked* ERP data suggests tactile stimuli are filtered out relatively early, in secondary somatosensory cortex, as indicated by the P100. Analysis of the *cue-target interval* demonstrated an ADAN in both single and dual tasks. The ADAN

effect was larger in the low versus high perceptual load task. This may indicate that increased perceptual load influences attentional control processes in the fronto-parietal attention network. Perceptual load also interacted with exogenous attention in the post-target interval. There was an N80 attention modulation in the single whilst not in the dual task. This suggests that attentional selection occurs earlier when perceptual load is low compared to high.

An interesting further area to explore would be to investigate varied tactile perceptual load upon processing of irrelevant tactile stimuli. That is, instead of investigating effects of load across modalities, to investigate whether similar results can be obtained by attending only within the tactile modality. Moreover, interesting would be to investigate how modality specific the load theory is. Tactile load could be manipulated whilst investigating the behaviour and electrophysiology of irrelevant visual stimuli. A supramodal view of the load theory would predict similar results to be obtained when the modalities were reversed.

CHAPTER VII

Summary and Conclusion

7.1 Introduction

A major distinction which has guided attention research over the past century is between endogenous (voluntary) and exogenous (stimulus driven) attention (James, 1890). Converging evidence from behavioural (e.g., Funes et al., 2005; Klein, 2004, for reviews), brain damaged patients (see Bartolomeo & Chokron, 2002, for a review), and neuroscientific methods (e.g., Macaluso, 2010, for a review) has further proposed a distinction between the two types of attention. The most popular method to investigate the effects of these two mechanisms has been using a Posner cue-target paradigm (Posner, 1978, 1980). The basis of this paradigm consists of a cue that is presented shortly before the imperative target. In the endogenous version, the cue is informative of where an upcoming target will appear. In the exogenous version, the cue is uninformative and serves as a distracting stimulus which may involuntarily capture our attention. The last three decades have seen countless variations of the cue-target paradigm. The relative simplicity of the cue-target paradigm has made this method of studying attention versatile. It has in particular been useful as similar versions of the paradigm have been adopted in vision, hearing, and touch. This allows for the possibility to compare attention effects across sensory modalities. The majority of research within the area of attention has investigated how we orient our attention in the visual and auditory modality and far less research has focused on our sense of touch (see Spence & Gallace, 2007, for a review of tactile attention).

The aim of this thesis was to explore tactile attention and the underlying neural correlates. In particular to investigate the neural correlates of exogenous tactile attention and inhibition of return (IOR). A few studies have explored the behavioural effects of exogenous tactile attention and a handful of studies have investigated the neural correlates of endogenous tactile attention. However, this thesis presents novel studies investigating the neural correlates of exogenous tactile attention. The first study (Chapter II) investigated the behavioural effects of whether exogenous attention interacts with endogenous orienting. The second study (Chapter III) aimed to explore the underlying neural correlates when IOR

was present versus absent. The study presented in Chapter IV addressed whether IOR is somatotopically or externally coded and how posture influenced tactile processing. The fourth study (Chapter V) aimed to investigate and contrast the neural correlates underlying exogenous and endogenous orienting. To isolate and compare the ERPs elicited by the two attention mechanisms an endogenous predictive and counter-predictive task was used in addition to an exogenous task. The final study (Chapter VI) addressed how varying perceptual load influenced the processing of irrelevant tactile stimuli.

ERP correlates of attentional control processes were analysed in all studies (apart from the behavioural study – Chapter II). This analysis focused on the lateralized waveforms in the cue-target interval. The more commonly investigated ERPs in the post-target interval - investigating tactile selective attention were also reported in all studies. Additionally, all ERP studies provided ample behavioural data. Consequently, any significant ERP attention modulations were correlated with behavioural response time effects (if present). This aimed to establish the presence of any direct link between brain responses and overt behaviour. All ERP studies are variations of the cue-target paradigm (Posner, 1978, 1980). The procedure employed - with a tactile cue-followed by a target after 800 ms stimulus onset asynchrony (SOA) - provided the possibility to compare ERP attention modulations and behavioural effects across studies. Moreover, the exogenous simple detection task was replicated in all ERP studies to provide a reliable picture of the somatosensory processing correlates of IOR.

7.2 Inhibition of return – behavioural effects

The common denominator throughout this thesis is IOR. Particular focus of the studies presented here was to investigate this behavioural effect in touch and to establish the neural pattern underlying this phenomenon. IOR is by nature a behavioural effect. To relate and link any ERP component(s) to IOR, it was imperative to firstly demonstrate the behavioural effect. The paradigm which has consistently demonstrated IOR in touch is a simple detection task. Simple detection tasks have demonstrated IOR at SOAs ranging from 100 ms to 6 seconds (Cohen et al., 2005; Lloyd et al., 1999; Röder et al., 2000; Röder et al., 2002). IOR is a result of slower response times at validly compared to invalidly cued locations. When interpreting this difference between valid and invalid trials it is not necessarily clear whether targets at validly cued locations are inhibited, or, whether invalidly cued targets are facilitated, or a combination of both. With the aim to resolve any

ambiguity, the study presented in Chapter III also included a neutral cue, consisting of a bilateral stimulation to both hands, cueing both possible target locations. The results from the detection task demonstrated that validly cued targets were significantly slower compared to the neutral trials, whilst there was no difference between invalid and neutral trials. This indicated that tactile IOR is due to, as the name implies, an inhibitory process. This is consistent with what has been demonstrated in the visual modality using similar bilateral stimuli as a neutral cue (Ayabe et al., 2008).

Although the main aim of this thesis was not to investigate whether IOR is an attentional, sensory, perceptual, motor, and/or response inhibition phenomena (see Berlucchi, 2006; and Chapter I for more detailed discussion of theoretical accounts), the different paradigms used may provide some insight into the debate.

An issue with IOR elicited by a simple detection task is that non-attentional explanations such as response inhibition (Poliakoff et al., 2002) or criterion shifts (Müller & Findlay, 1987) may explain the slowed response times for validly cued targets. Presence of IOR in discrimination tasks has suggested ameliorating or eliminating the possibility that IOR is not an attention effect (Miles et al., 2008). However, the discrimination task presented in Chapter III did not demonstrate IOR, thus raising the possibility that IOR in touch is not due to an underlying attention mechanism. Rather than suggesting IOR in this thesis (as demonstrated in studies presented in Chapters II-VI) is not due to an attention mechanism, the lack of IOR in the discrimination task is more likely a result of the particular SOA used in this task. The cue-target interval was set at 800 ms. Two recent studies have investigated the time-course of IOR in tactile discrimination tasks (Brown et al., 2010; Miles et al., 2008). Employing the same range of SOAs in both studies, they demonstrated facilitation of validly cued targets at 150 ms SOA (and also 350 ms in Miles et al.'s study). IOR did not develop until 1000 ms SOA, and at a cue-target interval of 550 ms there was no difference. At this intermediate SOA the valid cue facilitates and inhibits the subsequent target at the same location in the discrimination task resulting in no difference between valid and invalid trials. Based upon this time course the present results may suggest that IOR had not developed in the discrimination task at a SOA of 800 ms. The response pattern for the neutral cue in the discrimination task (Chapter III) may also be taken as support for a competing mechanisms theory of attention. The neutral trials were significantly faster compared to the valid trials, and although not significant, the invalid were also slower

compared to the neutral trials (see Figure 3.2). Taken together, the lack of IOR in the discrimination task was likely due to the specific SOA used. This contrasts an interpretation suggesting IOR is a non-attentional effect which disappears once response inhibition, criterion shifts, and sensory inhibition explanations are ameliorated using a discrimination task.

7.3 ERP correlates of attention selection

7.3.1 Neural correlates of exogenous attention and IOR

The aim of the studies in this thesis was to investigate the neural correlates of tactile attention, in particular exogenous orienting and IOR. ERP studies investigating IOR in vision have examined the neural correlates in the time window following target onset. ERPs in this time frame are thought to reflect attentional selection. Generally, a larger amplitude at a particular component is thought to reflect enhanced processing at that location, this logic is primarily based upon endogenous orienting studies (Luck et al., 2000). The ERPs of inhibitory processes are not as well established. However, Prime and Jolicoeur (2009) argue that if the "... inhibition of attention accounts are correct, attentional facilitation and IOR should arise from changes in the same stages of information processing" (p. 1278)¹². The following sections will discuss the somatosensory ERP components modulated by attention in the present thesis in light of previous endogenous tactile ERP studies. The somatosensory ERP modulations will also be compared to what has been demonstrated in ERP studies investigating IOR in vision. Importantly, the attention modulations in different studies of this thesis will be contrasted against each other. This will establish a more reliable pattern of the relationship between brain and behaviour.

7.3.2 The N80

The earliest component which demonstrated an attention effect in all ERP studies in this thesis was the N80. The N80 has been suggested to originate from the primary somatosensory cortex (SI), in the hemisphere contralateral to the side receiving tactile stimuli (e.g., Allison et al., 1992; Hari et al., 1984; Inui et al., 2004). The only previous studies which have demonstrated an attention modulation of this early component

¹² It is less clear exactly how inhibition is portrayed in the ERPs, whether inhibitory processes are manifested as suppressed components - for example, if the P100 reflects IOR then valid trials may be suppressed (i.e. less positive) compared to invalid trials, - whether inhibitory processes result in no difference between valid and invalid trials or an attentional difference with larger negativity for invalid trials compared to valid trials is not established.

employed a sustained endogenous attention paradigm. They demonstrated enhanced negativity for attended compared to unattended tactile stimuli (Eimer & Forster, 2003a; Michie et al., 1987; Schubert, Ritter, Wu, et al., 2008). Thus, indicating that endogenous orienting, at least using a sustained attention paradigm, can affect processing in SI.

The study presented in Chapter III aimed to assess the neural correlates of tactile selection when behaviourally IOR was present (in the simple detection task) and absent (in the discrimination task). Both tasks demonstrated this early N80 attention modulation with enhanced negativity for invalid over valid trials over contralateral hemisphere. Interestingly, this effect is opposite to that seen in previous endogenous studies which demonstrated enhanced negativity for valid over invalid trials (e.g., Eimer & Forster, 2003a). In the simple detection task exogenous attention leads to inhibition of response times, whilst endogenous attention leads to facilitation of responses to validly cued targets. The contrasting behavioural effects correspond to the contrasting polarity of the ERP modulation. This may indicate that the N80 in the exogenous paradigm reflects the inhibitory process. In other words, the slower condition in both endogenous (invalid) and exogenous (valid) tasks demonstrate reduced amplitude at the N80. In addition to a bilateral N80 attentional modulation in Chapter VI, a contralateral N80 attention effect was also replicated in Chapters III, IV and V together with IOR.

The study presented in Chapter IV investigated the effects of posture upon IOR. Regardless of the location of the hands in external space the results demonstrated IOR and an N80 attention modulation. This may not be surprising as the SI – where the N80 is proposed to originate – is somatotopically coded and not reliant upon external frame of reference (Penfield & Boldrey, 1937; Sutherland, 2006).

The N80 attention effect was again replicated in the study presented in Chapter V, which contrasted endogenous and exogenous orienting effects. In the exogenous task there was significant IOR and also enhanced negativity for invalid over validly cued targets at the N80, replicating the findings from Chapter III and IV. In the endogenous predictive task of this study the unilateral cues were made informative and the behavioural effect was reversed. That is, a target to the same side as the cue showed facilitation of response times as compared to IOR. Importantly, the N80 attention effect for the endogenous task also demonstrated enhanced negativity for invalid trials as seen in the exogenous tasks. The

present endogenous attention modulation of the N80 contrasts the N80 effect demonstrated in the sustained endogenous attention studies where valid trials showed enhanced amplitude (Eimer & Forster, 2003a; Michie et al., 1987). This may suggest the N80 attention modulation demonstrated throughout this thesis - using a transient paradigm - and the N80 demonstrated in previous sustained attention paradigms reflect qualitatively different processes. Likewise, Eimer and Forster (2003) concluded that sustained and transient modes of endogenous spatial attention affect different somatosensory processing stages.

Taken together the enhanced negativity for invalid over valid trials at the N80 component likely reflects a marker of exogenous tactile attention and/or perception related to cue location in a transient task. The attention modulation is unlikely directly linked to IOR as the same effect was demonstrated when IOR was absent (Chapter III – discrimination task), and also when the opposite behavioural effect was observed (facilitation of validly cued targets in endogenous predictive task – study presented in Chapter V).

7.3.3 *The P100 and IOR*

The general purpose of the study presented in Chapter III was to compare the neural correlates elicited in a task with IOR (detection task), to one where IOR was absent (discrimination task). As previously discussed, both tasks demonstrated an attention modulation at the N80. Following the N80, the P100 demonstrated a contralateral attention effect in the detection task whilst this contralateral effect was absent in the discrimination task. This was the only difference observed in the ERP pattern between the two tasks. This result was in line with the *a priori* prediction for the study presented in Chapter III suggesting that the P100 may, if any component, be associated with IOR. This hypothesis was based upon ERP studies of visual IOR which have demonstrated IOR and a significant reduced amplitude for valid compared to invalid trials at the P1 (McDonald et al., 1999; Prime & Jolicoeur, 2009; Prime & Ward, 2004, 2006; Tian & Yao, 2008; Wascher & Tipper, 2004).

Specifically, the results in the detection and discrimination task are comparable to findings from a recent exogenous visual attention study. Prime & Jolicoeur (2009) presented participants with an exogenous visual peripheral cue, followed by a target to the same or opposite side. In one task, during the cue-target interval, participants were required to re-orient attention back to the central fixation point prior to the target presentation. In a second

task no re-orienting was required. The hypothesis proposed that if attention is required to disengage from the cued location and subsequently re-orient to the target location, then this condition will maximize IOR. Prime and Jolicoeur demonstrated significant IOR in the re-orienting task whilst no behavioural difference between valid and invalid trials in their ‘re-orienting absent’ task. Importantly, they demonstrated a reduced P1 amplitude for valid compared to invalid trials only in the task which demonstrated IOR. The paradigms are not directly matched as Prime and Jolicoeur (2009) manipulated re-orienting, whilst the study in Chapter III compared a detection versus discrimination of targets (the two tasks also differ in terms of modalities investigated). However, the two studies may have elicited similar and comparable effects. Prime and Jolicoeur proposed that on a portion of trials in their re-orienting absent task, attention may have re-oriented back to fixation whilst not at other trials. In the trials when attention was disengaged then facilitation occurred for validly cued targets. When attention disengages and has to be re-oriented back to the cued location then inhibition for validly cued targets occur, and overall there is no difference. This account fits well with the discrimination task results were facilitation and inhibition for validly cued targets may have competed, resulting in no difference. Subsequently, there was no tactile P100 / visual P1 attention modulation in the discrimination task (Chapter III) and Prime and Jolicoeur’s ‘re-orient absent task’ where IOR and facilitation supposedly cancelled each other out.

The initial promise of a relationship between the P100 and IOR as demonstrated in the study presented in Chapter III was however not replicated. The exogenous tasks in Chapter IV and Chapter V – which were replications of the detection task in Chapter III – resulted in IOR whilst did not demonstrate an attention modulation of the contralateral P100 component. In the study presented in Chapter V the only condition which demonstrated an attention effect at the P100 was the endogenous predictive task. Importantly this condition resulted in the opposite behavioural effect to the exogenous task¹³.

¹³ The exogenous task in Chapter III and the endogenous task in chapter V demonstrated remarkably similar waveforms in and around the P100. Speculatively, it is possible that both P100 attention effects relate to opposite behaviour. The P100 in the exogenous task in Chapter III may be interpreted as suppression of the valid trials with enhanced negativity for invalid trials. On the other hand, the endogenous task in Chapter V may be interpreted as enhanced positivity for valid trials.

Collecting behavioural data in addition to the ERP recording provided the opportunity to correlate behaviour with ERP attention effects¹⁴. For the P100, if there was a clear relationship between the two measures then it would be hypothesised that the larger effect between response times for valid and invalid trials, the greater the amplitude difference between valid and invalid trials. Such a correlation was performed between all significant attention modulations and behavioural effects. However, there was no significant correlation between response time effect and ERP attention modulation at the P100, or at any other component, in the detection task. In other words, a direct link between behaviour and neural correlates at the somatosensory P100 was not established.

The research into the neural correlates of IOR in vision has also demonstrated mixed results. Studies have demonstrated a reduction in amplitude on valid trials without a behavioural IOR effect (Doallo et al., 2004; Hopfinger & Mangun, 1998). Other studies have shown a significant IOR effect but no P1 attention modulation (Prime & Ward, 2006). The mixed findings in visual attention literature have to some extent been attributed to variations in the paradigms used, rather than suggesting ambiguity in the link between IOR and the P1. The findings from this thesis indicate that the link between the P100 and IOR is not straight forward, at least not in the tactile modality. Evidence presented in this thesis therefore highlights the need for replication of studies linking the visual P1 to visual IOR using the same paradigm to establish the reliability of this relationship. Taken together, the somatosensory P100 is unlikely, at least on its own, directly related to tactile IOR.

7.3.4 The N140 and Nd

The visual N1 has previously been flagged as a potential “IOR component” as it has been found in studies which also showed behavioural IOR. A few studies have found a significantly enhanced negativity for invalid compared to valid trials together with a significant IOR effect (Prime & Ward, 2004, 2006; Tian & Yao, 2008). Other studies have found the opposite pattern with significant enhancement of valid over invalid trials when IOR was present (McDonald et al., 1999) and absent (Eimer, 1994; Hopfinger & Mangun,

¹⁴ The effects correlated were the attention effects for each individual subject - their average behavioural attention effect with their average attention modulation at a particular component. This resulted in a fairly small number to correlate, for example 18 data points in Chapter III as there were 18 participants. It was not possible to correlate the effects on a trial by trial basis as the effect needs to be calculated based upon at least two trials (one valid and one invalid). It was contemplated to correlate the effects of each experimental block to gain more data points. However, as all other analyses were based upon an average across task, this division of data could not be justified.

1998). Based upon the large diversity of results, the visual attention literature now seems to suggest that the N1 component is not directly linked to behavioural IOR (Prime & Ward, 2006). The N1 component demonstrated in visual attention research could arguably be compared to the N140 component in touch. Several tasks presented in this thesis demonstrated an attentional modulation of the N140. However, similar to the P100 and IOR, there was no clear relationship between the attention modulations of the N140 and IOR. There were similar attention modulation of the N140 when IOR was present (Chapter III – detection task; Chapter IV – all conditions; Chapter VI – low perceptual load task), and IOR was absent (Chapter III – discrimination task; Chapter VI – high perceptual load task). There was also no N140 effect when IOR was present (Chapter V – exogenous task). The reported N140 attention effects all demonstrated enhanced negativity for valid compared to invalid trials regardless of behavioural effects. This suggests that IOR is also not directly linked to this later stage of processing.

Along the same lines as the N140 findings and conclusions, several studies of visual attention have found IOR to be present together with an Nd attention effect (McDonald et al., 1999; Prime & Ward, 2004, 2006; Wascher & Tipper, 2004). In contrast, Prime and Jolicoeur (2009) did not find an attention modulation of the Nd when IOR was present and in their condition with no IOR, there was a significant Nd attention modulation. In all ERP studies presented in this thesis (apart from the exogenous task – Chapter V) there was an Nd effect with enhanced negativity for valid over invalid trials. Based upon the mixed behavioural results - similarly to the conclusion of the N140 – the Nd is likely to reflect processes not directly linked to the mechanisms underlying IOR. Instead, the Nd has been proposed to reflect deeper processing and indicate attentional influences at post-perceptual processing levels (Sambo & Forster, 2011).

7.4 Neural correlates of endogenous selective attention

The aim of the study presented in Chapter V was, in addition to explore the ERP pattern of IOR, to also investigate the neural correlates of endogenous attention. The effects of endogenous attention were measured in two tasks, an endogenous predictive and counter-predictive task. In the endogenous predictive task the cue indicated that the target would most likely appear at the same location. As previously stated, the N80 component showed an attention modulation with enhanced negativity for invalid over valid trials, a similar effect to all exogenous tasks in this thesis (apart from dual task in the study presented in

Chapter VI). When cue and target are presented at the same location it is not possible to isolate whether any observed effects are due to endogenous or exogenous processing. Any attention effects attributed to endogenous orienting could potentially be the result of exogenous processing elicited by the cue. To circumvent this problem the endogenous counter-predictive task required participants to attend to the opposite side to the cue. Interestingly, in this condition there was no contralateral attention effect at the N80 component. Thus, indicating endogenous attention can influence the early stages of tactile processing. This is in line with what has previously been demonstrated using a sustained attention paradigms (Eimer & Forster, 2003a; Michie et al., 1987).

The influence of endogenous attention upon the N80 component is possibly present in the perceptual load study (Chapter VI). In the single task (participants only responded to tactile targets) there was significant IOR and also a similar N80 effect as in the other exogenous tasks discussed. In the high perceptual load task participants also engaged their endogenous attention in a visual task. Behavioural results showed no IOR for this dual task and also no contralateral N80 attention modulation (see Figure 6.8). This may indicate that increased endogenous attention delayed the onset of the N80 in the dual compared to single task. However, the precise nature of the load manipulation in the study presented in Chapter VI is not clear leaving it open as to whether endogenous attention and/or increased perceptual load influenced the delayed N80 in the dual task. However, it may provide some support that endogenous and exogenous mechanisms can affect primary somatosensory cortex.

An attention modulation of the subsequent P100 component has been demonstrated in several endogenous tactile attention studies, with enhanced positivity for targets presented at attended over unattended locations (Eimer & Forster, 2003a; Schubert, Ritter, Wüstenberg, et al., 2008; Zopf et al., 2004). The endogenous predictive task presented in Chapter V similarly demonstrated enhanced positivity for valid over invalid trials at the P100. There was no P100 attention modulation in the exogenous task which may, in this particular study, suggest the P100 is a component more likely reflecting endogenous attention. However, the counter-predictive endogenous task did not demonstrate an attention effect at the P100 which argues against a clear-cut involvement of this component in endogenous orienting. Moreover, examination of the findings across studies and tasks in this thesis suggests the relationship is far from clear. The detection task presented in

Chapter III and single task in Chapter VI both demonstrated contralateral P100 attention modulations together with significant IOR.

Both endogenous tasks presented in Chapter V demonstrated attention modulations at the N140 and Nd components, respectively. Importantly both tasks showed the same bilateral effect with enhanced negativity for attended over unattended trials. In the endogenous predictive and counter-predictive tasks the attended targets appeared at opposite locations. This indicated that the attention modulation demonstrated could not be ascribed to cue location, but instead was dependent upon attended location. Similar attention modulations of the N140 and Nd components have been demonstrated in previous endogenous tactile attention studies (e.g., Eimer & Forster, 2003a; Forster & Eimer, 2004; Zopf et al., 2004). Moreover, for the first time a direct link between endogenous attention as measured by behaviour and ERPs was made. The N140 and Nd amplitude differences between valid and invalid trials were correlated with the behavioural response time effect of each participant. This showed; the larger the behavioural attention effect, the larger the ERP attention modulation at the N140 and Nd. This provides strong and novel empirical evidence that the N140 and Nd are directly related to behavioural outcomes of endogenous tactile orienting. Moreover, the relationship between the N140/Nd and behaviour in touch is consistent with similar findings in the visual modality. Increased N1 amplitude is proposed to reflect enhancement of attended stimuli (Talsma, et al 2005). For example, although the magnitude of the attention effects was not computed, Talsma, Mulckhuyse, Slagter, and Theeuwes (2007) demonstrated that larger N1 amplitude was associated (although not correlated) with faster response times.

7.5 The neural correlates of attentional capture

The study presented in Chapter VI aimed to investigate the effects of perceptual load on tactile processing. Participants engaged in two tasks, a high visual perceptual load and a low perceptual load task. The tactile stimuli were identical in the two different tasks, namely a simple detection task with an exogenous tactile cue followed by a tactile target. Behavioural results demonstrated IOR in the low perceptual load task whilst no difference between valid and invalid trials in the high perceptual load task. This result was consistent with the load theory of attention. This theory suggests that in a high perceptual load condition where our attentional capacity is fully engaged, then there is no spare capacity to process irrelevant stimuli. On the contrary, when we engage in a task with low perceptual

load, any capacity which has not been utilized in the relevant task is left over to automatically process task irrelevant stimuli (Lavie, 1995; Lavie et al., 2004). In other words, in the low perceptual load task there is spare capacity to process the irrelevant cue and it therefore influences response times in terms of IOR. In the high load task, then the cue does not influence response times as there are not sufficient attentional resources (see Santangelo & Spence, 2007, for comparable behavioural results). An interesting comparison between studies in this thesis is that the behavioural results from the perceptual load study (Chapter VI) and the results from the detection and discrimination task (Chapter III) can be viewed as similar. That is, IOR in the detection tasks whilst when discrimination of targets had to be performed, IOR disappeared. Whether the two studies manipulated the same underlying mechanisms is difficult to establish. The load study manipulated a cross-modal discrimination (between visual and tactile targets in the dual task) whilst a purely tactile discrimination in Chapter III.

In addition to investigating the somatosensory ERPs evoked by the target, the perceptual load study (Chapter VI) provided the opportunity to also investigate somatosensory ERPs elicited by the cue. The ERPs immediately following the cue were contrasted in the high versus low perceptual load task. This demonstrated reduced amplitude at the P100 in the high versus low perceptual load task. In other words, the irrelevant tactile stimuli demonstrated reduced neural processing when visual attention and perceptual load were increased. This finding is consistent with studies of visual attention: Studies using neuroimaging (Rees et al., 1997; Schwartz et al., 2005) and electrophysiology (Fu, Fedota, et al., 2010; Handy et al., 2001; Rauss et al., 2009) have shown decreased sensory processing for irrelevant peripheral stimuli when increasing a central load. Importantly, this shows for the first time how varying visual attentional load suppresses irrelevant tactile stimuli - not only through behaviour but now also observed in the neural processing.

7.6 Neural correlates of attentional orienting

The ERP studies in this thesis investigated for the first time, at least to the author's knowledge, the waveforms during the cue-target interval during exogenous orienting. After cue onset and during the cue-target interval orienting effects occur, either voluntarily or involuntarily. In endogenous attention research, two components¹⁵ have been highlighted to

¹⁵ A third early directing attention negativity (EDAN) was initially suggested to also reflect attention processing in the cue-target interval (Harter et al., 1989). However, more recent consensus is that the

reflect attentional control processes in the cue-target interval, namely the ‘anterior directing attention negativity’ (ADAN) and a ‘late directing attention positivity’ (LDAP). The ADAN appears at around 350 ms post cue onset and is a contralateral negativity demonstrated over anterior electrodes. This lateralized negativity contralateral to the attended side has been demonstrated in a number of visual (e.g., Hopfinger & Mangun, 2000), auditory (e.g., Green & McDonald, 2006) and tactile cue studies (Forster et al., 2009). The ADAN has been suggested to reflect supramodal attention mechanism in the frontal areas (Eimer, van Velzen, & Driver, 2002; Seiss, Gherri, Eardley, & Eimer, 2007). The LDAP appears later, at around 500 ms post cue onset, and is generated over posterior electrodes (Mathews et al., 2006). This enhanced positivity at contralateral compared to ipsilateral electrodes has been suggested to reflect attentional orienting mediated by external visual space (van Velzen, Eardley, Forster, & Eimer, 2006).

The ADAN and LDAP have been suggested to be components reflecting a fronto-parietal attention network. This attention network has in particular been investigated and mapped out using neuroimaging techniques (e.g. fMRI). A dorsal fronto-parietal (dFP) network has been associated with interpreting the cue and endogenously shifting and maintaining attention (Kelley et al., 2008). Brain activity following an exogenous cue which results in facilitation have failed to activate this dFP network suggesting a dissociation between endogenous and exogenous attention (Macaluso, 2010). However, simply concluding that endogenous and exogenous mechanisms activate different areas in the brain only tells half the story as exogenous attention can behaviourally lead to both facilitation and IOR. This point was demonstrated in an fMRI study comparing brain activity following endogenous and exogenous orienting when the exogenous orienting resulted in IOR (Mayer et al., 2004). In contrast to exogenous facilitation, they found exogenous IOR activated a similar dFP attention network as during endogenous orienting. Mayer and colleagues proposed the similar activation during endogenous attention and exogenous IOR is a result of functionally similar mechanisms operating in both conditions. Endogenous orienting aims to selectively direct attention to relevant information whilst at the same time limiting irrelevant stimuli. IOR is a mechanism used to save attention resources and reduce the influence of irrelevant stimuli.

EDAN reflects cue-specific properties rather than attention processing (van Velzen & Martin Eimer, 2003). No EDAN was present in any analysis of the cue-target interval of any study.

Analysis of the cue-target interval in both the detection and discrimination tasks presented in Chapter III demonstrated significant ADAN waveforms, starting at around 400 ms post cue onset. The ADAN was represented by enhanced negativity for anterior and central electrodes contralateral compared to ipsilateral to the stimulated hand. It should be noted that this may be conceptually different to the ADAN demonstrated in previous endogenous tasks. For the endogenous generated ADAN, the waveforms refer to enhanced negativity for the hemisphere contralateral to the attended side. There was no LDAP present in the cue-target interval in the detection or the discrimination task (Chapter III) and the ADAN continued until target onset. The lack of LDAP in this study may not be surprising as the hands were covered and limited ambient information was present. The LDAP has been suggested to be activated only when an external frame of reference is required (Eimer, Forster, et al., 2003). There was no particular requirement for the participants to use an external frame of reference to facilitate tactile processing in the study presented in Chapter III.

The ADAN has been suggested to be coded in a somatotopic frame of reference whilst the LDAP in an external reference frame. The former referring to where on the body stimuli appear, and the latter frame of reference referring to where the body part being stimulated is located in external space. Evidence for this spatial coding dissociation between the ADAN and LDAP has been derived from studies where hands are crossed over the body midline (e.g., Eimer, Forster, et al., 2003). This causes a conflict between the two frames of reference as compared to when hands are in a normal posture. It has been suggested that crossing the hands may induce qualitatively different processing as compare to how spatial coordinates are normally processed (Heed & Röder, 2010). The LDAP has however, been demonstrated to be affected by posture without crossing the hands. Eimer et al. (2004) demonstrated the LDAP to be attenuated when hands were close together compared to far apart. Posture did not affect the ADAN waveform in this endogenous tactile attention task.

The main purpose of the study presented in Chapter IV was to investigate how posture affects exogenous somatosensory processing. Hands were placed in front of the participant either close or far apart. A third condition included participants receiving tactile stimuli when the hands were behind their back. This condition aimed to investigate tactile processing in an external space which rarely is mediated by vision. Behaviour results demonstrated IOR in all conditions. The lack of posture effect upon IOR is in line with

previous findings suggesting the behavioural phenomena is anchored in somatotopic rather than external space (Röder et al., 2002). Analysis of the cue-target interval demonstrated an ADAN in all postures starting at around 400 ms and continuing until target onset. The ADAN was not manipulated by where the hands were located in space which is consistent with the ADAN being somatotopically coded (Eimer, Forster, et al., 2003). There was no LDAP present in any condition. This could be taken as support for the hypothesis that an external frame of reference was not employed during exogenous processing of tactile stimuli. However, and importantly, the presence or absence of an LDAP is not simply an indication of whether or not an external frame of reference was employed. The LDAP has also been demonstrated to relate to information about the ambient space. The hands were covered with a black cloth in all experiments which may also have had an influence on the presence of an LDAP.

A potential criticism towards the ADAN presented in the studies of Chapter III and IV is that the cues employed are unilateral. It is therefore not possible to establish whether the waveforms elicited are a result of the physical stimulation of one side or activation of an exogenous attention system. However, the ADAN waveform was nevertheless present during conditions which did not require or elicit endogenous attention, a finding previously not reported. Previous studies investigating endogenous tactile attention have used bilateral tactile cues to orient attention to one hand or the other (Forster et al., 2009). Bilateral cues are however not suitable when investigating exogenous attention in a cue-target paradigm.

The study presented in Chapter V aimed to compare exogenous with endogenous cue-target waveforms using the predictive and counter-predictive task, described earlier. The exogenous task presented in Chapter V replicated the previous findings demonstrating an ADAN waveform in the cue-target interval (studies presented in Chapter III and IV). The endogenous-predictive task also demonstrated an ADAN. Importantly, this ADAN effect was significantly larger compared to that in the exogenous task. Voluntarily orienting to the cued location therefore increased the ADAN effect. The presence of an ADAN in the endogenous-predictive tasks suggests that the ADAN is made up of both a stimulus driven and attention driven effect.

In the endogenous counter-predictive task there was no ADAN present. This is likely a result of the exogenous and endogenous ADAN effects cancel each other out. For example;

a cue presented to the left hand would evoke enhanced contralateral negativity over the right compared to the left hemisphere. The left cue also indicates to attend to the opposite side. Thus, the endogenously attended location is the right hand. The endogenously induced ADAN would therefore evoke enhanced contralateral negativity in the left hemisphere. Simultaneous endogenous and exogenous orienting therefore results in no difference in evoked activity between hemispheres (i.e. ADAN). Interestingly, at posterior electrodes an LDAP was present from approximately 600 ms post cue onset until target presentation, in the endogenous counter-predictive condition. That is, enhanced positivity for electrodes contralateral compared to ipsilateral to the attended side. A likely conclusion to be drawn may be that when attention is first directed to one hand and then needs to be shifted from that hand to the other, we engage an external frame of reference. This external frame of reference results in the presence of an LDAP, even when the hands are covered. However, there are alternative interpretations of the cue-target interval in Chapter V. It could be that the LDAP is present in all tasks but that the strong ADAN (exogenous or endogenous) masks any observed effect and only appears when the two ADANs cancel each other out. Moreover, the LDAP in the counter-predictive task is contralateral negativity to the location of the cue, similar to an ADAN. However, due to the posterior location and time window of the LDAP it seems most plausible that this cue-target waveform in the counter-predictive task is what previous research denotes an LDAP.

What can be established from investigating the cue-target interval in the exogenous tasks in this thesis is that a comparable waveform effect (the ADAN) to that seen following endogenous orienting is observed. This may indicate that a shared attention processing system for endogenous and exogenous (IOR) attention. At the very least, this thesis demonstrates novel findings that the ADAN waveform is not limited to endogenous attention but also elicited by unilateral exogenous cues. The ADAN elicited during exogenous tactile attention is not affected by varying posture. This is consistent with previous findings that the ADAN is somatotopically coded (e.g., Eimer et al., 2004). Furthermore, the stimulus driven ADAN can also be cancelled out by an ADAN elicited by endogenous orienting if the two waveforms are in conflict.

7.8 Conclusions and future direction

The studies presented in this thesis contribute to the field of tactile attention with novel behavioural and ERP findings. This thesis presents studies which for the first time

investigated the neural correlates of exogenous tactile attention and IOR. The first study of this thesis (Chapter II) demonstrated that exogenous irrelevant stimuli affects response times during an endogenous task. However, the two mechanisms did not interact suggesting the two orienting processes operate independently, at least during simple task demands. All ERP studies demonstrated an ADAN waveform in the cue-target interval in response to the unilateral cues. That is, enhanced negativity for the hemisphere contralateral to the stimulated hand. None of the exogenous tasks demonstrated an LDAP. This suggests that exogenous attention and IOR, at least in the present studies, is somatotopically coded. Adding endogenous orienting to unilateral cue (i.e. lateralized cues indicated the most likely target location instead of just acting as distractors; endogenous predictive task – Chapter V) increased the ADAN effect. Furthermore, the ADAN component was eliminated when the exogenous and endogenous orienting were in conflict (endogenous counter-predictive task – Chapter V). These results suggest the ADAN waveform can be made up of both endogenous and stimulus driven effects. An LDAP was only present during endogenous attention and when orienting was shifted from one side to the other.

A main conclusion to be drawn from the ERPs in the post-target time window is that not one component was demonstrated to be directly linked to IOR. The P100 component, which has in vision been proposed to reflect IOR processing, was not consistently modulated by attention when IOR was present in the studies across this thesis. The N80 was consistently modulated by attention with enhanced negativity for invalid compared to valid trials. Although not directly linked to behaviour, this modulation likely reflects early effects of exogenous rather than endogenous attention. The later components – N140 and Nd – showed to be directly linked to endogenous behavioural effects. This was demonstrated by significant correlations between response time and ERP effects in both the endogenous predictive and counter-predictive tasks (Chapter V). The perceptual load study (Chapter VI) demonstrated that increasing load leads to irrelevant stimuli being filtered out, as demonstrated by behavioural effects. The somatosensory evoked ERPs demonstrated the locus of selective attention to occur relatively early. The P100 of the irrelevant stimuli (the cue) was significantly smaller in the high versus the low perceptual load task. It can be concluded that varying visual perceptual load clearly affects tactile processing, demonstrated through both behavioural and ERP effects.

Both endogenous and exogenous versions of the Posner paradigm (Posner, 1978, 1980) were used in the studies presented in this thesis. The primary reason for choosing this paradigm was to provide results comparable with previous research. Previous ERP studies investigating visual IOR have employed a similar paradigm with peripheral cues and targets. Within tactile attention research the Posner paradigm is the most widely used method studying endogenous and exogenous attention. However, the cue-target paradigm has limitations. The exogenous nature of the tactile stimuli can be debated. The exogenous cue is arguably not the same as an unexpected tap on the shoulder which exogenous stimuli often is compared to. The cue in the cue-target paradigm is certainly to some degree expected. In the experiments in this thesis it appears at either one of only two locations. It may therefore be well founded to question whether results using a Posner paradigm in a laboratory setting reflects unexpected exogenous stimuli as it appears in the real world (see Kingstone, Smilek, Ristic, Kelland Friesen, & Eastwood, 2003, for further criticism of the Posner cueing paradigm). Future research may want to explore other paradigms investigating the neural correlates of exogenous tactile attention. For example, using paradigms where the stimuli are less expected which may be achieved by increasing the possible locations where stimuli could appear. The more locations should decrease the expectancy of exogenous stimuli and therefore better reflect exogenous attention as it may appear in a more natural setting.

A next stage would be to investigate how exogenous attention is processed across modalities. Behavioural studies have demonstrated crossmodal links for IOR (Ferris et al., 2008; Spence, Lloyd, et al., 2000). ERP studies have explored cross-modal links using endogenous attention paradigms (e.g., Eimer & Driver, 2000). However, no study has investigated the ERPs following exogenous cross-modal studies involving touch. It may be of particular interest to explore the cue-target interval during cross-modal exogenous orienting. Based upon endogenous attention research, the ADAN has been suggested to reflect a supramodal attentional control mechanisms (Seiss et al., 2007). Particularly interesting may be for future research to explore the cue-target waveforms in an exogenous cross-modal setting.

Continuing research into the neural correlates of tactile processing and attention may be of great practical and medical benefit. Medically unexplained symptoms (MUS) – symptoms lacking in any physical explanation - are common in medical settings (Nimnuan, Hotopf, &

Wessely, 2001). It has been proposed that disturbances in attention play a crucial role in MUS and chronic pain states (Brown, 2004; Crombez, van Damme, & Eccleston, 2005; Deary, Chalder, & Sharpe, 2007). Recently, Brown et al. (2010) demonstrated that people high in somatoform dissociation did not demonstrate the same cueing pattern as people with low somatoform dissociation. Specifically, people scoring high in somatoform dissociation did not demonstrate IOR in a tactile discrimination task (similar paradigm to that presented in Chapter III). Thus, emerging behavioural evidence suggest particular clinical populations demonstrate impaired processing using such cue-target paradigms as presented in this thesis. To map out the neural correlates of tactile attention may therefore benefit diagnosis of MUS. Before the leap of using ERPs as a diagnostic application can be made, it is imperative for future research to continue to map out reliable ERP patterns relating to exogenous and endogenous attention.

REFERENCES

- Adler, J., Giabbiconi, C.-M., & Müller, M. M. (2009). Shift of attention to the body location of distracters is mediated by perceptual load in sustained somatosensory attention. *Biological psychology*, *81*(2), 77-85.
- Allison, T., McCarthy, G., & Wood, C. C. (1992). The relationship between human long-latency somatosensory evoked potentials recorded from the cortical surface and from the scalp. *Electroencephalography and clinical neurophysiology*, *84*(4), 301-14.
- Allison, T., McCarthy, G., Wood, C. C., Darcey, T. M., Spencer, D. D., & Williamson, P. D. (1989). Human cortical potentials evoked by stimulation of the median nerve. Cytoarchitectonic areas generating short-latency activity. *Journal of neurophysiology*, *62*(3), 694-710.
- Axelrod, S., Thompson, L. W., & Cohen, L. D. (1968). Effects of senescence on the temporal resolution of somesthetic stimuli presented to one hand or both. *Journal of Gerontology*, *23*, 191-195.
- Ayabe, T., Ishizu, T., Kojima, S., Urakawa, T., Nishitani, N., Kaneoke, Y., & Kakigi, R. (2008). Neural processes of attentional inhibition of return traced with magnetoencephalography. *Neuroscience*, *156*(3), 769-80.
- Azañón, E., & Soto-Faraco, S. (2008). Changing reference frames during the encoding of tactile events. *Current biology*, *18*(14), 1044-9.
- Azañón, E., Longo, M. R., Soto-Faraco, S., & Haggard, P. (2010). The posterior parietal cortex remaps touch into external space. *Current biology*, *20*(14), 1304-9.
- Bartolomeo, P., & Chokron, S. (2002). Orienting of attention in left unilateral neglect. *Neuroscience and biobehavioral reviews*, *26*(2), 217-34.
- Berger, Andrea, Henik, Avishai, & Rafal, R. (2005). Competition between endogenous and exogenous orienting of visual attention. *Journal of experimental psychology. General*, *134*(2), 207-21.
- Berlucchi, G. (2006). Inhibition of return: A phenomenon in search of a mechanism and a better name. *Cognitive Neuropsychology*, *23*(7), 1065-1074.
- Broadbent, D. E. (1958). *Perception and communication*. London: Pergamon Press.
- Brown, R. J. (2004). Psychological mechanisms of medically unexplained symptoms: an integrative conceptual model. *Psychological Bulletin*, *130*(5), 793-812.
- Brown, R. J., Danquah, A. N., Miles, E., Holmes, E., & Poliakoff, E. (2010). Attention to the body in nonclinical somatoform dissociation depends on emotional state. *Journal of psychosomatic research*, *69*(3), 249-57.

- Cheal, M., & Chastain, G. (1999). Inhibition of Return: Support for Generality of the Phenomenon. *The Journal of General Psychology*, 126(4), 375 -390.
- Chica, A. B., & Lupiáñez, J. (2009). Effects of endogenous and exogenous attention on visual processing: an Inhibition of Return study. *Brain research*, 1278, 75-85.
- Chica, A. B., Sanabria, D., Lupiáñez, J., & Spence, C. (2007). Comparing intramodal and crossmodal cuing in the endogenous orienting of spatial attention. *Experimental brain research*, 179(3), 353-64.
- Chica, A. B., Taylor, T. L., Lupiáñez, J., & Klein, R. M. (2010). Two mechanisms underlying inhibition of return. *Experimental brain research*, 201(1), 25-35.
- Clark, V. P., & Hillyard, S. A. (1996). Spatial Selective Attention Affects Early Extrastriate But Not Striate Components of the Visual Evoked Potential. *Journal of Cognitive Neuroscience*, 8(5), 387-402.
- Cohen, J. C., Bolanowski, S. J., & Verrillo, R. T. (2005). A direct comparison of exogenous and endogenous inhibition of return and selective attention mechanisms in the somatosensory system. *Somatosensory & motor research*, 22(4), 269-79.
- Corbetta, M., Kincade, J M, Ollinger, J. M., McAvoy, M. P., & Shulman, G L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature neuroscience*, 3(3), 292-7.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature review Neuroscience*, 3(3), 201-15.
- Coward, R. S., Poliakoff, E, O'Boyle, D J, & Lowe, C. (2004). The contribution of non-ocular response inhibition to visual inhibition of return. *Experimental brain research*, 155(1), 124-8.
- Crombez, G., Van Damme, S., & Eccleston, C. (2005). Hypervigilance to pain: An experimental and clinical analysis. *Pain*, 116(1-2), 4-7.
- Danziger, S., Fendrich, R., & Rafal, R D. (1997). Inhibitory tagging of locations in the blind field of hemianopic patients. *Consciousness and Cognition*, 6(2-3), 291-307.
- Deary, V., Chalder, T., & Sharpe, M. (2007). The cognitive behavioural model of medically unexplained symptoms: A theoretical and empirical review. *Clinical Psychology Review*, 27, 781-797.
- Desmedt, J. E., & Tomberg, C. (1989). Mapping early somatosensory evoked potentials in selective attention: critical evaluation of control conditions used for titrating by difference the cognitive P30, P40, P100 and N140. *Electroencephalography and clinical neurophysiology*, 74(5), 321-46.
- Deutsch, J. A., & Deutsch, D. (1963). Attention: Some theoretical considerations. *Psychological Review*, 70(1), 80-90.

- Doallo, S., Lorenzo-López, L., Vizoso, C., Rodríguez Holguín, S., Amenedo, E., Bará, S., & Cadaveira, F. (2004). The time course of the effects of central and peripheral cues on visual processing: an event-related potentials study. *Clinical Neurophysiology*, *115*, 199-210.
- Dorris, M. C., Klein, R. M., Everling, S., & Munoz, D. P. (2002). Contribution of the primate superior colliculus to inhibition of return. *Journal of Cognitive Neuroscience*, *14*(8), 1256-1263.
- Eardley, A. F., & van Velzen, J. (2011). Event-related potential evidence for the use of external coordinates in the preparation of tactile attention by the early blind. *The European journal of neuroscience*, *33*(10), 1897-907.
- Egeth, H. E., & Yantis, S. (1997). Visual attention: Control, Representation, and Time Course. *Annual Review of Psychology*, *48*, 269-297.
- Eimer, M., & Driver, J. (2000). An event-related brain potential study of cross-modal links in spatial attention between vision and touch. *Psychophysiology*, *37*, 697-705.
- Eimer, M. (1994). An ERP study on visual spatial priming with peripheral onsets. *Psychophysiology*, *31*, 154-163.
- Eimer, M., & Forster, B. (2003a). Modulations of early somatosensory ERP components by transient and sustained spatial attention. *Experimental brain research*, *151*(1), 24-31.
- Eimer, M., & Forster, B. (2003b). The spatial distribution of attentional selectivity in touch: evidence from somatosensory ERP components. *Clinical Neurophysiology*, *114*(7), 1298-1306.
- Eimer, M., & van Velzen, J. (2002). Crossmodal links in spatial attention are mediated by supramodal control processes: evidence from event-related potentials. *Psychophysiology*, *39*(4), 437-49.
- Eimer, M., Forster, B., & van Velzen, J. (2003). Anterior and posterior attentional control systems use different spatial reference frames: ERP evidence from covert tactile-spatial orienting. *Psychophysiology*, *40*(6), 924-933.
- Eimer, M., Forster, B., Fieger, A., & Harbich, S. (2004). Effects of hand posture on preparatory control processes and sensory modulations in tactile-spatial attention. *Clinical neurophysiology*, *115*(3), 596-608.
- Eimer, M., van Velzen, J., & Driver, J. (2002). Cross-modal interactions between audition, touch, and vision in endogenous spatial attention: ERP evidence on preparatory states and sensory modulations. *Journal of cognitive neuroscience*, *14*(2), 254-71.
- Eimer, M., van Velzen, J., Forster, B., & Driver, J. (2003). Shifts of attention in light and in darkness: an ERP study of supramodal attentional control and crossmodal links in spatial attention. *Cognitive brain research*, *15*(3), 308-23.

- Ferris, T. K., Sarter, N. B., & Arbor, A. (2008). Cross-Modal Links Among Vision, Audition, and Touch in Complex Environments. *Human Factors*, 50(1), 17-26.
- Forss, N., & Jousmäki, V. (1998). Sensorimotor integration in human primary and secondary somatosensory cortices. *Brain research*, 781(1-2), 259-67.
- Forster, B., & Eimer, M. (2004). The attentional selection of spatial and non-spatial attributes in touch: ERP evidence for parallel and independent processes. *Biological psychology*, 66(1), 1-20.
- Forster, B., & Eimer, M. (2005). Covert attention in touch: behavioral and ERP evidence for costs and benefits. *Psychophysiology*, 42(2), 171-9.
- Forster, B., & Gillmeister, H. (2011). ERP investigation of transient attentional selection of single and multiple locations within touch. *Psychophysiology*, 48(6), 788-796.
- Forster, B., Eardley, A. F., & Eimer, M. (2007). Altered tactile spatial attention in the early blind. *Brain research*, 1131(1), 149-54.
- Forster, B., Sambo, C. F., & Pavone, E. F. (2009). ERP correlates of tactile spatial attention differ under intra- and intermodal conditions. *Biological psychology*, 82(3), 227-233.
- Frot, M., Garcia-Larrea, L., Guénot, M., & Mauguière, F. (2001). Responses of the suprasylvian (SII) cortex in humans to painful and innocuous stimuli. A study using intracerebral recordings. *Pain*, 94(1), 65-73.
- Frot, M., Rambaud, L., Guénot, M., & Mauguière, F. (1999). Intracortical recordings of early pain-related CO₂-laser evoked potentials in the human second somatosensory (SII) area. *Clinical neurophysiology*, 110(1), 133-45.
- Fu, S., Fedota, J. R., Greenwood, P. M., & Parasuraman, R. (2010). Dissociation of visual C1 and P1 components as a function of attentional load: an event-related potential study. *Biological psychology*, 85(1), 171-8.
- Fu, S., Fedota, J., Greenwood, P. M., & Parasuraman, R. (2010). Early interaction between perceptual load and involuntary attention: An event-related potential study. *Neuroscience letters*, 468(1), 68-71.
- Fu, S., Huang, Y., Luo, Y., Wang, Y., Fedota, J., Greenwood, P. M., & Parasuraman, R. (2009). Perceptual load interacts with involuntary attention at early processing stages: event-related potential studies. *NeuroImage*, 48(1), 191-9.
- Funes, M. J., Lupiáñez, J., & Milliken, B. (2005). The role of spatial attention and other processes on the magnitude and time course of cueing effects. *Cognitive processing*, 6(2), 98-116.

- Garcia-Larrea, L., Lukaszewicz, A. C., & Mauguiere, F. (1995). Somatosensory responses during selective spatial attention: the N120-to-N140 transition. *Psychophysiology*, *32*, 526–537.
- Gherri, E., & Eimer, M. (2008). Links between eye movement preparation and the attentional processing of tactile events: an event-related brain potential study. *Clinical neurophysiology*, *119*(11), 2587-97.
- Gibson, J. J. (1966). *The Senses Considered as Perceptual Systems*. Oxford, England: Houghton Mifflin.
- Graziano, M. S. A, & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia*, *44*(6), 845-59.
- Green, J. J., & McDonald, J. J. (2006). An event-related potential study of supramodal attentional control and crossmodal attention effects. *Psychophysiology*, *43*(2), 161-71.
- Haggard, P., Kitadono, K., Press, C., & Taylor-Clarke, M. (2006). The brain's fingers and hands. *Experimental brain research*, *172*(1), 94-102.
- Handy, T C, & Mangun, G R. (2000). Attention and spatial selection: electrophysiological evidence for modulation by perceptual load. *Perception & psychophysics*, *62*(1), 175-86.
- Handy, T. C., Soltani, M., & Mangun, G. R. (2001). Perceptual Load and Visuocortical Processing: Event-Related Potentials Reveal Sensory-Level Selection. *Psychological Science*, *12*(3), 213-218.
- Hari, R., & Forss, N. (1999). Magnetoencephalography in the study of human somatosensory cortical processing. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, *354*(1387), 1145-54.
- Hari, R., Karhu, J., Hämäläinen, M., Knuutila, J., Salonen, O., Sams, M., & Vilkmann, V. (1993). Functional organization of the human first and second somatosensory cortices: a neuromagnetic study. *The European journal of neuroscience*, *5*(6), 724-34.
- Hari, R., Reinikainen, K., Kaukoranta, E., Hamalainen, M., Ilmoniemi, R., Penttinen, A., Salminen, J., et al. (1984). Somatosensory evoked cerebral magnetic fields from SI and SII in man. *Electroencephalography and clinical Neurophysiology*, *57*(3), 254–263.
- Harter, M. R., Miller, S. L., Price, N. J., LaLonde, M. E., & Keyes, A. L. (1989). Neural processes involved in directing attention. *Journal of Cognitive Neuroscience*, *1*(3), 223-237.
- Heed, T. (2010). Touch perception: how we know where we are touched. *Current Biology*, *20*(14), R604-6.

- Heed, T., & Röder, B. (2010). Common anatomical and external coding for hands and feet in tactile attention: evidence from event-related potentials. *Journal of Cognitive Neuroscience*, 22(1), 184-202.
- Hernandez-Peon, R., Scherrer, H. & Jouvet, M. (1956) Modification of electrical activity in the cochlear nucleus during attention in unanesthetized cats. *Science*, 123, 331-332
- Hillyard, S. A., Vogel, E. K., & Luck, S. J. (1998). Sensory gain control (amplification) as a mechanism of selective attention: electrophysiological and neuroimaging evidence. *Philosophical Transactions of the Royal Society, Biological Sciences*, 353, 1257-1270.
- Ho, C., Santangelo, V., & Spence, C. (2009). Multisensory warning signals: when spatial correspondence matters. *Experimental Brain Research*, 195, 261-272
- Hopf, J. M., & Mangun, G R. (2000). Shifting visual attention in space: an electrophysiological analysis using high spatial resolution mapping. *Clinical neurophysiology*, 111(7), 1241-57.
- Hopfinger, J. B., Buonocore, M. H., & Mangun, G R. (2000). The neural mechanisms of top-down attentional control. *Nature neuroscience*, 3(3), 284-91.
- Hopfinger, J. B., & Mangun, G. R. (1998). Reflexive Attention Modulates Processing of Visual Stimuli in Human Extrastriate Cortex. *Psychological Science*, 9(6), 441-447.
- Indovina, I., & Macaluso, E. (2007). Dissociation of stimulus relevance and saliency factors during shifts of visuospatial attention. *Cerebral Cortex*, 17(7), 1701-1711.
- Inui, K., Wang, X., Tamura, Y., Kaneoke, Yoshiki, & Kakigi, Ryusuke. (2004). Serial processing in the human somatosensory system. *Cerebral cortex*, 14(8), 851-7.
- Ivanoff, J., & Klein, R. M. (2003). Orienting of attention without awareness is affected by measurement-induced attentional control settings. *Journal of vision*, 3(1), 32-40.
- James, W. (1890). *The principles of psychology*. New York: Holt
- Jonides, J. (1981). Voluntary versus automatic control over the mind's eyes. In J. Long & A. Baddeley (Eds.), *Attention and performance IX* (pp. 187–203). Hillsdale, NJ: Erlbaum.
- Kakigi, R, Hoshiyama, M., Shimojo, M., Naka, D., Yamasaki, H., Watanabe, S., Xiang, J., et al. (2000). The somatosensory evoked magnetic fields. *Progress in neurobiology*, 61(5), 495-523.
- Karnath, H.-O., Fruhmann Berger, M., Küker, W., & Rorden, C. (2004). The anatomy of spatial neglect based on voxelwise statistical analysis: a study of 140 patients. *Cerebral Cortex*, 14(10), 1164-1172.

- Kelley, T. A., Serences, J. T., Giesbrecht, B., & Yantis, S. (2008). Cortical mechanisms for shifting and holding visuospatial attention. *Cerebral cortex*, *18*(1), 114-25.
- Kennett, S., Eimer, M., Spence, C., & Driver, J. (2001). Tactile-visual links in exogenous spatial attention under different postures: convergent evidence from psychophysics and ERPs. *Journal of cognitive neuroscience*, *13*(4), 462-78.
- Kennett, S., van Velzen, J., Eimer, M., & Driver, J. (2007). Disentangling gaze shifts from preparatory ERP effects during spatial attention. *Neuroscience*, *44*, 69-78.
- Kincade, J. M., Abrams, R. A., Astafiev, S. V., Shulman, G. L., & Corbetta, M. (2005). An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. *The Journal of neuroscience*, *25*(18), 4593-604.
- Kingstone, A., Smilek, D., Ristic, J., Kelland F., C., & Eastwood, J. D. (2003). Attention, researchers! it is time to take a look at the real world. *Current Directions in Psychological Science*, *12*(5), 176-180.
- Klein, R. (2004). On the control of visual orienting. In M I Posner (Ed.), *Cognitive neuroscience of attention* (pp. 29-44). New York: Guildford press.
- Klein, R. M., & Taylor, T. (1994). Categories of cognitive inhibition with reference to attention. In D. Dagenbach & T. Carr (Eds.), *Inhibitory processes in attention, memory, and language* (pp. 113-150). San Diego: Academic.
- Klein, Raymond M. (2000). Inhibition of return. *Trends in cognitive sciences*, *4*(4), 138-146.
- Kóbor, I., Füredi, L., Kovács, G., Spence, Charles, & Vidnyánszky, Z. (2006). Back-to-front: improved tactile discrimination performance in the space you cannot see. *Neuroscience letters*, *400*(1-2), 163-7.
- Lavie, N. (1995). Perceptual load as a necessary condition for selective attention. *Journal of experimental psychology. Human perception and performance*, *21*(3), 451-68.
- Lavie, N., Hirst, A., de Fockert, J. W., & Viding, E. (2004). Load theory of selective attention and cognitive control. *Journal of experimental psychology. General*, *133*(3), 339-54.
- Lewis, J. W., & Van Essen, D. C. (2000). Corticocortical connections of visual, sensorimotor, and multimodal processing areas in the parietal lobe of the macaque monkey. *The Journal of comparative neurology*, *428*(1), 112-37.
- Lloyd, D. M., Bolanowski Jr, S. J., Howard, L., & McGlone, F. (1999). Mechanisms of attention in touch. *Somatosensory & Motor Research*, *16*(1), 3-10.

- Losier, B. J., & Klein, R. M. (2001). A review of the evidence for a disengage deficit following parietal lobe damage. *Neuroscience and biobehavioral reviews*, 25(1), 1-13.
- van der Lubbe, R. H. J., & Postma, A. (2005). Interruption from irrelevant auditory and visual onsets even when attention is in a focused state. *Experimental brain research*, 164(4), 464-71.
- Luck, S.J., Hillyard, S.A., Mouloua, M., Woldorff, M.G., Clark, V.P., Hawkins, H.L., (1994). Effects of spatial cueing on luminance detectability: Psychophysical and electrophysiological evidence for early selection. *Journal of Experimental Psychology Human Perception and Performance*, 20, 887-904.
- Perform. 20, 887–904. Luck, S., Woodman, G., & Vogel, E. (2000). Event-related potential studies of attention. *Trends in cognitive sciences*, 4(11), 432-440.
- Lupiáñez, J, Milán, E. G., Tornay, F. J., Madrid, E., & Tudela, P. (1997). Does IOR occur in discrimination tasks? Yes, it does, but later. *Perception And Psychophysics*, 59(8), 1241-1254.
- Macaluso, E. (2010). Orienting of spatial attention and the interplay between the senses. *Cortex*, 46(3), 282-97.
- Martínez, A., Anllo-Vento, L., Sereno, M. I., Frank, L. R., Buxton, R. B., Dubowitz, D. J., Wong, E. C., et al. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature neuroscience*, 2(4), 364-9.
- Mathews, S., Ainsley Dean, P. J., & Sterr, A. (2006). EEG dipole analysis of motor-priming foreperiod activity reveals separate sources for motor and spatial attention components. *Clinical neurophysiology*, 117(12), 2675-83.
- Mauguière, F., Merlet, I., Forss, N., Vanni, S., Jousmäki, V., Adeleine, P., & Hari, R. (1997). Activation of a distributed somatosensory cortical network in the human brain. A dipole modelling study of magnetic fields evoked by median nerve stimulation. Part I: Location and activation timing of SEF sources. *Electroencephalography and clinical neurophysiology*, 104(4), 281-9.
- Mayer, A. R., Dorflinger, J. M., Rao, S. M., & Seidenberg, M. (2004). Neural networks underlying endogenous and exogenous visual-spatial orienting. *NeuroImage*, 23(2), 534-41.
- McDonald, J. J., Ward, L. M., & Kiehl, K. A. (1999). An event-related brain potential study of inhibition of return. *Perception & psychophysics*, 61(7), 1411-1423.
- Medina, J., & Coslett, H. B. (2010). From maps to form to space: touch and the body schema. *Neuropsychologia*, 48(3), 645-54.
- Mele, S., Savazzi, S., Marzi, C. A., & Berlucchi, G. (2008). Reaction time inhibition from subliminal cues: is it related to inhibition of return? *Neuropsychologia*, 46(3), 810-9.

- Mesulam, M. M. (1999). Spatial attention and neglect: parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philosophical Transactions of the Royal Society of London - Series B: Biological Sciences*, 354(1387), 1325-1346.
- Michie, P. T. (1984). Selective attention effects on somatosensory event-related potentials. *Annals Of The New York Academy Of Sciences*, 425, 250-255.
- Michie, P. T., Bearpark, H. M., Crawford, J. M., & Glue, L. C. (1987). The effects of spatial selective attention on the somatosensory event-related potential. *Psychophysiology*, 24, 449-463.
- Miles, E., Poliakoff, E., & Brown, R. J. (2008). Investigating the time course of tactile reflexive attention using a non-spatial discrimination task. *Acta psychologica*, 128(2), 210-5.
- Mima, T., Nagamine, T., Nakamura, K., & Shibasaki, H. (1998). Attention modulates both primary and second somatosensory cortical activities in humans: a magnetoencephalographic study. *Journal of neurophysiology*, 80(4), 2215-2221.
- Mondor, T. A., & Amirault, K. J. (1998). Effect of same- and different-modality spatial cues on auditory and visual target identification. *Journal of Experimental Psychology: Human Perception and Performance*, 24(3), 745-755.
- Motter, B. C. (1993) Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *Journal of Neurophysiology*, 70, 909-919.
- Mulckhuyse, M., & Theeuwes, J. (2010). Unconscious attentional orienting to exogenous cues: A review of the literature. *Acta psychologica*, 134(3), 299-309.
- Müller, H. J., & Findlay, J. M. (1987). Sensitivity and criterion effects in the spatial cuing of visual attention. *Perception and Psychophysics*, 42(4), 383-399.
- Müller, H. J., & Humphreys, G. W. (1991). Luminance-increment detection: Capacity-limited or not? *Journal of Experimental Psychology Human Perception and Performance*, 17(1), 107-124.
- Müller, H. J., & Rabbitt, P. M. (1989). Reflexive and voluntary orienting of visual attention: time course of activation and resistance to interruption. *Journal of experimental psychology. Human perception and performance*, 15(2), 315-30.
- Natale, E., Marzi, C. A., Girelli, M., Pavone, E. F., & Pollmann, S. (2006). ERP and fMRI correlates of endogenous and exogenous focusing of visual-spatial attention. *The European journal of neuroscience*, 23(9), 2511-21.
- Nicoletti, R., Anzola, G. P., Luppino, G., Rizzolatti, G., & Umiltà, C. (1982). Spatial compatibility effects on the same side of the body midline. *Journal of Experimental Psychology: Human Perception and Performance*, 8(5), 664-73.

- Nimnuan, C., Hotopf, M., & Wessely, S. (2001). Medically unexplained symptoms: an epidemiological study in seven specialities. *Journal of Psychosomatic Research*, *51*(1), 361-367.
- Nobre, A. C., Sebestyen, G. N., & Miniussi, C. (2000). The dynamics of shifting visuospatial attention revealed by event-related potentials. *Neuropsychologia*, *38*(7), 964-74.
- Occelli, V., Spence, C., & Zampini, M. (2011). Audiotactile interactions in front and rear space. *Neuroscience and biobehavioral reviews*, *35*(3), 589-98.
- O'Connell, R. G., Schneider, D., Hester, R., Mattingley, J. B., & Bellgrove, M. A. (2011). Attentional load asymmetrically affects early electrophysiological indices of visual orienting. *Cerebral cortex*, *21* (5), 1056-1065.
- Paillard, J. (1999). Body schema and body image - A double dissociation in deafferented patients. In G. N. Gantchev, S. Mori, & J. Massion (Eds.), *Motor control, today and tomorrow* (pp. 197-214). Sofia: Academicno Izdatelstov.
- Penfield, W., & Boldrey, E. (1937). Somatic Motor and Sensory Representation in the Cerebral Cortex of Man As Studied By Electrical Stimulation. *Brain*, *60*(4), 389-443.
- Poliakoff, E., Spence, C., McGlone, F. P., & Cody, F.W.J. (2002). Tactile inhibition of return: non-ocular response inhibition and mode of response. *Experimental brain research*, *146*(1), 54-59.
- Poliakoff, E., O'Boyle, D. J., Moore, A. P., McGlone, F. P., Cody, F. W. J., & Spence, C. (2003). Orienting of attention and Parkinson's disease: tactile inhibition of return and response inhibition. *Brain*, *126*, 2081-2092.
- Posner, M. I, Cohen, Y., & Rafal, R. D. (1982). Neural systems control of spatial orienting. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, *298*(1089), 187-98.
- Posner, M I. (1978). *Chronometric explorations of mind*. Hillsdale: Erlbaum.
- Posner, M I. (1980). Orienting of Attention. *Quarterly Journal of Experimental Psychology*, *32*, 3-25.
- Posner, M. I. & Driver, J. (1992) The neurobiology of selective attention. *Current Opinion in Neurobiology*, *2*, 165-169.
- Posner, M I, & Cohen, Y. (1984). Components of visual orienting. In H. Bouma & D. G. Bouwhuis (Eds.), *Attention and performance X* (pp. 531-556). Hillsdale: Lawrence Erlbaum Assoc.
- Posner, M I, Snyder, C. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of experimental psychology*, *109*(2), 160-74.

- Posner, M. I., Rafal, R. D., Choate, L. S., & Vaughan, J. (1985). Inhibition of return: Neural basis and function. *Cognitive Neuropsychology*, 2(3), 211-228.
- Posner, M. I., Walker, J. A., Friedrich, F. J., & Rafal, R. D. (1984). Effects of parietal injury on covert orienting of attention. *Journal of Neuroscience*, 4(7), 1863-1874.
- Praamstra, P., Boutsen, L., & Humphreys, G. W. (2005). Frontoparietal control of spatial attention and motor intention in human EEG. *Journal of neurophysiology*, 94(1), 764-74.
- Prime, D. J., & Jolicoeur, P. (2009). On the relationship between occipital cortex activity and inhibition of return. *Psychophysiology*, 46(6), 1278-87.
- Prime, D. J., & Ward, L. M. (2004). Inhibition of return from stimulus to response. *Psychological science*, 15(4), 272-6.
- Prime, D. J., & Ward, L. M. (2006). Cortical expressions of inhibition of return. *Brain research*, 1072(1), 161-74.
- Quinlan, P. T., & Bailey, P. J. (1995). An examination of attentional control in the auditory modality: Further evidence for auditory orienting. *Perception & Psychophysics*, 57, 614-628.
- Rafal, R. D., Calabresi, P. A., Brennan, C. W., & Sciolto, T. K. (1989). Saccade preparation inhibits reorienting to recently attended locations. *Journal of experimental psychology. Human perception and performance*, 15(4), 673-85.
- Rafal, R. D., Posner, M. I., Friedman, J. H., Inhoff, A. W., & Bernstein, E. (1988). Orienting of visual attention in progressive supranuclear palsy. *Brain*, 111 (2), 267-280.
- Rauss, K. S., Pourtois, G., Vuilleumier, P., & Schwartz, S. (2009). Attentional load modifies early activity in human primary visual cortex. *Human brain mapping*, 30(5), 1723-33.
- Rees, G., Frith, C. D., & Lavie, N. (1997). Modulating irrelevant motion perception by varying attentional load in an unrelated task. *Science*, 278(5343), 1616-1619.
- Riggio, L., Gawryszewski, L. D. G., & Umiltà, C. (1986). What is crossed in crossed-hand effects? *Acta Psychologica*, 62(1), 89-100.
- Robin, D. A., & Rizzo, M. (1992). Orienting attention in audition and between audition and vision: young and elderly subjects. *Journal of Speech and Hearing Research*, 35, 701-707.
- Roggeveen, A. B., Prime, D. J., & Ward, L. M. (2005). Inhibition of return and response repetition within and between modalities. *Experimental brain research*, 167(1), 86-94.

- Rorden, C., Greene, K., Sasine, G., & Baylis, G. (2002). Enhanced tactile performance at the destination of an upcoming saccade. *Current Biology*, *12*(16), 1429-1434.
- Ruz, M., & Lupiáñez, J. (2002). A review of attentional capture: On its automaticity and sensitivity to endogenous control. *Psicológica*, 283-309.
- Röder, B., Spence, C., & Rösler, F. (2000). Inhibition of return and oculomotor control in the blind. *Neuroreport*, *11*(13), 3043-5.
- Röder, B., Föcker, J., Hötting, K., & Spence, C. (2008). Spatial coordinate systems for tactile spatial attention depend on developmental vision: evidence from event-related potentials in sighted and congenitally blind adult humans. *The European journal of neuroscience*, *28*(3), 475-83.
- Röder, B., Rösler, F., & Spence, C. (2004). Early vision impairs tactile perception in the blind. *Current Biology*, *14*(2), 121-124.
- Röder, B., Spence, C., & Rösler, F. (2002). Assessing the effect of posture change on tactile inhibition-of-return. *Experimental brain research*, *143*(4), 453-62.
- Sakata, H., Takaoka, Y., Kawarasaki, A., & Shibutani, H. (1973). Somatosensory properties of neurons in the superior parietal cortex (area 5) of the rhesus monkey. *Brain Research*, *64*, 85-102.
- Sambo, C. F., & Forster, B. (2011). Sustained spatial attention in touch: modality-specific and multimodal mechanisms. *TheScientificWorldJournal*, *11*, 199-213.
- Santangelo, V., Ho, C., & Spence, C. (2008). Capturing spatial attention with multisensory cues. *Psychonomic Bulletin & Review*, *15*(2), 398-403.
- Santangelo, Valerio, & Spence, Charles. (2007). Assessing the automaticity of the exogenous orienting of tactile attention. *Perception*, *36*(10), 1497-1505.
- Santangelo, V., & Spence, C. (2008). Is the exogenous orienting of spatial attention truly automatic? Evidence from unimodal and multisensory studies. *Consciousness and cognition*, *17*(3), 989-1015.
- Santangelo, V., Botta, F., Lupiáñez, J., & Spence, C. (2011). The time course of attentional capture under dual-task conditions. *Attention, perception, & psychophysics*, *73*(1), 15-23.
- Sapir, A., Soroker, N., Berger, A., & Henik, A. (1999). Inhibition of return in spatial attention: direct evidence for collicular generation. *Nature Neuroscience*, *2*(12), 1053-1054
- Schiller, P. H. (1977). The effect of superior colliculus ablation on saccades elicited by cortical stimulation. *Brain Research*, *122*(1), 154-156.

- Schmidt, W. C. (1996). Inhibition of return without visual input. *Neuropsychologia*, 34(10), 943-952.
- Schubert, R., Ritter, P., Wüstenberg, T., Preuschhof, C., Curio, G., Sommer, W., & Villringer, A. (2008). Spatial attention related SEP amplitude modulations covary with BOLD signal in S1--a simultaneous EEG--fMRI study. *Cerebral cortex*, 18(11), 2686-700.
- Schwartz, S., Vuilleumier, P., Hutton, C., Maravita, A., Dolan, R. J., & Driver, J. (2005). Attentional load and sensory competition in human vision: modulation of fMRI responses by load at fixation during task-irrelevant stimulation in the peripheral visual field. *Cerebral cortex*, 15(6), 770-86.
- Seiss, E., Gherri, E., Eardley, A. F., & Eimer, M. (2007). Do ERP components triggered during attentional orienting represent supramodal attentional control? *Psychophysiology*, 44(6), 987-90.
- Shepherd, M., & Müller, H. J. (1989). Movement versus focusing of visual attention. *Perception And Psychophysics*, 46(2), 146-154.
- Shore, D. I., Gray, K., Spry, E., & Spence, C. (2005). Spatial modulation of tactile temporal-order judgments. *Perception*, 34(10), 1251-1262.
- Shore, D. I., Spry, E., & Spence, C. (2002). Confusing the mind by crossing the hands. *Cognitive brain research*, 14(1), 153-63.
- Spalek, T. M., Falcon, L. J., & Di Lollo, V. (2006). Attentional blink and attentional capture: endogenous versus exogenous control over paying attention to two important events in close succession. *Perception & psychophysics*, 68(4), 674-84.
- Spence, C., & McGlone, F. P. (2001). Reflexive spatial orienting of tactile attention. *Experimental brain research*, 141(3), 324-30.
- Spence, C., Pavani, F., & Driver, J. (2000). Crossmodal links between vision and touch in covert endogenous spatial attention. *Journal of experimental psychology. Human perception and performance*, 26(4), 1298-319.
- Spence, C., & Gallace, A. (2007). Recent developments in the study of tactile attention. *Canadian Journal of Experimental Psychology*, 61(3), 196-207.
- Spence, C., Lloyd, D., McGlone, F., Nicholls, M. E. R., & Driver, J. (2000). Inhibition of return is supramodal: a demonstration between all possible pairings of vision, touch, and audition. *Experimental Brain Research*, 134(1), 42-48.
- Sutherland, M. T. (2006). The hand and the ipsilateral primary somatosensory cortex. *Journal of Neuroscience*, 26(32), 8217-8218.

- Talsma, D., Slagter, H.A., Nieuwenhuis, S., Hage, J., & Kok, A., (2005). The orienting of visuospatial attention: an event-related brain potential study. *Cognitive Brain Research*, 25, 117–129.
- Talsma, D. Mulckhuysen, M., Slagter, H. A., & Theeuwes, J. (2007). Faster, more intense! The relation between electrophysiological reflections of attentional orienting, sensory gain control, and speed of responding. *Brain Research*, 92-105.
- Tanaka, Y., & Shimojo, S. (1996). Location vs feature: reaction time reveals dissociation between two visual functions. *Vision Research*, 36(14), 2125-2140.
- Tassinari, G., & Campara, D. (1996). Consequences of covert orienting to non-informative stimuli of different modalities: a unitary mechanism? *Neuropsychologia*, 34(3), 235-45.
- Tassinari, G., Campara, D., Benedetti, C., & Berlucchi, G. (2002). The contribution of general and specific motor inhibitory sets to the so-called auditory inhibition of return. *Experimental brain research*, 146(4), 523-30.
- Taylor, T. L., & Klein, R. M. (2000). Visual and motor effects in inhibition of return. *Journal of experimental psychology. Human perception and performance*, 26(5), 1639-56.
- Terry, K. M., Valdes, L. A., & Neill, W. T. (1994). Does “inhibition of return” occur in discrimination tasks? *Perception & psychophysics*, 55, 279-286.
- Theeuwes, J. (1991). Exogenous and endogenous control of attention: the effect of visual onsets and offsets. *Perception & psychophysics*, 49(1), 83-90.
- Thomas, L. E., Ambinder, M. S., Hsieh, B., Levinthal, B., Crowell, J. A., Irwin, D. E., Kramer, A. F., et al. (2006). Fruitful visual search: inhibition of return in a virtual foraging task. *Psychonomic bulletin & review*, 13(5), 891-5.
- Tian, Y., & Yao, D. (2008). A study on the neural mechanism of inhibition of return by the event-related potential in the Go/NoGo task. *Biological psychology*, 79(2), 171-8.
- Tipper, S. P., Rafal, Robert D, Reuter-Lorenz, P. A., Stareveld, Y., Ro, T., Egly, R., & Weaver, B. (1997). Object Based Facilitation and Inhibition from Visual Orienting in the Human Split Brain. *Journal of Experimental Psychology. Human Perception and Performance*, 23(5), 1522-1532.
- Turatto, M., Benso, F., Galfano, G., & Umiltà, C. (2002). Nonspatial attentional shifts between audition and vision. *Journal of Experimental Psychology Human Perception and Performance*, 28(3), 628-639.
- van Velzen, J., Eardley, A. F., Forster, B., & Eimer, M. (2006). Shifts of attention in the early blind: an ERP study of attentional control processes in the absence of visual spatial information. *Neuropsychologia*, 44(12), 2533-46.

- van Velzen, J., & Eimer, M. (2003). Early posterior ERP components do not reflect the control of attentional shifts toward expected peripheral events. *Psychophysiology*, *40*(5), 827-31.
- Wascher, E., & Tipper, S. P. (2004). Revealing effects of noninformative spatial cues: an EEG study of inhibition of return. *Psychophysiology*, *41*(5), 716-28.
- Welsh, T. N., & Pratt, J. (2006). Inhibition of return in cue-target and target-target tasks. *Experimental brain research*, *174*(1), 167-75.
- Woldorff, M. G. (1993). Distortion of ERP averages due to overlap from temporally adjacent ERPs: analysis and correction. *Psychophysiology* *30*, 98– 119.
- Yamamoto, S., & Kitazawa, S. (2001). Reversal of subjective temporal order due to arm crossing. *Nature neuroscience*, *4*(7), 759-65.
- Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: voluntary versus automatic allocation. *Journal of experimental psychology. Human perception and performance*, *16*(1), 121-34.
- Yantis, S., Schwarzbach, J., Serences, J. T., Carlson, R. L., Steinmetz, M. A., Pekar, J. J., & Courtney, S. M. (2002). Transient neural activity in human parietal cortex during spatial attention shifts. *Nature neuroscience*, *5*(10), 995-1002.
- Zhu, Z., Disbrow, E. a, Zumer, J. M., McGonigle, D. J., & Nagarajan, S. S. (2007). Spatiotemporal integration of tactile information in human somatosensory cortex. *BMC neuroscience*, *8*, 21.
- Zopf, R., Giabbiconi, C. M., Gruber, T., & Müller, M. M. (2004). Attentional modulation of the human somatosensory evoked potential in a trial-by-trial spatial cueing and sustained spatial attention task measured with high density 128 channels EEG. *Cognitive Brain Research*, *20*(3), 491-509.