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The effect of perceptual load on tactile spatial attention

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The effect of perceptual load on tactile spatial attention:

Evidence from Event-Related Potentials

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Abstract

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To investigate whether tactile spatial attention is modulated by perceptual load, behavioural and electrophysiological measures were recorded during two spatial cuing tasks in which the difficulty of the target/non-target discrimination was varied (High and Low load tasks). Moreover, to study whether attentional modulations by load are sensitive to the availability of visual information, the High and Low load tasks were carried out under both illuminated and darkness conditions. ERPs to cued and uncued non-targets were compared as a function of task (High vs. Low load) and illumination condition (Light vs. Darkness). Results revealed that the locus of tactile spatial attention was determined by a complex interaction between perceptual load and illumination conditions during sensory-specific stages of processing. In the Darkness, earlier effects of attention were present in the High load than in the Low load task, while no difference between tasks emerged in the Light. By contrast, increased load was associated with stronger attention effects during later post-perceptual processing stages regardless of illumination conditions. These findings demonstrate that ERP correlates of tactile spatial attention are strongly affected by the perceptual load of the target/non-target discrimination. However, differences between illumination conditions show that the impact of load on tactile attention depends on the presence of visual information. Perceptual load is one of the many factors that contribute to determine the effects of spatial selectivity in touch.

Keywords:

Highlights

- Perceptual load modulates the mechanisms of tactile spatial attention

- In the darkness, effects of attention emerged earlier under high than low load In the light, attentional modulations of the N140 were not affected by load

- Earlier effects of tactile attention depend on both load and visual information

- Later attentional modulations are stronger under high load regardless of vision

Acknowledgements

Introduction

Tactile spatial attention refers to our ability to prioritize the processing of stimuli that are presented at relevant body locations. There is now convincing evidence that spatial attention improves the speed and accuracy of responses to attended tactile stimuli as compared to unattended ones in healthy humans (e.g. Sathian and Burton, 1991; Spence et al., 2000). To investigate which stages of processing are modulated by tactile attention, a number of electrophysiological studies have compared event related potentials (ERPs) elicited by tactile stimuli at cued and uncued locations. In these studies, participants attend to the cued body location to respond to infrequent target stimuli but not to frequent non-target stimuli (i.e. performing a tactile discrimination), while ignoring both target and non-targets delivered to the other uncued location. The mechanical stimulations of the fingers elicits clear sensory specific ERP components (P45, N80, P100 and N140). The early P45 and N80 components are generated in contralateral SI (e.g. Hari et al., 1984; Hamalainen et al., 1988; Zhu et al., 2007) while tactile processing is implemented by brain areas in and beyond SII from about 90 ms post-stimulus onset (corresponding to the time range of the mid latency P100 and N140 components; e.g. Allison et al., 1992; Barba et al., 2002; Frot and Maguiere, 1999). Importantly, (some of) these early components together with longer latencies ERPs are selectively modulated during tactile spatial tasks, revealing that the effects of attention can be observed during both perceptual and post-perceptual stages of somatosensory processing (for reviews, see Johansen-Berg and Lloyd, 2000; Sambo and Forster, 2011; Gomez-Ramirez et al, 2016).

However, the neural mechanisms mediating the spatial selection of stimuli in the somatosensory system remain poorly understood. In particular, the time course of the

attentional modulations varies quite considerably across studies. For instance, some cuing studies reported the earliest attention effects on the mid-latency P100 or N140 components (e.g. Eimer and Forster, 2003; Forster and Eimer, 2005a; Zopf et al., 2004) while others did so at longer latencies (from the descending flank of the N140, e.g. Van Velzen et al., 2002; Foster et al., 2009). One factor that might contribute to these differences is the perceptual load that determines the difficulty of the discrimination between targets and non-targets at cued locations. Differences in the discriminability of these stimuli might result in different amount of attentional resources at the cued body locations, which in turn might affect the locus of attentional selectivity and the size of the effects of attention on sensory processing.

In the visual domain, ERP studies on spatial attention demonstrated that the effect of attention on visual processing is sensitive to variations of the difficulty of the target/non-target discrimination (i.e. perceptual load) (e.g., Handy and Mangun, 2000). Larger modulations of the P1 and N1 components were observed for high load discrimination than for low load discrimination tasks (e.g., Handy and Mangun, 2000). Furthermore, the amplitude of these components increased with the amount of attentional resources voluntarily allocated to the spatial location of the ERP-eliciting stimulus (Mangun and Hillyard, 1991; Alho et al., 1992). Thus, increased perceptual demands have a systematic impact on visual processing.

No study to date has directly investigated whether analogous effects of perceptual load on attention can be observed in the tactile domain. Indirect evidence suggests that changes in the target/non-target attributes affect the efficiency of the tactile discrimination and modulate tactile spatial attention (Michie et al., 1987). In this early ERP study different intensities defined tactile targets and non-targets (weak vs. strong stimuli). Earlier effects of spatial attention and worst behavioural performance were

observed when participants had to detect a weak target among strong non-targets as compared to when a strong target was presented amongst weak non-targets (effects of attention observed in the N80 and P100 time range, respectively) (Michie et al., 1987). While this study was not designed to investigate the effect of load on tactile spatial attention (the frequent non-targets analysed in the two conditions are physically different stimuli which cannot be directly compared), these observations suggest that the difficulty of the target/non-target discrimination might modulate spatial selectivity in touch.

The aim of the study reported here was to investigate the effects of perceptual load on tactile spatial attention. We used a spatial cuing task in which tactile targets and non-targets were vibro-tactile stimuli defined by different frequencies. We varied systematically the difficulty of the target/non-target perceptual discrimination by decreasing or increasing the targets frequency while leaving unchanged that of non-targets. The *low load task* was characterised by a wide difference between the frequencies of target and non-target tactile stimuli (100 Hz vs. 25 Hz, respectively). In contrast, this difference was reduced in the *high load task* (40 Hz for targets and 25 Hz for non-targets). Thus, increased perceptual demands characterised the high load task as compared to the low load task. ERPs elicited by physically identical non-target tactile stimuli presented to the cued and uncued hand were compared as a function of the different load tasks (high vs. low). If the manipulation of perceptual load - operationally defined as the increased or reduced difference between targets and non-targets - affects attention by changing the locus of attentional selectivity in touch and/or by increasing the attentional resources deployed to the cued body location, we expect to observe earlier and/or stronger attentional modulations in the high load task.

An additional aim of the present study was to investigate whether the effects of perceptual load on tactile spatial attention are modulated by the presence or absence of visual information during the task. The visual system is often engaged during tactile spatial attention tasks. Even when the experimental task involves exclusively tactile stimuli, participants often receive visual cues about the tactually stimulated body part. Increasing evidence has demonstrated that the operations of tactile attention are strongly affected by this incoming visual information about the body (for a review see Sambo and Forster, 2011). Electrophysiological studies have now reported modulatory effects of vision on tactile selectivity (c.f. Eimer et al., 2003; Gillmeister et al., 2010; Sambo et al., 2009). In one of these studies, attentional modulations of somatosensory processing emerged earlier when visual information was available suggesting that tactile selectivity was facilitated by visual information (specifically, the sight of the stimulated hand)(Sambo et al., 2009). Tactile spatial attention is mediated by representations of the relevant body location not only in somatotopic coordinates but also in external coordinates which are likely to be based on visual information (e.g. Eardley and Van Velzen, 2011; Eimer et al., 2001; 2003; Röder et al., 2008). Because vision provides highly detailed spatial information, viewing the touched body part has been suggested to facilitate the remapping of tactile stimuli in external coordinates, aiding tactile spatial selectivity (e.g. Sambo et al., 2009; Gillmesiter et al., 2010).

Interestingly, behavioural studies investigating the effect of vision on tactile perception revealed that the difficulty of the perceptual task plays a relevant mediatory role in these effects. Visual information about the touched body part can improve tactile spatial acuity but these facilitatory effects of vision on touch depend on the difficulty of the task (e.g. Kennett et al., 2001; Press et al., 2004). Despite the fact that different mechanisms might be responsible for the effects of vision on tactile percep-

tion and on tactile selectivity (e.g. Sambo & Forster, 2011), these observations provide indirect evidence for interactive effects between vision and task difficulty. In the present study, we systematically manipulated not only the load of the perceptual task but also the availability of visual information. Different participants performed the same high and low load tactile attention tasks in the light or in the darkness[i]. Because both the effects of vision and perceptual load might impact the time course and the amount of attentional resources engaged during the task, we investigated whether these factors contribute separately or jointly to determine the operations of tactile spatial attention.

2. Results

2.1. Behavioural Results

Performance was more accurate in the Low load than in the High load task (mean accuracy 91% vs. 77.5%, respectively; $F(1,22) = 34.5$; $p < .001$; $\eta_p^2 = .6$). Accuracy levels were comparable across illumination conditions (no main effect of illumination condition, $F(1,22) < 1$; $p = .4$; 96% accuracy in both illumination conditions), and similar differences between high and low load tasks were present in the light and in the darkness (no task x illumination condition, $F(1,22) < 1$; $p = .5$).

The analysis of response times revealed a main effect of task ($F(1, 22) = 34.4$; $p<.001$; $\eta_p^2 = .6$). Vocal responses to target stimuli presented to the cued hand were significantly faster in the low load than in the high load task (608 ms vs. 682 ms, respectively). No reliable difference emerged between illumination conditions ($F(1, 22) < 1$; $p = .7$; 654 ms in the light and 637 ms in the darkness). Although differences between the low and high load tasks were numerically more pronounced in the darkness

condition (596 vs. 677 ms, respectively) than in the light condition (620 ms low load task vs. 687 ms for the and high load tasks), no reliable task x illumination condition interaction was observed (F(1, 22) < 1 ; p = .6).

<u>2.2. ERP Results</u>

Grand-averaged somatosensory ERPs elicited by non-target stimuli presented to the cued (solid line) and uncued hand (dashed line) are shown separately for the low load and high load tasks and for the light and darkness condition in Figure 1. In this figure, ERPs elicited over electrode sites contralateral and ipsilateral to the stimulated hand as well as midline electrodes are represented in the top, central and bottom panels, respectively. The differences in the time course of attentional ERP modulations in the high load and low load tasks are further illustrated in the difference waveforms (right panels) obtained by subtracting ERPs in response to tactile stimuli presented at cued locations from ERPs elicited by tactile stimuli at uncued locations, in each of the two load tasks. Figures 2 shows the scalp distributions of the attentional modulations of mid- (N140) and longer latencies (early and late phases of the Nd) ERP components, respectively. In this figure, bar graphs (right panels) represent the mean amplitude values and standard error of the means of ERPs elicited by cued and uncued tactile stimuli computed at midline electrodes separately for the different tasks and illumination conditions.

As can be seen in Figures 1, the load manipulation seems to affect attentional modulations emerged during both sensory specific as well as post-perceptual stages of processing. Importantly, the effect of load on spatial attention appears to be strongly modulated by the presence or absence of visual information (illumination condition: light vs. darkness). In the darkness, attentional modulations appear more pronounced

in the high load as compared to the low load task, see Figure 1 and 2 (right panels). In contrast, in the light the effects of attention on touch seem stronger in the low load as compared to the high load task until about 260 ms post-stimulus (Figure 1 and 2, left panels). However, during the late phase of the Nd (280 – 400 ms), similar effects of load are observed regardless of illumination condition with stronger attentional modulations for the high than low load task.

2.2.1. P45 (35-55 ms), N80 (65-85 ms) and P100 (90-125)

No main effect of attention or interaction involving attention emerged for the time windows of the early P45 and N80 components (measured in the 35-65 ms and 65-85 ms post-stimulus time windows, respectively) as well as for the mid-latency P100 component (90-125ms). In the N80 time window a main effect of task was observed at lateral and midline electrodes (both $F(1, 22) > 4.6$; both $p < .044$; both $\eta_p^2 > .17$), revealing that ERPs elicited in the high load task were more negative than those in the low load task.

2.2.2. N140 (130-170 ms)

In the N140 time window (130-170 ms), main effects of attention were observed at both lateral and midline sites, both $F(1, 22) > 11.3$; both $p < .003$; both $\eta_p^2 > .34$). Significant attention x task x illumination condition interactions at midline sites ($F(1, 22) = 5$; $p = .036$; $\eta_p^2 = .18$; approaching significance at lateral sites $F(1, 22) = 3.3$; $p = .082$; $\eta_p^2 = .13$) revealed systematic differences between the attention effects measured in the high and low load tasks under different illumination conditions. As can be seen in Figure 2, a different pattern of attentional modulations by load emerged under dif-

ferent illumination conditions. To explore this three-way interaction follow-up analyses were conducted separately for the different illumination conditions. In the *darkness*, an attention x task interaction emerged at midline electrodes $F(1, 11) = 5.6$; $p = .036$; $\eta_p^2 = .34$). This modulation of tactile attention by load was due to the fact that N140 attentional modulations were present in the <u>high load task </u>(main effects of attention emerged at both lateral and midline sites, both $F(1, 11) > 7.5$; all $p < .019$; $\eta_p^2 > .4$), but not in the <u>low load task</u> (both sites, $F(1,11) < 2.5$; $p > .13$; $\eta_p^2 = .19$). In contrast, in the *light*, differences between tasks were less evident as revealed by the absence of significant attention x task interactions (both midline and lateral sites, $F(1,11) = 0.6$, $p = .4$, ; $\eta_p^2 < .05$). Effects of attention on the N140 component were statistically reliable in the <u>low load task</u> (main effects of attention observed at both lateral and midline sites, both $F(1, 11) > 11.1$; both $p < .007$; both $\eta_p^2 > .5$), and just failed to reach significance in the <u>high load task</u> (both lateral and midline sites $F(1, 11) < 4.08$; all $p > .069$; $\eta_p^2 < .27$).

2.2.3. Nd1 (200-260 ms)

Between 200 and 260 ms post-stimulus onset, main effect of tasks at midline and lateral electrodes revealed the presence of more negative ERPs in the high load than in the low load condition (both $F(1, 22) > 6.4$; both $p < .018$; both $\eta_p^2 > .22$). In addition, main effects of attention were present at lateral and midline sites (both $F(1, 22) > 32.1$; both $p < .001$; both $\eta_p^2 < .59$), reflecting the earlier phase of the enhanced negativity that characterizes cued stimuli as compared to uncued ones (negative difference, Nd). Three-way interactions between attention, task and illumination condition were present at lateral and midline electrodes (both $F(1, 22) > 5.6$; both $p < .027$; both $\eta_p^2 > .2$). Follow-up analyses were carried out separately in the light and darkness conditions. In

the *darkness,* significant attention x task interactions emerged at midline sites ($F(1, 11)$ = 6.4; p = .028; η_p^2 = .36; approaching significance at lateral electrodes $F(1, 11)$ = 3.38; p = .093; η_p^2 = .23), reflecting the fact that the attentional negativities were larger in the high load than in the low load task. This was confirmed by follow up analyses conducted separately for each task which revealed reliable main effects of attention in the <u>low load task</u> (both sites $F (1, 11) > 8.3$, both $p < .015$; both $\eta_p^2 > .43$), as well as in the <u>high load task</u> (both $F (1, 11) > 20.1$; both $p < .001$; both $\eta_p^2 > .64$). In the *light,* no significant attention x task interactions emerged at any of the electrode sites (attention x task interactions, both $F (1, 11) < 2.3$; both $p > .15$; both $\eta_p^2 < .17$) and follow-up analyses confirmed that significant effects of attention were present at all electrodes sites in both the <u>low load</u> (both lateral and midline sites $F (1, 11) > 16.5$; both $p < .002$; $\eta_p^2 < .6$) and the <u>high load task</u> (both sites $F (1, 11) > 10.8$; both $p < .007$; both $\eta_p^2 < .49$).

2.2.4. Nd2 (280-400 ms)

In the final time interval (280-400 ms), ERPs were more negative in the high than in the low load task, as reflected by main effects of task at midline and lateral electrodes (both $F(1, 22) > 5.6$; both $p < .027$; both $\eta_p^2 > .2$). The later phase of the Nd component (Nd2) was strongly modulated by attention (main effect of attention at both lateral and midline sites, both $F(1, 22) > 64.3$; both $p < .001$; both $\eta_p^2 > .74$). As can be seen in Figure 2, stronger effects of attention were present in the high load as compared to the low load task and this difference was unaffected by the illumination conditions. Significant attention x task interactions were present at lateral and midline sites, both $F(1, 22) > 18.5$; both $p < .001$; both $\eta_p^2 > .45$), while no three-way interactions emerged at any of the electrode sites (both $F(1, 22) < 0.6$; both $p > .4$; both $\eta_p^2 <$

.03). Follow-up analyses conducted separately for the high and low load tasks confirmed the presence of highly significant attention effects for both the high load task (both lateral and midline sites $F(1, 23) > 82.07$; both $p < .001$; both $\eta_p^2 > .78$) and the low load task (both lateral and midline sites $F(1, 23) > 26.07$; both $p < .001$; both $\eta_p^2 > .53$).

3. Discussion

ERP studies investigating tactile spatial selective attention often require participants to attend to one of their hands to detect infrequent targets presented amongst frequent non-targets, while ignoring all stimuli to the unattended hand. That is, participants perform a perceptual discrimination between tactile targets and non-targets presented to the cued hand. The purpose of the present study was twofold. First, we investigated whether the perceptual demands of this tactile discrimination impact the operations of tactile spatial attention. Perceptual load was manipulated by increasing (low load task) or decreasing (high load task) the differences between the frequencies of targets and non-targets tactile vibrations. In addition, because visual information appears to impact the mechanisms that determine the locus of tactile selectivity and the amount of attentional resources available (c.f. Sambo et al., 2009; Eimer et al., 2003), we investigated whether modulations of tactile spatial attention by perceptual load were sensitive to the availability of visual information about the stimulated body part. To this aim, the same high and low load tasks were carried out under different illumination conditions (light vs. darkness). ERPs elicited by physically identical non-target tactile stimuli presented to the cued and uncued hand were compared as a function of the different load tasks (high vs. low) and illumination conditions (light vs. darkness).

Results revealed differential processing of cued and uncued tactile non-targets for both sensory-specific as well as longer latencies tactile ERPs, in line with previous ERP studies on tactile attention (e.g. Michie, 1984; Michie et al., 1987; Garcia-Larrea et al., 1995; Forster and Eimer, 2005). Crucially, these attentional modulations of somatosensory processing were strongly affected by changes in the perceptual load of the task both in the light and in the darkness, but the specific pattern of these modulations differed systematically between illumination conditions and these differences were particularly evident during earlier stages of processing.

In the darkness, effects of spatial attention on touch were present during sensory specific stages of processing (N140 time range) in the high load task, while they become statistically reliable only in the time range of the following Nd component in the low load task. Effects of load on tactile attention were not restricted to the onset of the attentional modulations during sensory-specific stages of tactile processing, but were also observed during post-perceptual stages. The processing negativity which typically follows the sensory specific N140 component in discrimination tasks is characterised by more negative ERPs for cued than uncued stimuli (e.g. Eimer and Forster, 2003; Forster and Eimer, 2004; Zopf et al., 2004). Importantly, the amplitude of the resulting 'negative difference' (Nd) was larger in the high load than in the low load task, revealing that higher perceptual load resulted in stronger Nds. In contrast, in the light no systematic difference emerged between the attentional modulations observed in the high and low load tasks during the N140 and early Nd time windows. The first reliable effect of load on tactile attention was only observed during the late phase of the Nd (between 280-400 ms), during which larger attention effects were present for more difficult tactile discriminations similarly to what was observed in the darkness.

Taken together, the results of the present study demonstrated for the first time that increasing the perceptual load of a tactile discrimination task changes the operations of tactile spatial attention. Differences between the attentional modulations in the high and low load tasks were observed in terms of time course as well as amplitude of the attentional modulations and affected multiple stages of tactile processing. This is not only in line with previous evidence in the visual (e.g. Handy and Mangun, 2000) and auditory domains (e.g.Woldorff et al., 1987; Woldorff et al., 1993), but also with earlier indirect observations within the tactile domain (Michie et al., 1987). Importantly, however, these differences were shaped by the presence or absence of visual information. Before discussing the possible mechanisms responsible for the differences observed between illumination conditions, we will first consider the effect of load on the modality-specific mechanisms of tactile spatial attention in the absence of visual information.

In the dark, reliable effects of attention were present in the high load but not in the low load task during sensory specific processing stages (N140 time window). The observation that earlier effects of attention were present for difficult target/non-target discriminations (high load task) as compared to easy ones (low load task) suggest that the manipulation of perceptual load affects the time course of tactile spatial attention and contributes to determining the locus of attentional selectivity in touch. This observation can provide a theoretical explanation as to why some ERP studies in touch have found attention effects earlier than others. While a number of studies have shown attentional modulations of the sensory-specific ERP components (typically the mid-latency P100 or N140 components, e.g. Desmedt and Robertson, 1977; Eimer and Forster, 2003; Hötting et al., 2003; Eimer et al., 2004; Forster and Eimer, 2005a; Forster and Gillmeister, 2011; Gherri and Forster, 2012; but also the P45 and N80 e.g.

Eimer and Forster, 2003; Jones and Forster, 2014; Schubert et al., 2008; Zopf, et al., 2004), others have only observed effects of spatial attention during post-perceptual processing stages (Nd time window, Van Velzen et al., 2002; Forster et al., 2009). The factors that might contribute to determining the locus of tactile attention have only just started to be identified. For instance, sustained attention tasks in which the same body location was attended to throughout a block of trials resulted in earlier effects of attention as compared to transient studies of attention where the task-relevant body location was cued on a trial-by-trial basis (c.f. Eimer and Forster, 2003; Zopf, et al., 2004). However, even within cuing studies, results appear to be inconsistent, with some reporting the earliest attention effects on the P100 (e.g. Eimer and Forster, 2003) while others on the following N140 component (e.g. Eimer et al 2004; Forster and Eimer, 2004; 2005; Eardley and van Velzen, 2011), or even at longer latencies (from the descending flank of the N140, e.g. Van Velzen et al., 2002; Forster et al., 2009). Because different types of target vs. non-target discriminations were used in previous ERP studies of tactile spatial attention (gap/non-gap, frequency, intensity, etc.), it is conceivable that they required different amounts of attentional resources, resulting in different onset times of the attention effects. Thus, in addition to the specific attentional requirements (transient vs. sustained attention tasks; c.f. Eimer and Forster, 2003; Zopf et al., 2004), the discriminability of the tactile stimuli (high vs. low load) also contributes to determine the time course of tactile spatial attention.

Importantly, however, the effect of load on tactile spatial attention differed as a function of illumination condition during early sensory-specific processing stages. This observation provides additional evidence for the claim that tactile attention operates in a multimodal fashion because its operations are sensitive to the availability of visual information. Neuroimaging studies have suggested that the presence of visual

information during a tactile attention task activates multi-modal mechanisms of tactile attention in addition to the modality-specific ones which are typically engaged regardless of visual information (Macaluso et al., 2000; 2002; for a review, see Macaluso and Driver, 2005). Furthermore, electrophysiological studies have shown that visual information impacts the mechanisms that determine the locus of tactile selectivity and the amount of attentional resources engaged during tactile processing (c.f. Eimer et al., 2003; Sambo et al., 2009; Gillmeister et al., 2010). For example, viewing the hands resulted in earlier and stronger attentional modulations of tactile processing as compared to experimental conditions in which participants were blind-folded or their hands were hidden from view, revealing that visual information facilitates the spatial selection of the task-relevant hand (Sambo et al., 2009). Because the attentional mechanisms that modulate sensory processing in modality-specific somatosensory areas are not only mediated by somatotopic representations of the task relevant body location but also by visual representations of the body in external space (e.g. Eardley and Van Velzen, 2011; Eimer et al., 2001; 2003; Röder et al., 2008), it has been suggested that non-informative visual information about the stimulated hand might facilitate the re-mapping of tactile locations in external coordinates (e.g. Sambo et al., 2009; Gillmesiter et al., 2010). The exact neural mechanisms responsible for this visual facilitation of tactile spatial attention remains largely unknown. The fronto-parietal areas involved in attentional control and the multisensory areas responsible for visuo-tactile integration are likely to modulate the activity of somatosensory areas, possibly through converging but independent back-projections or through common back-projections regulated by direct connections between these higher-level areas (e.g. Sambo and Forster, 2011; Sambo et al., 2009).

In addition to the effect of visual information on tactile spatial attention, non-informative visual cues about the touched body part can also directly modulate the processing of tactile events, improving tactile acuity (e.g. Kennett et al., 2001; Press et al., 2004). This perceptual enhancement might be mediated by early crossmodal interactions within somatosensory areas (e.g. Cardini et al., 2011; 2012; Forster and Eimer, 2005b; Longo et al., 2011; Taylor-Clark et al., 2002), possibly through backward projections from higher level multisensory areas to early somatosensory areas as well as by direct connections between visual and somatosensory areas (e.g. Driver and Noesselt, 2008). Thus, the presence of visual information can have a direct impact not only on tactile spatial attention, but also on the processing of tactile events at least under certain experimental conditions.

It is likely that a combination of these factors might have contributed to the pattern of results observed in the present study in which the effects of tactile selectivity during sensory-specific stages of processing was modulated by load in the absence but not in the presence of visual information. The presence of visual information might have facilitated tactile selectivity, resulting in earlier effects of attention in the light as compared to the darkness. The fact that a statistically reliable attentional modulation of the N140 component was present in the low load task of the illuminated condition but not in the darkness is in line with existing ERP evidence measured during easy perceptual tasks (e.g. Sambo et al., 2009) and provide support for the hypothesis that tactile selectivity operates earlier when visual information is available. In addition, the presence of visual information might have directly modulated the processing of tactile stimuli. Importantly, evidence from behavioural and neuropsychological studies has shown that vision facilitates tactile perception almost exclusively when the tactile task is close to the limit of tactile performance, that is, during difficult tasks (Press et al.,

2004; Serino et al., 2007). Thus, if visual information facilitated tactile processing in the high load task (but not in the low load task), it is conceivable that reduced attentional resources might have been initially recruited under high load, reducing the differences between the high and the low load tasks. While this hypothesis is in line with existing evidence (Press et al., 2004; Serino et al., 2007), it is relevant to note that we did not observe main effects of vision in the general analysis nor in the analysis of the high load task. The lack of evidence for a direct effect of vision on tactile processing is likely due to the fact different participants performed the task under different illumination conditions. ERPs recorded in different groups of participants can differ quite substantially with respect to the exact shape of their waveforms (see Luck, 2005; Woodman, 2010, for an exhaustive discussion of individual differences in the early sensory ERP components). For this reason it is not surprising that a subtle perceptual effects such as the visual enhancement of touch is not evident in the ERP waveforms when manipulated as a between-subjects variable. It is worth noting that Sambo and colleagues (Sambo et al., 2009) did not observed a direct effect of vision on touch, most likely because their task involved an easy tactile discrimination. Future studies should investigate whether early tactile processing is directly modulated by visual information when the tactile attention task is perceptually challenging and whether under these experimental conditions the effects of vision and attention contribute independently or jointly to the modulation of touch.

In contrast to the sensory-specific processing stages during which interactive effects of perceptual load and visual information on tactile spatial attention were observed, during later post-perceptual processing stages increasing the target/nontarget discrimination difficulty (perceptual load) resulted in increased attentional engagement. Stronger effects of attention were present for challenging perceptual

target/nontarget discriminations and this difference was observed regardless of illumination condition, although differences between tasks emerged earlier in the darkness. This finding suggests that in order to deal with a more challenging perceptual discrimination, additional resources were recruited during the high load task.

To find out whether these stronger attention effects observed in the high load tasks were caused by differential processing at cued or uncued body locations, we compared directly cued as well as uncued ERPs elicited in the high and low load tasks. ERPs elicited by cued stimuli were more negative in the high than in the low load task (main effect of task for cued stimuli at lateral and midline electrodes, both $F(1, 22) > 13.9$; both $p < .001$; both $\eta_p^2 > .38$). In contrast, no difference emerged between tasks for uncued stimuli (both lateral and midline electrodes $F(1, 22) < 0.2$; both $p > .6$; both $\eta_p^2 < .009$). These results reveal that the additional attentional resources recruited in the high load task were not equally distributed across cued and uncued body locations. Instead, the increased resources necessary for the in-depth elaboration of the non-spatial features of stimuli (their frequency) were directed selectively to the cued hand during post-perceptual processing stages of perceptually demanding tasks. The idea that increased attentional resources were directed to the attended hand in the high load task to perform difficult discriminations is further supported by the results of the behavioural analysis which showed slower and less accurate responses to attended targets in the high load as compared to the low load task. Interestingly, the behavioural effect of load was not modulated by illumination condition mirroring the pattern of ERP results observed during the later phase of the Nd component (measured between 280 and 400 ms post-stimulus). This is line with existing observations suggesting that the behavioural performance is more strongly related to attentional modulations ob-

served during later post-perceptual stages of somatosensory processing (e.g. Jones & Forster, 2014).

Attentional modulations of touch in the Nd time range have been linked to the suppression of tactile processing at uncued rather than cued body locations (c.f. Forster and Eimer, 2005a; Forster and Gillmeister, 2011). ERP investigations of costs and benefits in tactile selective attention - in which both informative and non-informative (neutral) cues were presented - showed increased positivities for tactile ERPs on uncued as compared to neutral trials (costs) in the Nd time range, but no difference between cued and neutral trials (benefits) (c.f. Forster and Eimer, 2005; Forster and Gillmeister, 2011). The fact that we observed enhancement of processing of cued information during the Nd time range in the high load task might suggest that the specific pattern of costs/benefits observed in the Nd time range depends also on the perceptual difficulty of the task. Low perceptual demands might result primarily in attentional costs (suppression of uncued information) while high perceptual demands might result in both costs and benefits (suppression of uncued information and enhancement of cued information, respectively).

Finally, it is interesting to note that previous studies have typically reported delayed and/or reduced effects of attention on touch when the spatial selection of the task-relevant body location was more challenging. For example, the operations of spatial attention are 'disrupted' whenever there is a conflict or a mis-alinement between different spatial representations defining a task-relevant body location. This is typically observed during manipulations of body posture when tactile stimuli are delivered to the left or right hand and the position of the body is changed across experimental conditions. For instance, placing the hands close together rather than far apart reduces the amplitude of the N140 component (Eimer et al., 2004; Gillmeister et al., 2010; Gill-

meister and Forster, 2012). Similarly when the hands are positioned at the same distance but are crossed the effect of attention is delayed and reduced (Eimer et al., 2001; 2003; Eardley and van Velzen, 2011; Gherri and Forster, 2012; Röder et al., 2008). Furthermore, smaller attentional modulations of the Nd component are present when participants direct their gaze to the side as compared to a neutral central position (Gherri and Forster, 2014). Importantly, however, the results of the present study demonstrate that reduced effects of tactile spatial attention (in the time range of the Nd component) do not necessarily reflect a disruption in its operations. When the difficulty of the perceptual target/nontarget discrimination is manipulated rather than the difficulty of the spatial selection of the task-relevant body location, smaller attentional modulations correspond to easier tasks which require reduced attentional resources[ii].

In summary, the present study shows for the first time that perceptual load selectively modulates the mechanisms of tactile spatial attention. In particular, the reduced discriminability of targets and non-targets in the high load task results in larger attentional modulations during post-perceptual stages. This effect of load on tactile spatial attention is caused by systematic changes in the cognitive operations associated with the processing of stimuli at cued locations and is independent from the availability of visual cues about the body. By contrast, attentional modulations by load during perceptual processing stages are strongly affected by the availability of visual information. Earlier effects of attention during perceptually demanding tactile tasks (high load) are only observed in the absence of visual information (darkness condition), while no such difference is present when visual cues about the body are available (light condition). Thus, a complex interplay between vision and tactile perceptual load determines the effects of spatial attention on the perceptual stages of tactile processing. Overall, our results demonstrate that perceptual load is one of the

many factors that contribute to shape the specific time-course and strength of the attention effect in touch.

4. Method

4.1. Participants

Thirty-seven paid volunteers gave informed consent to participate in the experiment and they were assigned to two experimental groups which carried out the same experimental task under different illumination conditions (light vs. darkness conditions). Eighteen participants took part in the light condition. Four were excluded due to poor eye fixation control in the cue–target interval (see below for details) and two could not complete the task due to a technical problem with the tappers. Thus, 12 participants (9 women, 3 men; aged 18-35; all right-handed) remained in the sample. The remaining nineteen volunteers participated in the darkness condition. Seven were excluded due to poor eye fixation control (see below). Thus, 12 participants remained in the sample (7 women, 5 men; aged 18–32; 11 participants were right-handed, 1 was left-handed). All participants had normal or corrected-to-normal vision by self-report. Ethical approval was granted by the Psychology Research Ethics Committee, University of Edinburgh. The studies followed the guidelines laid down in The Code of Ethics of the World Medical Association (Declaration of Helsinki; British Medical Journal, 18 July 1964).

4.2. Stimuli and Materials

Participants sat at a table in an experimental chamber. Their hands were positioned on the table palm down with their index fingers 20 cm to the left and right of

the body midline. Tactile stimuli were presented using 12-V solenoids, driving a metal rod with a blunt conical tip. The solenoids were attached to the radial side of the middle phalanx of the index fingers with white medical tape. Whenever a current was passed through the solenoids, the tip made contact with the finger. White noise (65 dB SPL) was continuously present to mask any sound made by the activation of the tactile stimulators. Participants were instructed to keep their gaze on a central fixation point which was located approximately 52 cm from the participant's viewpoint, at about participants' eye level, and present continuously during the experiments. In the light condition, the fixation point consisted in a white cross (1°x1°) presented on a screen against a black background; in the darkness condition, the fixation point consisted in a dim LED light mounted on a black panel. A microphone placed next to the participant was used to collect vocal responses, and an infrared camera was used to monitor participants during the experiment.

Each trial started with the bilateral presentation of the tactile cue (60 ms) followed by a unilateral tactile stimulus (target or non-target, 205 ms duration), 950 ms after cue offset. The inter-trial interval varied randomly between 1200 and 1300 ms. The bilateral cues (presented simultaneously to both hands) consisted in either single (the rod continuously contacting the skin for 60 ms) or double taps (skin contact interrupted for 50 ms after a duration of 5 ms). The following tactile stimuli consisted in unilateral vibrations presented to the left or right hand and were composed of a rapid sequence of pulses during which the rod was in contact with the skin for 5 ms and followed by a variable inter-pulse interval. Non-target stimuli (i.e. standard) consisted in 'slow' vibrations and were characterized by 5 ms inter-pulse interval (each cycle repeated 5 times, 25 Hz frequency) in both the low and high load tasks. Target stimuli consisted in 'fast' vibrations with inter-pulse interval set to 35 ms in the low load task

(each cycle repeated 20 times, 100Hz vibration) and to 20 ms in the high load task (each cycle repeated 8 times, 40 Hz frequency).

4.3. Design and Procedure

In both the light and darkness conditions, the experiment consisted of 12 blocks, with 80 trials per block. In each block, a non-target tactile stimulus (slow vibrations) was presented with equal probability to the left or right hand and to the cued or uncued hand on 60 of the trials. A target stimulus (fast vibration) was presented on the remaining 20 trials. Twelve of these targets were delivered to the cued hand (6 on the left hand and 6 on the right hand) and required a vocal response. On eight trials per block, tactile targets were presented to the uncued hand (4 on the left hand and 4 on the right hand), and no response was required on these trials.

Participants performed two experimental tasks, the low and high load tasks, each consisting of six successive blocks (task order was counterbalanced across participants). The difference between the low vs. high load tasks consisted in the physical distance between the frequencies that characterized targets stimuli. Target frequency was 100Hz in the low load task and 40Hz in the high load task, while non-target frequency was 25Hz in both tasks. Participants were instructed to covertly attend to the hand placed on the side indicated by the tactile cue (stimulus-hand mapping was counterbalanced across participants) and to respond by saying 'pa' whenever a tactile target stimulus (fast vibrations) was delivered to the hand on the cued side, while ignoring target stimuli (fast vibrations) presented to the uncued hand as well as all non-target stimuli (slow vibrations).

In the darkness condition, participants were blindfolded before entering the completely dark experimental room. Blindfolds were removed prior to EEG recording

and participants were asked to close their eyes anytime an experimenter was about to enter the room (which the experimenter would signal by knocking on the door). All experimental blocks were conducted in darkness, only the dim LED fixation point being visible. Thus, participants had no direct visual information throughout the darkness condition about their hands or the testing environment.

4.5. EEG recording and data analysis

EEG was recorded using a BIOSEMI system from 64 active electrodes (Fpz, Fp1,Fp2, AFz, AF7, AF3, AF4 AF8, Fz, F7, F5, F3, F1, F2, F4, F6, F8, FCz, FT7, FC5, FC3, FC1, FC2, FC4 FC6, FT8, Cz, T7, C5, C3, C1, C2, C4, C6, T8, CPz, TP7, CP5, CP3, CP1, CP2, CP4, CP6, TP8, Pz, P9, P7, P5, P3, P1, P2, P4, P6, P8, P10, POz, PO7, PO3, PO4, PO8, Oz, O1, O2, Iz) positioned according to the 10-20 system. Two additional electrodes were attached to the earlobes and were used as offline references. Horizontal eye movements (HEOG) were recorded from two electrodes placed at the outer canthi of each eye and vertical eye movements (VEOG) were recorded from two electrodes positioned above and below the right eye. Electrode impedance was kept below 15 kΩ. EEG and EOG were sampled with a 512 Hz digitization rate and stored on a computer for offline analysis. Data were analysed using the Brain Vision Analyser software (version 2.0.4.368). EEG was digitally re-referenced to the average of the left and right earlobe and was digitally filtered offline (high-pass filter 0.53 Hz, low-pass filter 40 Hz and notch filter 50 Hz). EEG was epoched into 500ms intervals starting 100ms before and ending 400ms after non-target onset. Trials with eye blinks (voltage exceeding ±60μV on the VEOG channel), horizontal eye movements (voltage exceeding ±40μV on the HEOG channel) and other artefacts (voltage exceeding ±80μV at all other electrode sites) were excluded from further analysis, as

were trials with response errors. Because gaze direction can alter the processing of tactile information (Gherri and Forster, 2015) and modulate tactile attention (Gherri and Forster, 2014), we excluded participants that were not able to maintain a central gaze direction. Averaged HEOG waveforms obtained in the cue-target interval in response to cues directing tactile attention to the left or right hand were scored for systematic deviations of eye positions. Residual HEOG deflections exceeding $\pm$ 3.8 µV led to the exclusion of four participants in the light condition and seven participants in the darkness condition. Visual inspection of these residual HEOG deflections confirmed the presence of systematic ocular activity in the excluded participants.

To avoid contamination by vocal responses to the cued targets, only ERPs elicited by non-targets stimuli (slow vibrations) were included in the ERP analysis (note that non-targets were physically identical in the low and high load tasks). These were averaged relative to a 100ms pre-stimulus baseline for all combinations of task (low load vs. high load), attention (stimulus presented to the cued vs. uncued hand) and stimulated hand (left vs. right hand). ERP mean amplitudes were computed for each participant within successive measurement windows centred on the P45 (35-55 ms post-stimulus onset), N80 (65-85 ms), P100 (90 – 125 ms) and the N140 (130 - 170 ms) components, and for longer latencies (Nd1, 200 – 260 ms and Nd2, 280 - 400 ms post-stimulus onset).

Statistical analyses were carried out for the twelve lateral electrode pairs located close to and over the somatosensory areas FC1/2, FC3/4, FC5/6, C1/2, C3/4, C5/6, CP1/2, CP3/4, CP5/6, P1/2, P3/4, P5/6, and for the corresponding midline electrodes Fcz, Cz, Cpz and Pz. Separate analyses were conducted for lateral electrodes (ipsilateral and contralateral to the stimulated hand, FC1/2, FC3/4, FC5/6, C1/2, C3/4, C5/6, CP1/2, CP3/4, CP5/6, P1/2, P3/4, P5/6) and for midline electrodes (Fcz, Cz, Cpz and

Pz). Mean amplitude values were analysed using mixed ANOVAs, including the within subjects factors task (low load vs. high load), attention (stimulus presented to the cued vs. uncued hand), electrode site (FC1/2, FC3/4, FC5/6, C1/2, C3/4, C5/6, CP1/2, CP3/4, CP5/6, P1/2, P3/4, P5/6 for lateral electrodes and Fcz, Cz, Cpz and Pz for midline electrodes), and hemisphere (contralateral vs. ipsilateral to the stimulated hand for lateral electrodes only) and the between subject factor illumination condition (light vs. darkness). In these mixed ANOVAs, the presence of systematic effects of perceptual load on attention were reflected by significant attention x task interactions while attention x task x illumination condition interactions showed systematic differences between the effects of load on attention in the different illumination conditions. Whenever these three ways interactions were present separate analyses were carried out for each illumination conditions to evaluate the presence of significant attention x task interactions. Following significant attention x task interactions, follow-up analyses were carried out separately for the low and high load tasks to determine the presence and strength of the attention effect on touch for each task. Greenhouse–Geisser adjustments to the degrees of freedom were performed when appropriate, and adjusted p values were reported.

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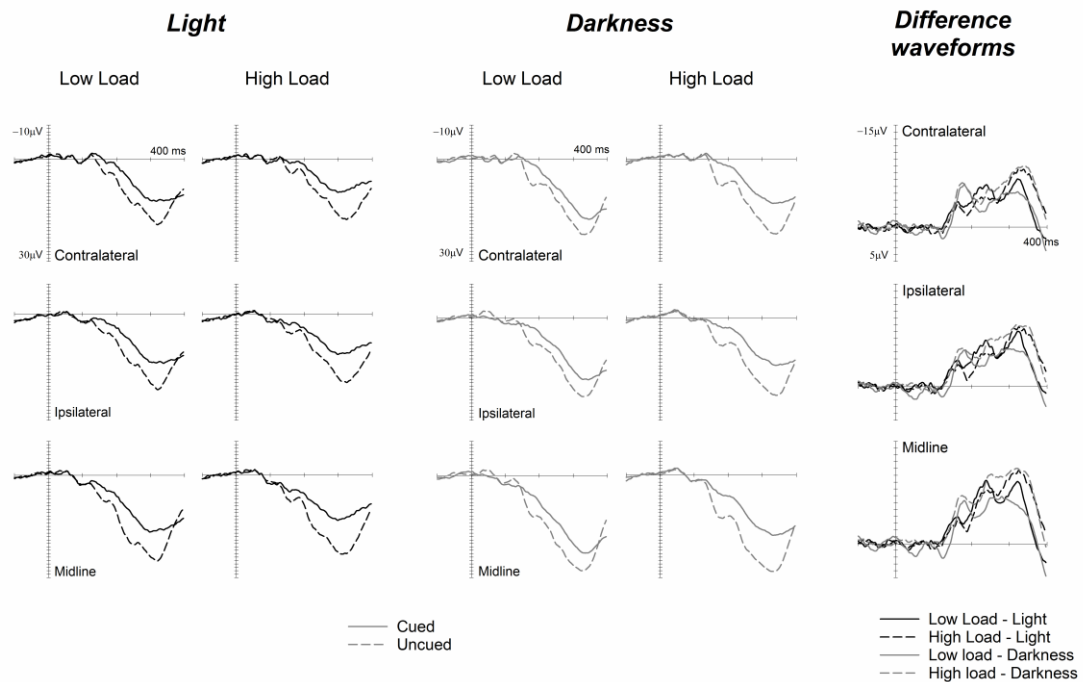
Figures

Figure 1. Grand-averaged tactile ERPs elicited by non-target tactile stimuli presented at cued locations (solid lines) and uncued locations (dashed lines) at electrode sites contralateral and ipsilateral to the stimulated hand (top and middle panels) as well as midline electrodes sites in the 400-ms interval following the onset of the tactile stimulus. Separate graphs show ERPs recorded in the Low load and High load tasks in the Light and Darkness conditions. The corresponding difference waveforms represent the cuing effect (obtained by subtracting the tactile ERPs elicited by cued stimuli from those elicited by uncued stimuli) separately for the Light and Darkness conditions (black and grey lines, respectively)and for the Low Load (solid line) and the High Load tasks (dashed line), pooled across sites contralateral and ipsilateral to the stimulated hand (FC1/2, FC3/4, FC5/6, C1/2, C3/4, C5/6, CP1/2, CP3/4, CP5/6, P1/2, P3/4, P5/6) and midline sites (Fcz, Cz, Cpz, Pz).
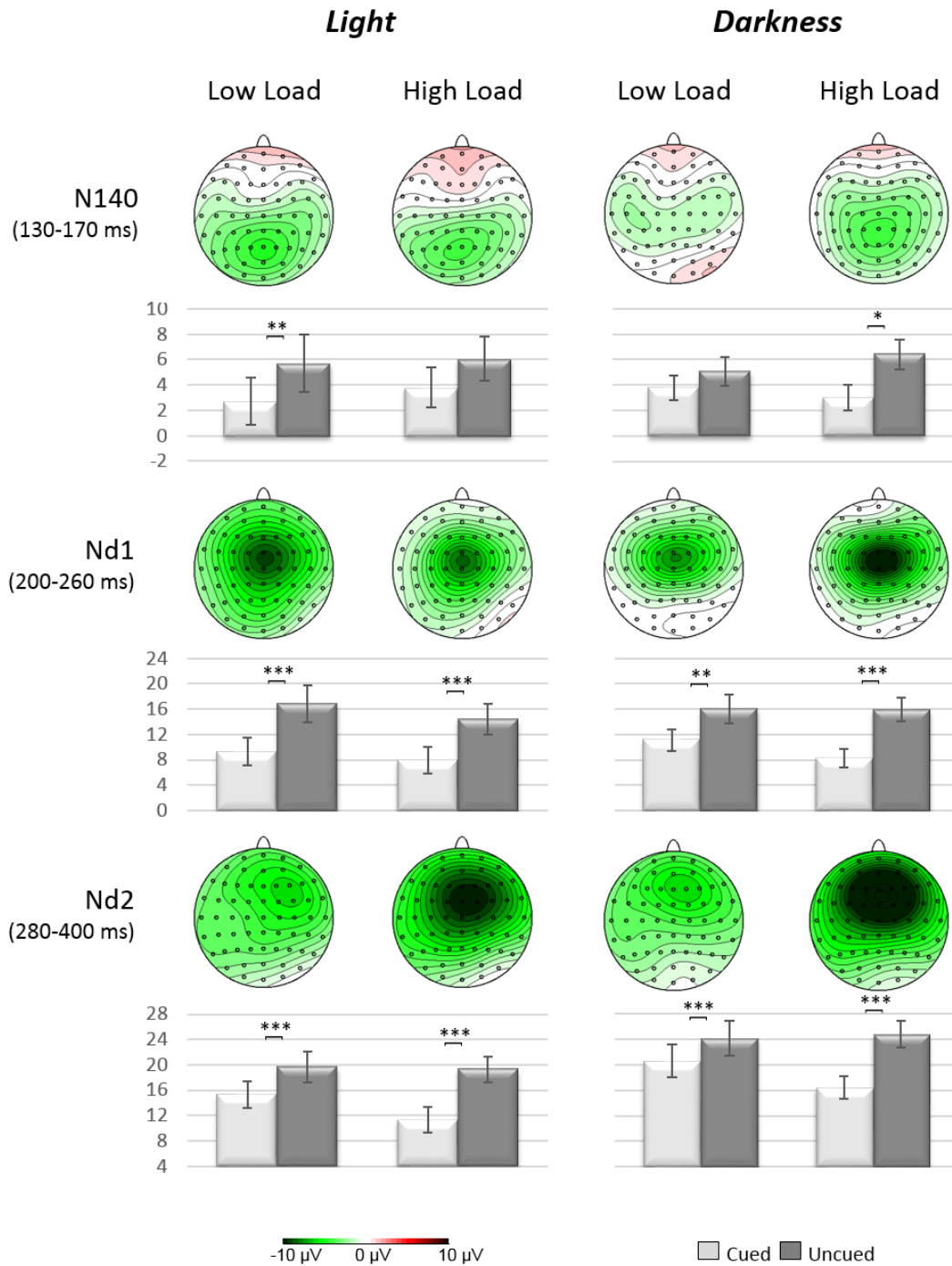
Figure 2. Attentional modulations of tactile processing observed under illuminated and darkness conditions (left and right panels, respectively) in the High and Low Load tasks. Top panels show the topographical voltage maps of the attention effects for the N140, Nd1 and Nd2 components. These maps display the voltage distributions of the cuing effect obtained by subtracting ERPs to uncued non-target stimuli from ERPs to cued stimuli. Electrodes on the left hemisphere are contralateral to the

stimulated hand, while those on the right hemisphere are ipsilateral to the stimulated hand. The bar graph below each topographical map shows the mean amplitude values of the corresponding cued and uncued ERPs (white and grey bars respectively) for the same ERP components averaged across midline electrodes (Fcz, Cz, Cpz, Pz) where attention effects were stronger. Asterisks in the bar graphs denote the presence of significant cuing effects as revealed by planned comparisons conducted in each task and for each illumination condition (* p < .05; ** p < .01; *** p < .001).

Footnotes:

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[i] Because our main focus was the effect of perceptual load on tactile spatial attention, the variable illumination condition (light vs. dark) was manipulated between participants. This mixed experimental design eliminated issues related to practice/training effects (the same participants executing the high load task twice under different illumination conditions) and avoided multiple recording sessions given the substantial lengths of the experiment.

[ii] One additional aspect of our results which is worth noting is the presence of a direct effect of task (perceptual load) on tactile processing. This was characterised by enhanced negativities for ERPs elicited by stimuli in the high as compared to the low load condition, during sensory-specific (N80 time range) as well as later processing stages (Nd1 and Nd2). Because participants were instructed to attend to a specific frequency (tar-get frequency) while ignoring another one (non-target frequency), the main effect of task reflects, at least in part, non-spatial attention (i.e. attention to frequency). The observation that the main effect of task was present in the N80 time window, before any reliable spatial attention effect, provides further evidence that non-spatial selectivity in touch operates independently from spatial attention (Forster & Eimer, 2004).