



The attentional selection of spatial and non-spatial attributes in touch: ERP evidence for parallel and independent processes

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Abstract

To investigate the functional relationship between spatial and non-spatial attentional selectivity in somatosensory processing, event-related potentials (ERPs) were recorded to mechanical tactile stimuli, which were delivered to the right or left hand, and were low or high in frequency (Experiment 1), or soft or strong in intensity (Experiment 2). Participants' task was to attend to a specific combination of one stimulus location and one non-spatial attribute. Spatial attention was reflected in enhanced N140 components followed by a sustained attentional negativity. ERP effects of non-spatial attention (enhanced negativities to the attended frequency or intensity) were observed in the same latency range, suggesting that the attentional selection of relevant spatial and non-spatial attributes occurs in parallel. Most importantly, ERP correlates of attention directed to stimulus frequency and intensity were unaffected by the current focus of spatial attention. In contrast to vision, where the selective processing of non-spatial attributes is hierarchically dependent on selection by location, but similar to auditory attention, spatial and non-spatial attentional selectivity appear to operate independently in touch.

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1. Introduction

While selective attention has been studied intensively in the visual and auditory modality, the processes underlying attentional selectivity in somatosensation are still poorly

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understood. The aim of the ERP study reported here was to investigate the attentional selection of spatial and non-spatial attributes of tactile stimuli, in order to obtain insights into the mechanisms involved in the selective attentional processing of different tactile stimulus attributes.

Directing visual attention in space results in faster detection and more accurate discrimination of visual stimuli at currently attended locations (Posner et al., 1980). ERP studies have provided evidence that early stages of visual processing are modulated by visual-spatial attention (Mangun and Hillyard, 1990). Enhanced early sensory-specific ERP components (P1 and N1) are elicited over posterior visual cortical areas in response to visual stimuli at currently attended as compared to unattended locations (e.g. Mangun, 1995; Mangun et al., 1987; Mangun and Hillyard, 1987; Eimer, 1995), and these amplitude modulations start as early as 80 ms after stimulus onset. In contrast, visual attention to non-spatial features, such as colour or shape, result in an enhanced sustained negativity that starts much later (at about 150 ms post-stimulus; e.g. Eimer, 1995; Helsenfeld et al., 1997).

To investigate whether the selective attentional processing of non-spatial visual stimulus attributes depends on prior selection for spatial location, Hillyard and Münte (1984) presented their participants with visual stimuli defined by both location and color. The participants' task was to detect infrequent target stimuli that matched both the attended color and the attended location. ERP waveforms elicited by non-target stimuli with the attended color and/or location were compared to non-targets with the unattended color and/or location. ERPs elicited by stimuli at attended locations showed enhanced P1, N1 and N2 components compared to stimuli at unattended locations, and these spatial attention effects were independent of stimulus colour. Effects of attention directed to colour were associated with a broad negativity starting around 150 ms after stimulus onset. Most importantly, these ERP effects of selective colour processing were only found in response to stimuli at the attended location, thus suggesting that spatially selective processing not only precedes the selective processing of non-spatial attributes of visual stimuli (i.e. color), but also that non-spatial attention effects are contingent upon the prior selection of visual stimuli on the basis of their location (see also Eimer, 1995; Omoto et al., 2001).

Similar to vision, selective spatial attention also facilitates auditory processing (Spence and Driver, 1994, 1998). However, recent behavioral studies have shown that the attentional processing of auditory stimulus locations is influenced by stimulus frequency even when frequency is irrelevant (Mondor et al., 1998), and that auditory targets defined by frequency or by the conjunction of frequency and location are identified faster than targets defined by location only (Woods et al., 2001). These findings suggest that unlike in vision, the attentional selection of spatial does not precede the selection of non-spatial attributes of auditory stimuli. To examine the mechanisms underlying the selective processing of auditory spatial and non-spatial attributes, Woods and Alain (2001) recorded ERPs in response to tones defined by a combination of location, frequency and duration, under conditions where targets were defined by a specific combination of location, frequency and duration attributes. When ERP waveforms elicited by stimuli possessing none of the attended attributes with ERPs elicited by stimuli possessing one, two or all of the attended attributes were compared, both attention to location and attention to frequency were reflected in enhanced early attentional negativities starting at about 60 ms post-stimulus. In line with the behavioural evidence described above, these results suggest that the attentional selection of spatial and non-spatial

auditory stimulus attributes takes place in parallel and independently (see also Hansen and Hillyard, 1983; Woods et al., 1994).

Only few ERP studies to date have investigated mechanisms of selective attention in touch. In most studies on tactile spatial attention, participants were instructed to attend to one hand versus the other while electrical or mechanical stimuli were delivered to the left or right hand. Spatial attention was found to modulate the sensory-specific somatosensory N140 component, with enhanced N140 amplitudes for tactile stimuli delivered to the attended hand (Desmedt and Robertson, 1977; Michie et al., 1987; García-Larrea et al., 1995; Eimer and Driver, 2000; Eimer et al., 2001, 2002; Eimer and Forster, 2003). In addition, effects of tactile spatial attention on the somatosensory P100 component (Josiassen et al., 1982; Michie, 1984; Eimer and Forster, 2003), and a later sustained processing negativity (Desmedt and Robertson, 1977; Michie, 1984) have also been observed. The fact that tactile spatial attention affects early, sensory-specific somatosensory ERP components clearly suggests that, analogous to visual and auditory spatial attention, spatial selectivity in touch can modulate relatively early perceptual stages of somatosensory processing.

ERP correlates of non-spatial attentional selectivity in touch have not yet been investigated systematically. Michie et al. (1987) found that ERP effects of tactile spatial attention were modulated by a non-spatial attribute (intensity) defining infrequent target stimuli. In this experiment, participants had to report infrequent weak stimuli delivered among stronger stimuli, or infrequent strong stimuli delivered among weaker stimuli, when these infrequent targets were presented to the currently attended hand. Spatial attention affected the N80 component when weak stimuli had to be detected among strong non-targets, and an effect of spatial attention on the P105 when infrequent strong targets were presented among weak non-targets. However, ERP correlates of tactile attention directed to stimulus intensity were not measured directly in this study.

The present experiment was designed to investigate for the first time ERP correlates of selective attention directed to non-spatial attributes of tactile stimuli, as well as the relationship between spatial and non-spatial selective attention in somatosensation. Mechanical vibratory tactile stimuli were delivered to the left or right hand, and these stimuli also differed with respect to one non-spatial attribute. In Experiment 1, stimulus frequency was either low or high. In Experiment 2, stimulus intensity was either strong or soft. Participants' task was to direct attention to one side, and to one non-spatial stimulus attribute, in order to detect and respond to infrequent targets (which were longer than non-targets) when these possessed both relevant attributes. Thus, in separate blocks, selective attention was directed to one of the four possible combinations of location (left versus right) and frequency (high versus low, in Experiment 1) or intensity (strong versus soft, in Experiment 2). ERPs were computed in response to non-targets possessing both, one, or neither of these task-relevant attributes.

In vision, ERP effects of spatial attention precede ERP effects of non-spatial attentional selectivity, and ERP correlates of the selective processing of a non-spatial visual attribute are only observed in response to visual stimuli at currently attended locations, thus demonstrating that the attentional processing of non-spatial visual features is hierarchically dependent on prior selection of stimulus location (Hillyard and Münte, 1984; Eimer, 1995). If the same hierarchical dependency also exists for selective attention in the somatosensory modality, ERP effects of attention directed to stimulus frequency or intensity should emerge later

than ERP effects of tactile-spatial attention, and any effects of non-spatial attention should only be present for tactile stimuli presented to the currently attended hand. In addition, the attentional processing of spatial and non-spatial stimulus attributes appears to be based on parallel and independent mechanisms (Woods et al., 1994, 2001; Woods and Alain, 2001). If this was also the case for somatosensation, ERP modulations reflecting attention to spatial and non-spatial tactile stimulus attributes should be elicited concurrently. More importantly, ERP correlates of non-spatial tactile attention should not only be elicited in response to stimuli delivered to the currently attended hand, but also for tactile stimuli presented to the unattended hand.

2. Experiment 1

2.1. Methods

2.1.1. Participants

Seventeen paid volunteers participated in Experiment 1. Two participants had to be excluded because of too many eye-blinks contaminating more than 70% of trials. Three additional subjects had to be excluded because of a lack of clearly defined early somatosensory components (see below). Thus 12 participants (4 males, 8 females), aged 19–41 years (mean age: 25.6 years) remained in the sample. All participants were right-handed and had normal or corrected vision.

2.1.2. Stimuli and apparatus

Participants sat in a dimly lit experimental chamber, wearing a head-mounted microphone, and facing a computer screen. Tactile stimuli were presented using 12 volt solenoids, driving a metal rod with a blunt conical tip to one finger, making contact with the skin whenever a current was passed through the solenoid. Two tactile stimulators were used. These were attached to the radial side of the second phalanx of the index fingers. Participants were instructed to place their hands in a comfortable position on the tabletop in front of them. Care was taken that the arms were placed parallel to the right and left of the body midline. Throughout the experimental blocks a fixation cross was presented at the centre of a computer screen at a distance of about 45 cm from the participants' fingertips. White noise (62 dB SPL) was continuously delivered to mask any sound made by the tactile stimulators.

Two different rectangular frequencies (29.4 and 58.8 Hz) of vibratory stimulation were used. To create low and high frequency vibrations, the contact time between the rod and the skin was set to 3 ms, followed by a 31 or 14 ms interpulse interval, for low and high frequency, respectively. On each trial, a single vibratory stimulus was presented at either the left or right hand. Stimulus duration was 340 ms for non-targets, and 680 ms for targets. The intertrial interval between successive stimuli varied randomly between 750 and 1050 ms with a mean intertrial interval of 900 ms.

2.1.3. Procedure

The experiment consisted of 16 experimental blocks. Tactile stimuli were high-frequency or low-frequency stimuli presented either to the left or right hand. Before the start of

each experimental block, participants were instructed to direct attention to one of the four possible combinations of stimulus frequency and location. They were reminded to keep gaze direction focussed on the central fixation cross and to respond vocally (by saying “yes”) whenever an infrequent relevant target (a long-duration stimulus possessing both task-relevant features) was detected. Four blocks were run for each frequency/location combination. The order in which these blocks were delivered was randomised for each participant. Each block consisted of 120 trials. In 100 trials, non-target stimuli were delivered equiprobably for each of the four possible combinations of stimulus location and frequency. In the remaining randomly intermingled 20 trials, longer target stimuli were presented. Eight of these possessed both currently relevant attributes, and thus required a response. The other 12 target stimuli had only one, or neither of the task-relevant features, and thus could be ignored.

Before the start of the experiment, participants received a demonstration to familiarize them with the two vibratory stimulus frequencies. Additionally, they received one training block randomly selected from one of the four possible combinations of stimulus attributes.

2.1.4. Recording and data analysis

EEG was recorded with Ag–AgCl electrodes and linked-earlobe references from midline electrodes FPz, Fz, Cz, Pz, Oz, electrodes F4, F8, FC6, C4, T8, CP6, P4, P8 and homologous electrode sites over the left hemisphere (according to the 10–20 system), and from OL and OR (located halfway between O1 and P7, and O2 and P8, respectively). Horizontal EOG (HEOG) was recorded bipolarly from the outer canthi of both eyes. Impedance for all electrodes was kept below 5 k Ω . The amplifier bandpass was 0.1–40 Hz and digitisation rate was 200 Hz. Trials immediately following a vocal response were discarded to avoid any contamination of averaged ERPs by movement-related artefacts (this led to the exclusion of 7% of all trials). Trials with eyeblinks, horizontal eye movements, and muscle artefacts were excluded (this resulted in an exclusion of 24% of all trials, averaged across participants). As the aim of the study was to investigate attentional effects on early somatosensory components, somatosensory ERP components elicited by left-hand and right-hand stimulation (collapsed across both stimulus frequencies and all attention instructions) were sourced individually for each participant. For two participants, early somatosensory components (P45, N80, P100) were not clearly visible over contralateral electrodes C3/C4 and CP5/CP6, and for one participant, these components were delayed (>10 ms) relative to the group mean. These three participants were excluded from further analysis.

ERPs to non-target stimuli (short duration) were averaged relative to a 100 ms pre-stimulus baseline for all combinations of attention instruction, stimulus location, and stimulus frequency. ERP mean amplitudes were computed within measurement windows centred on the latency of somatosensory N80 (65–85 ms), P100 (90–125 ms) and N140 (130–165 ms) components. To investigate longer-latency effects of spatial and non-spatial attention, mean amplitudes were also computed between 185 and 285 ms post-stimulus. Mean amplitudes were analysed with repeated measures ANOVAs. Analyses of ERP data were restricted to electrode sites contralateral to the stimulated hand located close to and over somatosensory cortex (F3/4c, FC5/6c, C3/4c, CP5/6c), where somatosensory ERPs are maximal. Initial analysis included the factors attention to location (stimulus presented at currently attended versus unattended side), attention to frequency (stimulus in the currently attended versus

unattended frequency), stimulus location (left versus right), stimulus frequency (high versus low), and electrode site.

The latency of vocal responses was measured relative to the duration of the shorter non-target stimuli (340 ms), as target/nontarget discriminations were only possible after this interval. For vocal responses to tactile targets, mean response times (RT) for each participant were calculated for each combination of target location and frequency. A repeated measures ANOVA was performed on mean RTs with the factors stimulus frequency and location. Additionally, the same analysis was performed on the percentage of missed relevant targets.

2.2. Results

2.2.1. Behavioural performance

Vocal responses were faster to high frequency than to low frequency tactile target stimuli (mean RTs of 697 and 731 ms for high and low frequency targets, respectively; $F(1, 11) = 8.5$; $P < .02$). In contrast, stimulation location did not affect response latency (mean RTs of 711 and 717 ms for left and right hand target stimuli, respectively). There was no interaction between stimulus location and frequency. Participants missed on average 12% of all relevant targets, with no significant difference between high and low frequency targets, or between left and right targets. The rate of False Alarms to irrelevant tactile targets and non-target stimuli was on average below 1%.

2.2.2. Effects of attention to location and frequency on somatosensory ERP components

The left panel of Fig. 1 shows ERPs elicited at electrodes contralateral to the stimulated hand in response to tactile stimuli delivered at currently attended (solid lines) and unattended (dashed lines) locations, collapsed across both stimulus frequencies. Spatial attention showed a clear effect at all electrode sites, with an enhanced N140 component followed by a sustained negativity for tactile stimuli at the attended location. The right panel of Fig. 1 shows ERPs elicited at the same electrodes in response to stimuli with the currently attended (solid lines) and unattended (dashed lines) frequency, collapsed across attended and unattended locations. Attention to frequency was reflected in an enhanced early negativity for attended stimulus frequencies overlapping with the N80, P100 and N140 component, as well as a later sustained negativity, which was smaller than the late negativity observed for spatial attention.

These observations were substantiated by statistical analysis. No significant effects of attention to location were found in the N80 (65–85 ms after stimulus onset) or P100 time range (90–125 after stimulus onset). In the subsequent N140 time window (130–165 ms after stimulus onset), as well as in the late processing time range (185–285 ms after stimulus onset), significant effects of attention to location were present ($F(1, 11) = 15.1$; $P < 0.03$; and $F(1, 11) = 35.3$; $P < 0.001$, respectively), reflecting an enhanced negativity for stimuli at attended relative to unattended locations.

Unlike the spatial attention effect, an attention to frequency effect emerged already in the P100 time range (90–125 after stimulus onset; $F(1, 11) = 4.9$; $P < 0.05$), and this effect was also present as a late processing effect beyond 185 ms after stimulus onset ($F(1, 11) = 10.4$; $P < 0.01$), reflecting an enhanced negativity for tactile stimuli in the attended frequency.

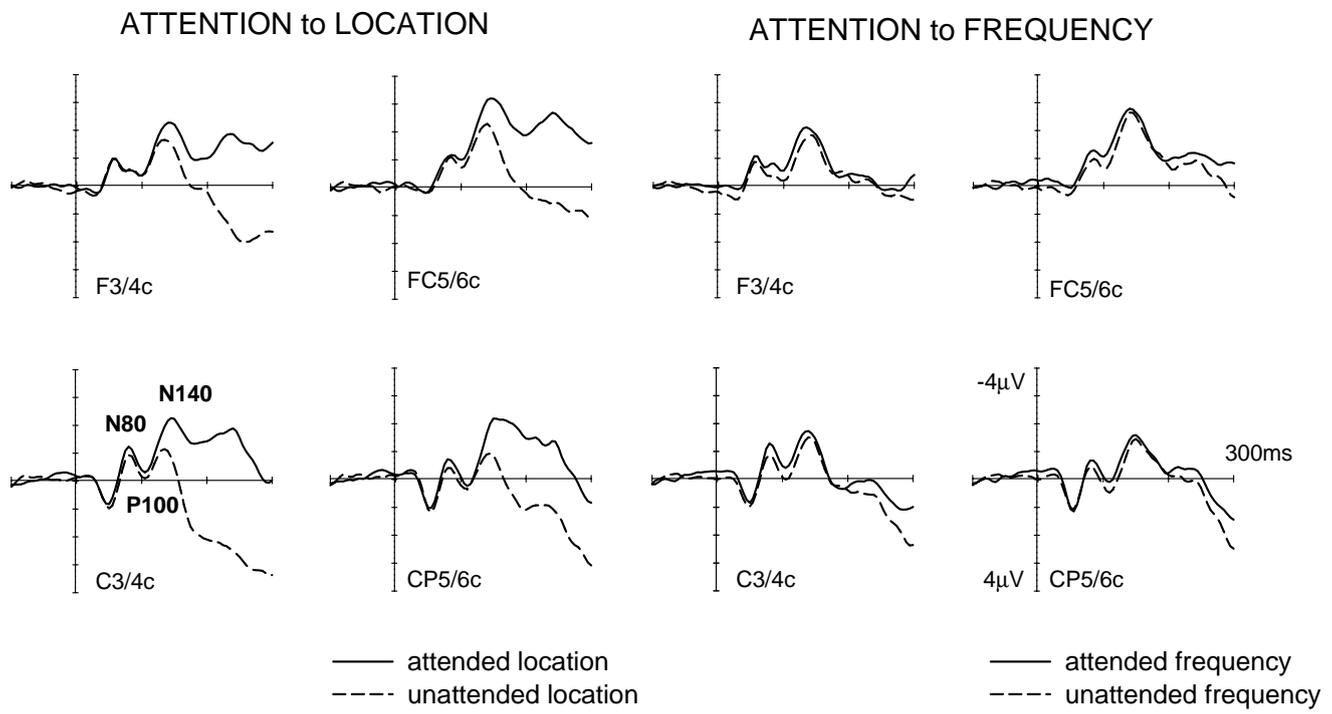


Fig. 1. Grand-averaged somatosensory ERPs elicited in Experiment 1 by tactile non-target stimuli in the 300 ms interval following stimulus onset over the hemisphere contralateral to the stimulated hand close to somatosensory cortex. Left panel: ERPs obtained in response to stimuli at attended (solid lines) and unattended (dashed lines) locations, collapsed across attended and unattended frequencies. Right panel: ERPs obtained in response to stimuli with the currently attended (solid lines) and unattended (dashed lines) frequency, collapsed across attended and unattended stimulus locations.

There was no main effect of attention to frequency at the N80 (65–85 ms after stimulus onset; $F(1, 11) = 2.7$, n.s.) or N140 time range (130–165 ms after stimulus onset; $F(1, 11) = 3.5$, n.s.). However, an interaction of stimulus frequency and attention to frequency ($F(1, 11) = 7.6$; $P < 0.02$) was observed in the N140 time range. To further investigate this interaction, separate analyses were performed for low and high frequency stimuli.

Fig. 2 contrasts ERPs to high (left panel) and low (right panel) frequency stimuli under conditions when this particular frequency was attended (solid lines) or unattended (dashed lines), collapsed across attended and unattended locations. As can be seen from this Figure, ERP effects of attention to frequency differed as a function of stimulus frequency. For low-frequency stimuli, an early enhanced negativity was elicited when this frequency was attended, as compared to blocks where attention was directed to high frequency stimuli. This effect overlapped with the N80, P100 and N140 components (Fig. 2, right). In contrast, these early frequency attention effects were attenuated or entirely absent (for the N140 component) in response to high frequency tactile stimuli (Fig. 2, left). Statistical analyses, conducted separately for low and high frequency stimuli, found significant effects of attention to frequency for low frequency stimuli in the N80 (65–85 ms after stimulus onset; $F(1, 11) = 5.7$; $P < 0.04$), P100 (90–125 ms after stimulus onset; $F(1, 11) = 17.5$; $P < 0.01$) and N140 (130–165 ms after stimulus onset; $F(1, 11) = 9.3$; $P < 0.02$) time range. In contrast, no significant effects of attention to frequency were present in any analysis window for high frequency stimuli (all $F(1, 11) < 1$). However, Fig. 2 (left) suggests that a late sustained attentional negativity was in fact elicited for high frequency stimuli beyond 200 ms post-stimulus. This was confirmed by an additional analysis based on mean amplitudes between 220 and 300 ms after stimulus onset. In this latency range, a significant effect of attention to frequency was present for high frequency stimuli ($F(1, 11) = 13.2$; $P < 0.01$).

If effects of non-spatial selective attention were contingent upon a previous selection by location, ERP effects of attention to frequency should only be elicited in response to stimuli at currently attended locations, and this should be reflected by significant attention to location \times attention to frequency interactions. Importantly, there were no such interactions in the N80 ($F(1, 11) = 4.2$; n.s.), P100 ($F(1, 11) = 1.8$; n.s.), and N140 ($F(1, 11) < 1$) time windows, nor in the 185–285 ms analysis interval ($F(1, 11) < 1$), thus indicating that ERP effects of attention to frequency were unaffected by the current focus of tactile spatial attention. This is also illustrated in Fig. 3, which shows ERPs elicited by stimuli with the attended and unattended frequency at currently attended (right panel) and unattended (left panel) locations. An enhanced negativity in response to stimuli in the attended frequency panel was present regardless of whether stimuli were presented to the currently relevant hand (left panel) or to the currently unattended hand (right panel).

2.3. Discussion

The aim of Experiment 1 was to assess the time course of somatosensory ERP modulations due to the selective processing of stimulus location and stimulus frequency. More specifically, we investigated whether, analogous to vision, the selective processing of a non-spatial tactile stimulus attribute (frequency) is hierarchically dependent upon a prior selection of stimulus location, or whether, analogous to audition, spatial and non-spatial

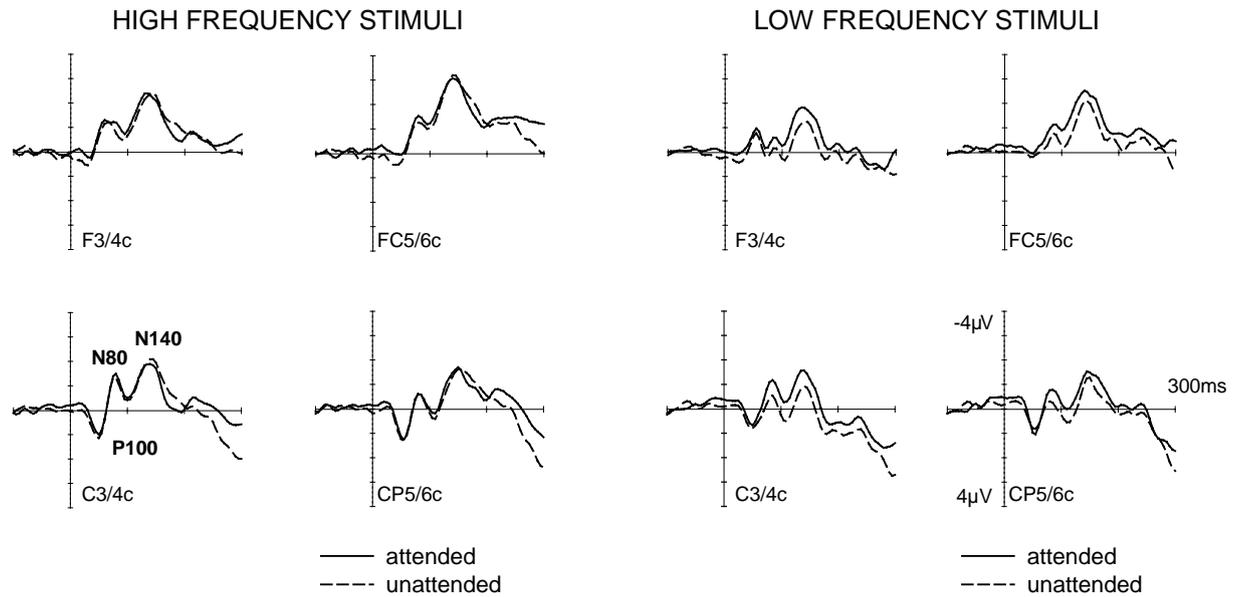


Fig. 2. Grand-averaged somatosensory ERPs elicited in Experiment 1 by tactile non-target stimuli in the 300 ms interval following stimulus onset over the hemisphere contralateral to the stimulated hand close to somatosensory cortex. Left panel: ERPs obtained in response to high frequency stimuli when these were attended (solid lines) and unattended (dashed lines), collapsed across attended and unattended stimulus locations. Right panel: ERPs obtained in response to low frequency stimuli when these were attended (solid lines) and unattended (dashed lines), collapsed across attended and unattended stimulus locations.

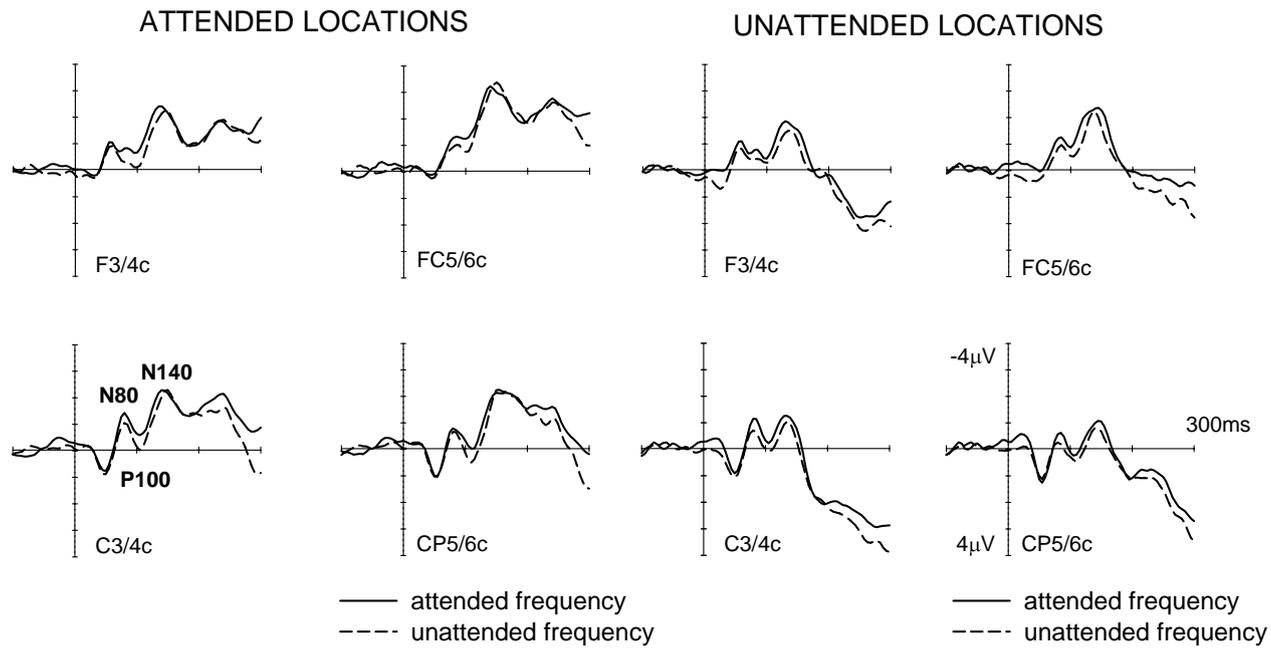


Fig. 3. Grand-averaged somatosensory ERPs elicited in Experiment 1 by tactile non-target stimuli in the 300 ms interval following stimulus onset over the hemisphere contralateral to the stimulated hand close to somatosensory cortex. Left panel: ERPs obtained in response to stimuli at attended locations with the currently attended (solid lines) and unattended (dashed lines) frequency. Right panel: ERPs obtained in response to stimuli at unattended locations with the currently attended (solid lines) and unattended (dashed line) frequency.

attributes of tactile stimuli are selected in parallel and independently. Participants were attending to one of the four possible combinations of stimulus location and stimulus frequency in order to detect rare tactile target stimuli characterized by these attributes.

As expected, tactile spatial attention was reflected by an enhanced N140 component in response to stimuli at the attended location, confirming results from earlier ERP studies (Desmedt and Robertson, 1977; Michie et al., 1987; García-Larrea et al., 1995; Eimer and Driver, 2000; Eimer et al., 2001, 2002; Eimer and Forster, 2003). Additionally, a late processing negativity for stimuli at attended as compared to unattended locations was observed. In contrast to these spatial attention effects, the selective processing of stimulus frequency affected ERP waveforms already in the P100 time range, with an enhanced negativity for stimuli in the attended frequency. Similar to spatial attention, attention to frequency also showed longer-latency effects with an enhanced negativity for stimuli in the attended frequency.

This observation that ERP correlates of tactile spatial attention do not precede ERP modulations reflecting non-spatial attentional selectivity appears to suggest, analogous to the auditory modality, that spatial and non-spatial attention operate in parallel in the somatosensory modality. In line with this interpretation, no interaction between spatial attention and attention to frequency was obtained, indicating that the current locus of spatial attention did not modulate ERP effects of non-spatial attention (Fig. 3). While the selection of non-spatial stimulus attributes in vision is hierarchically dependent on visual spatial attention (e.g. Hillyard and Münte, 1984), the selection of non-spatial attributes (such as stimulus frequency) and the selection of location appear to occur not only in parallel, but also independently in touch. This important difference in the functional properties of attentional selectivity in vision and somatosensation will be further investigated in Experiment 2.

It should be noted that ERP correlates of non-spatial attention were not equivalent for high and low frequency stimuli. For low frequency stimuli, a sustained attentional negativity was elicited in the N80, P100 and N140 time range when these stimuli were task-relevant, as compared to blocks where attention was directed to high frequency stimuli. No such early attentional modulations were observed for high frequency stimuli (Fig. 2). In other words, selecting low frequency stimuli against a background of irrelevant high frequency stimuli was reflected by systematic modulations of early ERP components, whereas selecting high frequency stimuli against irrelevant low frequency stimuli was not.

These unexpected differential effects of attention to frequency for low frequency versus high frequency stimuli could be due to differences in the perceived intensity of these two stimulus types. Although absolute intensity was constant, it is well known that the subjective intensity of vibratory stimuli depends on their frequency. Increasing stimulus frequency results in an increase of subjective intensity, for tactile stimulus frequencies up to 200 Hz (Burton and Sinclair, 1996). Thus, in Experiment 1, low frequency stimuli were subjectively less intensive than high frequency stimuli. It is possible that non-spatial attention acts to boost the processing of less salient stimuli when these have to be selected against a background of more salient events. In contrast, when task-relevant stimuli are already more salient than irrelevant stimuli (as was the case when attention was directed to high frequency stimuli), there may be less need for further selective contributions of attentional mechanisms. This issue was further explored in Experiment 2.

3. Experiment 2

This experiment was conducted to provide additional evidence for the independence of spatial and non-spatial selectivity in touch. Now, stimulus frequency was kept constant, while stimulus intensity was varied. Thus, participants had to attend to specific combinations of stimulus location (left versus right) and stimulus intensity (strong versus soft) to detect infrequent targets characterized by these two features. In all other respects, design and procedure was identical to Experiment 1.

3.1. Methods

3.1.1. Participants

Sixteen paid volunteers participated in Experiment 2. Two participants took part in Experiment 1. One participant had to be excluded because of too many eye-blinks contaminating more than 70% of trials. Three additional subjects had to be excluded because of a lack of clearly defined early somatosensory components (see above). Thus 12 participants (8 males, 4 females), aged 19–48 years (mean age: 28.6 years) remained in the sample. All participants were right-handed and had normal or corrected vision.

3.1.2. Apparatus, procedure, recording, and data analysis

The experimental setup and procedures were the same as in Experiment 1, except that stimulus frequency was kept constant at 58.8 Hz, and two different intensities of vibratory stimulation were used. To create soft and strong intensity stimuli, the contact time between the rod and the skin was 2 ms (followed by a 15 ms interpulse interval) for soft vibrations, and 3 ms (followed by a 14 ms interpulse interval) for strong vibrations. This difference in contact time created the subjective perception of clearly distinct soft and strong stimuli. EEG recording and data analyses were identical to Experiment 1. Artefact rejection procedures resulted in an exclusion of 20% of all trials, averaged across participants.

3.2. Results

3.2.1. Behavioural performance

There was no significant main effects of stimulus intensity (mean RT of 679 ms versus 663 ms for low and high intensity targets, respectively; $F(1, 11) = 2.4$, n.s.), and stimulus location (mean RT of 671 ms versus 670 ms for left and right targets, respectively; $F(1, 11) < 1$), nor an interaction between intensity and location ($F(1, 11) < 1$). Participants missed on average 9% of rare targets, without any significant differences between strong and soft, or left and right targets. The overall rate of False Alarms to irrelevant targets and non-targets was below 1%.

3.2.2. Effects of attention to location and intensity on somatosensory ERP components

As in Experiment 1, ERP modulations related to spatial attention (Fig. 4, left panel) were obtained by comparing ERP waveforms elicited by tactile stimuli at the attended and unattended locations, collapsed across currently attended and unattended stimulus intensities.

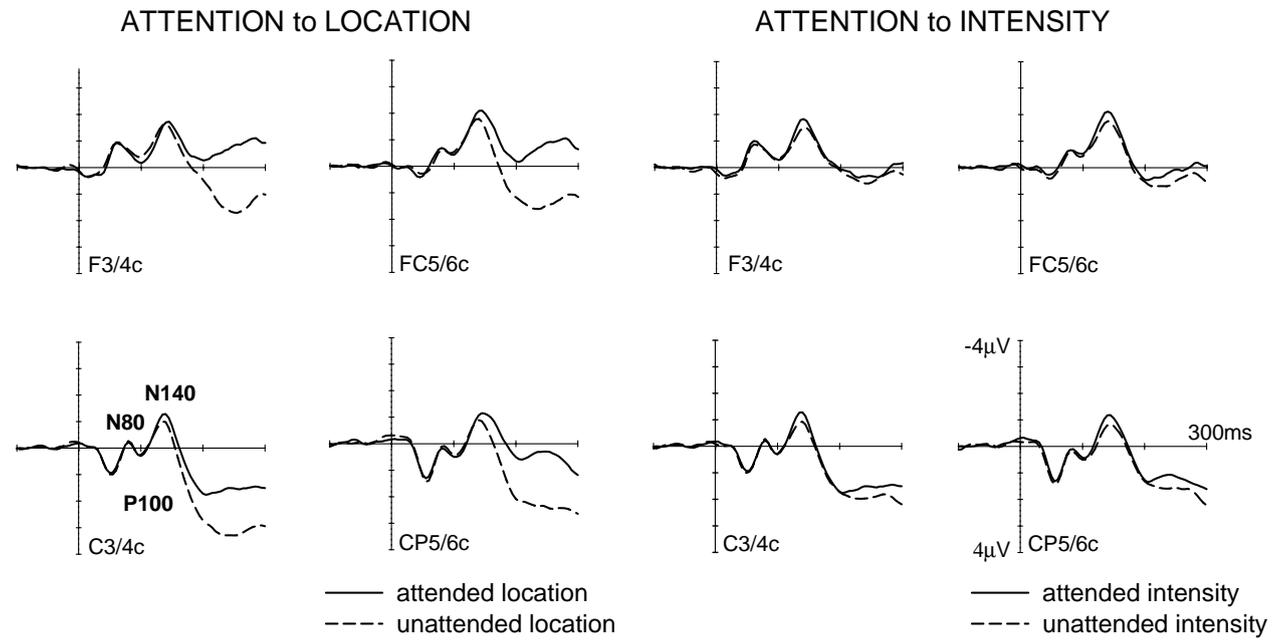


Fig. 4. Grand-averaged somatosensory ERPs elicited in Experiment 2 by tactile non-target stimuli in the 300 ms interval following stimulus onset over the hemisphere contralateral to the stimulated hand close to somatosensory cortex. Left panel: ERPs obtained in response to stimuli at attended (solid lines) and unattended (dashed lines) locations, collapsed across attended and unattended intensities. Right panel: ERPs obtained in response to stimuli with the currently attended (solid lines) and unattended (dashed lines) intensity, collapsed across attended and unattended locations.

ERP effects of attention to intensity (Fig. 4, right panel) were obtained by comparing ERP waveforms elicited by tactile stimuli with the currently attended versus unattended intensity, collapsed across attended and unattended stimulus locations.

The left panel of Fig. 4 shows that, analogous to Experiment 1, spatial attention affected the N140 component, with enhanced N140 amplitudes, followed by a sustained negativity for tactile stimuli presented at the attended location. These observations were confirmed by statistical analyses. No significant effect of attention to location was present in the time range of the N80 or P100 component. There was a significant effect of attention to location in the N140 time range (130–165 ms after stimulus onset; $F(1, 11) = 7.3$; $P < 0.03$), and for the time range of long-latency effects (185–285 ms after stimulus onset; $F(1, 11) = 30.7$; $P < 0.001$).

The right panel of Fig. 4 shows no attention to intensity effect prior to the N140 component. In contrast to attention to location effects, an attention to intensity effect appeared to be already present to the ascending flank of the N140 component. However, this effect was confined to the N140 component and reappeared later around 220 ms after stimulus onset showing an enhanced negativity for stimuli in the attended intensity. These observations were substantiated by statistical analyses. There was no significant effect of attention to intensity in the N80 or P100 time range. For the N140 time range, an attention to intensity effect was present ($F(1, 11) = 5.7$; $P < 0.04$). There was also an attention to intensity effect in the time range of long-latency effects (185–285 ms after stimulus onset; $F(1, 11) = 4.9$; $P < 0.05$).

When analysing ERP amplitudes separately within time windows centred on the ascending and descending flank of the N140 component (110–140 ms, and 145–170 ms after stimulus onset, respectively), an attention to intensity effect ($F(1, 11) = 6.6$; $P < 0.03$) was already present for the ascending flank, while an attention to location effect ($F(1, 11) = 13.9$; $P < 0.01$) emerged only for the descending flank of the N140 component.

If the attentional selection of stimulus intensity was dependent on tactile spatial attention, an interaction between attention to intensity and attention to location would be expected, indicating that ERP effects of attention to intensity were confined to tactile stimuli presented at currently attended locations. No such interaction was found in any of the time windows investigated (all $F(1, 11) < 1$), thus indicating, analogous to Experiment 1, that effects of non-spatial attention were not affected by the current focus of tactile spatial attention. This is further illustrated in Fig. 5, which shows ERPs elicited by stimuli with the currently attended (solid lines) and unattended intensity (dashed lines), separately for stimuli at attended (left panel) and unattended locations (right panel). Attention to intensity resulted in enhanced N140 amplitudes regardless of whether stimuli were presented to the currently attended or unattended hand.

In Experiment 1, an interaction of stimulus frequency and attention to frequency was observed, indicating that early effects of attention to frequency were elicited in response to low, but not to high frequency stimuli. This difference was tentatively attributed to differences in the subjective intensity of low frequency and high frequency stimuli. However, in the present experiment, no interaction between stimulus intensity and attention to intensity was present in any of the analysis windows investigated (all $F(1, 11) < 1$), indicating that the ERP effects of attention to intensity were equivalent for soft and for strong tactile stimuli.

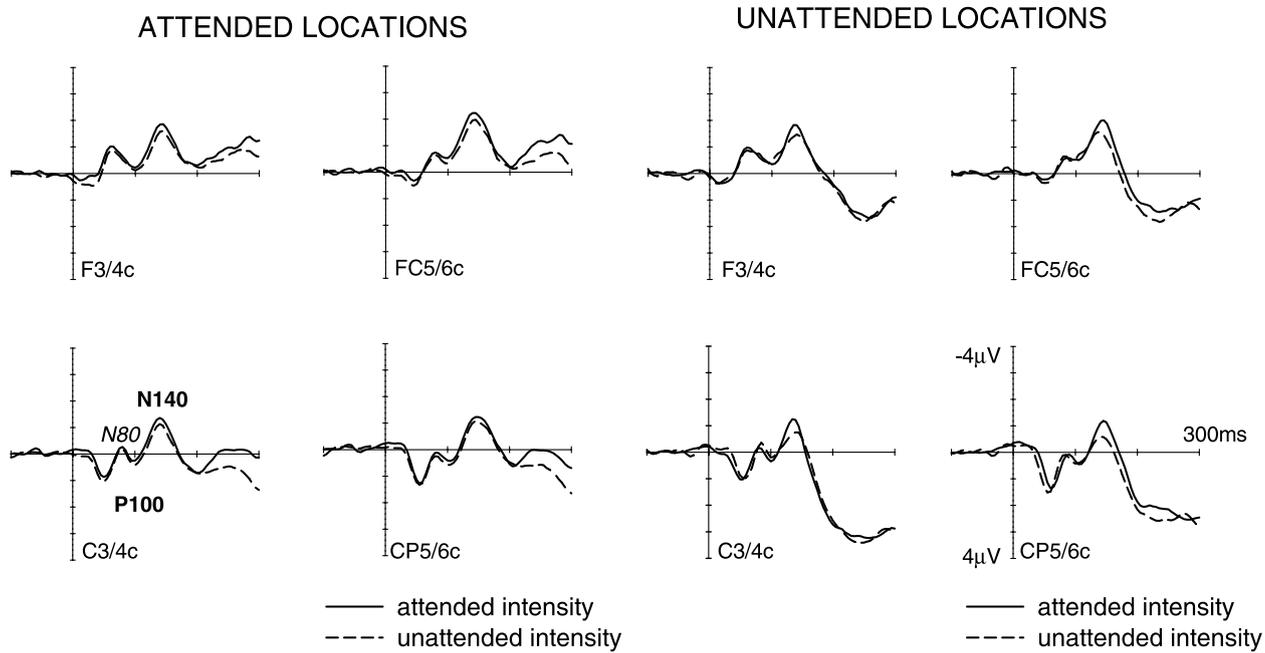


Fig. 5. Grand-averaged somatosensory ERPs elicited in Experiment 2 by tactile non-target stimuli in the 300 ms interval following stimulus onset over the hemisphere contralateral to the stimulated hand close to somatosensory cortex. Left panel: ERPs obtained in response to stimuli at attended locations with the currently attended (solid lines) and unattended (dashed lines) intensity. Right panel: ERPs obtained in response to stimuli at unattended locations with the currently attended (solid lines) and unattended (dashed lines) intensity.

3.3. Discussion

The aim of Experiment 2 was to provide further evidence for the independence of spatial and non-spatial attentional selectivity in touch. Additionally, this experiment was conducted to clarify whether the differential effects of attention to frequency in response to low and high frequency stimuli observed in Experiment 1 were due to differences in the subjective intensity of these stimuli. In Experiment 2, stimuli were either soft or strong in intensity, and were presented to the right or left hand, while participants directed their attention to a specific combination of stimulus intensity and stimulus location.

As in Experiment 1, tactile spatial attention resulted in an enhanced N140 component, followed by a sustained negativity for stimuli at attended compared to unattended locations. Attention to intensity was reflected by a similar pattern of ERP modulations, with enhanced N140 amplitudes for stimuli in the attended intensities. This selective effect of non-spatial attention was already present for the ascending flank of the N140 component, while ERP modulations produced by spatial attention only emerged for the descending flank of the N140 component (Fig. 4). This pattern of results again indicates that the selective processing of tactile stimulus locations does not precede the selective processing of a non-spatial attribute such as stimulus intensity. Importantly, ERP effects of attention directed to stimulus intensity were present at both attended and unattended locations (Fig. 5), and this was reflected by the absence of any interactions between spatial attention and attention to intensity. This result indicates that the attentional selection of a non-spatial tactile stimulus attribute (intensity) takes place irrespective of the current focus of tactile spatial attention.

In Experiment 1, ERP effects of selective frequency processing were present only when participants were attending to low frequency stimuli presented among task-irrelevant high frequency stimuli, but not when high frequency stimuli had to be selected among irrelevant low frequency stimuli. In contrast, Experiment 2 revealed no systematic differences between ERP correlates of attention to stimulus intensity for soft and strong intensity stimuli. The selection of soft stimuli against a background of irrelevant strong stimuli was reflected in similar ERP modulations as the selection of strong stimuli under conditions where soft stimuli were task-irrelevant. This finding is inconsistent with the hypothesis that the differential effects of attention to low frequency versus high frequency observed in Experiment 1 were due to the fact that low frequency stimuli were subjectively less intensive and thus less salient.

3.4. General discussion

Previous ERP studies investigating electrophysiological correlates of spatial and non-spatial attentional selectivity, and the functional relationship between spatial and non-spatial attention have been restricted to the auditory and visual modality. Although several ERP experiments have studied spatial attention in touch (Desmedt and Robertson, 1977; Michie et al., 1987; García-Larrea et al., 1995), very little is known about ERP correlates of selective non-spatial processing in somatosensation. The present study was conducted to investigate whether, when, and how selective non-spatial attention (i.e., attention directed to the frequency or intensity of tactile stimuli) modulates somatosensory ERP waveforms, and whether or not such ERP effects of non-spatial tactile attention are hierarchically dependent

upon a prior selection of tactile events in virtue of their location. In two experiments, participants were directing their attention to either the left or right hand and to one non-spatial stimulus attribute. Non-spatial stimulus attributes were low versus high frequency in Experiment 1, and soft versus strong intensity in Experiment 2.

In line with previous findings (Desmedt and Robertson, 1977; Michie et al., 1987; García-Larrea et al., 1995; Eimer and Driver, 2000; Eimer et al., 2001, 2002; Eimer and Forster, 2003), tactile spatial attention was found to modulate the modality-specific somatosensory N140 component, with enhanced N140 amplitudes for tactile stimuli at attended compared to unattended locations. This effect was followed by a sustained processing negativity for stimuli at attended locations, again in line with observations of previous ERP studies on spatial attention in touch (Desmedt and Robertson, 1977; Michie, 1984).

More importantly, the present experiments have revealed for the first time systematic ERP correlates of selective non-spatial attention effects in somatosensation. In Experiment 1, attention directed to stimulus frequency was reflected by an enhanced negativity in the P100 time range, followed by a sustained negativity for stimuli in the attended compared to stimuli in the unattended frequency. In Experiment 2, attention to intensity was reflected in an enhanced N140 component for stimuli in the attended compared to stimuli in the unattended intensity, again followed by a later sustained attentional negativity.

When comparing the onset latencies of ERP modulations reflecting the selection of spatial and non-spatial attributes of tactile stimuli, it is obvious that these effects were elicited at about the same time, analogous to results previously found for the auditory modality (cf., Woods and Alain, 2001). In vision, ERP correlates of spatial attention typically precede ERP effects of non-spatial attention by at least 50 ms (Hillyard and Münte, 1984). In sharp contrast to these observations for the visual modality, the present study has provided no evidence whatsoever that a similar temporal asymmetry also exists in somatosensation. If anything, ERP effects of attention to frequency (Experiment 1) or attention to intensity (Experiment 2) were observed slightly earlier than ERP effects of tactile spatial attention. This pattern of results strongly suggests that in contrast to vision, but analogous to audition, the attentional selection of spatial and non-spatial stimulus attributes of tactile stimuli occurs in parallel.

Another important new finding of the present study was that the selective attentional processing of non-spatial attributes of tactile stimuli such as their frequency or intensity was unaffected by the current focus of tactile spatial attention. This was confirmed by the absence of any interactions between attention to stimulus location and attention to either stimulus frequency (Experiment 1) or stimulus intensity (Experiment 2), indicating that ERP effects of selective non-spatial attention were present regardless of whether tactile stimuli were presented at currently attended or unattended locations. Again, this pattern of results is very different from the results of analogous ERP experiments investigating interactions between spatial and non-spatial attention in the visual modality (Eimer, 1995; Hillyard and Münte, 1984). In these studies investigating mechanisms of selective processing in vision, effects of non-spatial attention were confined to currently attended locations, suggesting that the attentional selection of non-spatial visual attributes is hierarchically dependent upon the prior selection of stimulus location (Anllo-Vento and Hillyard, 1996; Eimer, 1995; Hillyard and Münte, 1984; Omoto et al., 2001). No such evidence for a hierarchical dependence of non-spatial upon spatial selectivity was obtained in the present experiments, thus strongly suggesting that the mechanisms underlying attentional processing in the somatosensory

modality differ substantially from the mechanisms implementing attentional selectivity in vision. The finding that ERP effects of non-spatial tactile attention were present for tactile stimuli presented at unattended locations is analogous to observations from ERP studies investigating spatial and non-spatial attention in the auditory modality (Woods et al., 1994; Woods and Alain, 2001). Thus, the present results indicate that the mechanisms governing attentional selectivity in touch may be more similar to the mechanisms underlying selective attention in audition than to the processes responsible for visual selective attention.

This latter conclusion may seem surprising, given that both in vision and in somatosensation, stimulus location is represented explicitly via the spatial pattern of activity on the receptor surface (retina and skin) as well as in retinotopic and somatotopic maps in primary sensory cortical areas. In contrast, auditory information is initially represented tonotopically. Given this primacy of spatial representation in vision and in touch, but not in audition, it would seem intuitively more plausible to assume that the mechanisms underlying attentional processing in touch should be more similar to visual attention (with a hierarchical dependence of non-spatial upon spatial selectivity) than to auditory attention.

It could be argued that although both touch and vision are primarily ‘spatial’ in the encoding of information, there are important differences in the spatial representation of events in these two modalities (3D representations of visual objects in external space versus two-dimensional representations of tactile events impinging on a specific part of the body surface), which may explain why selection by location is less dominant in touch than in vision. Visual perception usually deals with objects distant from the observer, which need to be selected from other surrounding objects. Under these conditions, selection by location is most efficient, with subsequent attentional processing of non-spatial attributes confined to the object previously selected on the basis of its location. In contrast, a rapid evaluation of non-spatial features of tactile stimuli impinging on the body surface may be as important as their localization. Tactile perception implies direct interaction with proximal objects, thus often demanding their immediate and complete analysis. The fact that non-spatial attributes of tactile events such as frequency and intensity appear to be represented in primary somatosensory cortex (SI) in parallel with somatotopic spatial information (Harrington and Downs, 2001; Iguchi et al., 2001; Jousmäki and Forss, 1998) may make it possible for these features to be directly accessible to attentional selection, independently of their spatial location.

Another unexpected result from Experiment 1 was that ERP correlates of attention selectively allocated to stimulus frequency depended on stimulus frequency: While systematic early modulations of somatosensory ERP components were observed for low-frequency stimuli, these early effects were absent for high frequency stimuli. The hypothesis that this difference was due to a systematic difference in the subjective intensity (and salience) of low and high frequency stimuli was not confirmed in Experiment 2, where ERP effects of attention directed to stimulus intensity were equivalent in response to soft and to strong stimuli. At present, it is unclear why ERP effects elicited by attention directed to a specific stimulus frequency should be more pronounced in response to low as compared to high frequency stimuli. It is conceivable that this difference is linked to differences in the receptors and afferent pathways sensitive to low frequency and high frequency vibration. The stimulus frequencies employed in Experiment 1 (29.4 and 58.8 Hz) fall within the encoding characteristics of two different receptor types. Meissner corpuscles are mainly sensitive

to frequencies below 40 Hz, while Pacini corpuscles respond to frequencies above 40 Hz (Burton and Sinclair, 1996). Each receptor type is linked to separate afferent pathways and activates different cortical areas within the somatosensory cortex (Burton and Sinclair, 1996; Hämäläinen et al., 1990; Harrington and Downs, 2001). The results of Experiment 1 appear to suggest that tactile attention primarily acts to enhance the processing of low frequency stimuli encoded by Meissner corpuscles when these have to be selected among high frequency stimuli encoded by Pacini corpuscles, but not vice versa. Reasons for this possible difference in the allocation of attentional resources in the processing of different stimulus frequency ranges in touch need to be elucidated by further research.

In summary, the present study demonstrates for the first time systematic ERP correlates of tactile attention directed to non-spatial attributes of tactile stimuli such as frequency and intensity. Attention directed to one specific task-relevant stimulus frequency or intensity resulted in modulations of early modality-specific somatosensory components. In marked contrast to previous observations from ERP studies investigating the relationship between spatial and non-spatial selectivity in the visual modality, but in line with findings from experiments investigating mechanisms of auditory attention, these non-spatial attentional effects were elicited in parallel with ERP modulations reflecting spatially selective processing, and were entirely independent of the current focus of tactile spatial attention. Overall, this pattern of results suggests that in contrast to vision but analogous to audition, the mechanisms underlying spatial and non-spatial selective attention in the somatosensory modality can operate in parallel and independently.

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