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The spatial distribution of attentional selectivity in touch: evidence from somatosensory ERP components

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Abstract

Objective: Somatosensory event-related brain potentials (ERPs) were measured to investigate the spatial distribution of selective attention in touch, and whether the focus of tactile attention can be split between non-contiguous areas of the body surface.

Methods: On each trial, vibratory tactile stimuli were delivered to one of 4 possible locations of the right hand. Participants had to attend to either one or two locations in order to detect infrequently presented target stimuli there. ERPs were recorded to tactile non-targets at attended and unattended locations.

Results: Attention directed to one finger versus another was reflected by amplitude modulations of the sensory-specific P100 component and a subsequent attentional negativity (Nd). These effects were smaller for within-finger as compared to between-finger selection. When attention was directed simultaneously to non-adjacent fingers, ERPs in response to stimuli delivered to spatially and anatomically intervening fingers showed no attentional modulations whatsoever.

Conclusions: Allocating tactile–spatial attention to one finger versus another affects early modality-specific somatosensory processing stages, and these effects of within-hand attentional selectivity decrease gradually with increasing distance from the current attentional focus. Unlike vision, the focus of tactile attention can be split, and directed simultaneously to non-adjacent areas, thus excluding spatially and anatomically intermediate regions from attentional processing.

Keywords: Selective attention; Somatosensory; Event-related brain potential; Spatial cognition

1. Introduction

While mechanisms of spatial attention have been investigated intensively in the visual and auditory domain, relatively little is known about the processes responsible for spatial selectivity in touch. In one early study, Posner (1978) failed to find any effect of spatial attention on response latencies in a tactile detection task. However, more recent experiments have demonstrated that similar to vision and audition, spatial attention can facilitate both accuracy (Sathian and Burton, 1991) and speed (Spence et al., 2000) of performance in response to tactile stimulation. Now that systematic behavioural effects of tactile–spatial attention have been documented, it is time to begin to uncover the processes underlying the operation of spatial selectivity in touch.

In order to gain insights into the mechanisms involved in spatially selective somatosensory processing, the process of allocating attention to specific regions of the body surface, and its relationship to cortical representations of tactile information, needs to be investigated in more detail. It is well known that somatosensory cortex is organised in a somatotopic fashion, with separate detailed maps of the cutaneous body surface in areas 3b, 1, 3a and 2 (cf. Merzenich et al., 1978; Kaas, 1983). For example, the digit zones of S1 form ordered maps where the medial to lateral axis represents the ulnar to radial axis of digits and hand, and the rostrocaudal dimension is mapped onto the proximal to distal axis of individual digits (cf. Pons et al., 1985). It is possible that properties of these somatotopic cortical maps constrain the allocation of tactile–spatial attention. The somatotopic organisation of somatosensory cortex may provide natural boundaries for the spread of spatial attention, and thus determine the size of the attentional focus when tactile attention is allocated to

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specific parts of the body surface. For example, while attention may be directed selectively to single fingers, narrowing the attentional focus further to include only parts of a finger may not be possible. Along similar lines, somatotopic maps may also constrain the allocation of attention to two or more spatially and anatomically non-contiguous areas of the body surface. For example, when attention is directed simultaneously on two non-adjacent fingers (for example, index and little fingers), spatially and anatomically intervening digits (for example, middle and ring fingers) may be automatically included within a single ‘unitary spotlight’ of tactile attention.

Questions such as whether there is a minimal attentional focus size, or whether spatial attention can be divided between non-adjacent locations, have been studied in detail for the visual modality (cf. Eriksen and Eriksen, 1974; Downing and Pinker, 1985; Hughes and Zimba, 1985, 1987; Eriksen and Yeh, 1985; Heinze et al., 1994), but have not yet been raised for the case of somatosensation. The present experiment was conducted to initiate the investigation of these issues, and to gain first insights into the spatial distribution of selective attention in touch. More specifically, we asked whether tactile attention can be directed selectively to single fingers, and whether the attentional focus can be narrowed further to include only one specific phalanx (finger segment), but not other parts of the same finger. In addition, we investigated whether tactile attention can be directed simultaneously to two non-adjacent fingers, while excluding intervening fingers from attentional processing, or whether tactile attention is always allocated in the form of a unitary attentional spotlight, and thus cannot be divided to include only non-adjacent positions on the body surface. To investigate these questions, somatosensory event-related brain potentials (ERPs) were recorded to tactile stimuli at attended and unattended locations, and attentional ERP modulations were measured to obtain insights into the spatial distribution of tactile attention.

In most previous ERP studies of tactile–spatial attention, electrical or mechanical stimuli were delivered to one hand or the other, with attention focused on one designated hand (Desmedt and Robertson, 1977; Josiassen et al., 1982; Michie, 1984: Michie et al., 1987; García-Larrea et al., 1995; Eimer and Driver, 2000; Eimer et al., 2001, 2002). These studies found that early sensory-specific ERP components (N80, P100, N140) were enhanced for tactile stimuli delivered to the attended hand, suggesting that spatial attention can modulate tactile information processing in modality-specific somatosensory cortical areas. In addition, a sustained negativity (‘Nd’) for stimuli at attended locations was also observed (cf. Michie, 1984), which may reflect the in-depth processing of task-relevant features of attended stimuli.

The experimental manipulations used in these earlier ERP studies (directing attention to one hand versus the other) precluded any insights into the spatial tuning of tactile attention within a single hand or a single finger. In the present experiment, tactile stimuli were delivered to one of 4 possible locations, all on the right hand. On each trial, a single vibratory stimulus (58.8 Hz) was delivered to one of these locations. Participants’ task was to detect and respond to infrequent target stimuli (slightly less intense vibrations) when these were presented at prespecified relevant (attended) locations, and to ignore all other stimuli. The experiment consisted of two parts. One part (one-location task) was designed to study whether tactile attention can be allocated selectively to single fingers, or even to individual finger phalanxes. The aim of the other part (two-location task) was to find out whether the focus of tactile attention can be divided, with attention allocated simultaneously to two non-adjacent fingers, while excluding intervening fingers from attentional processing.

In the one-location task, tactile stimuli were delivered to the middle or bottom phalanx of the right index or middle finger. In each block, attention had to be directed to one of these 4 locations to detect infrequent targets presented there. Attended locations were varied across blocks. ERPs were recorded to non-target stimuli at currently attended as well as the 3 unattended locations. The first question to be investigated was whether tactile attention can not only be selectively directed to one hand versus another (as was demonstrated in previous ERP experiments), but also to one specific finger versus another. If this was the case, there should be systematic differences between ERPs in response to tactile stimuli presented to attended locations relative to ERPs to stimuli delivered to another, irrelevant finger of the same hand. Next, we compared ERPs elicited by attended-location stimuli and ERPs to stimuli delivered to the same (relevant) finger, but to the phalanx that was currently ignored. If whole fingers constitute the basic unit of attentional selection in touch, the location of the task-relevant phalanx within the attended finger should have no effect on ERP waveforms. In contrast, systematic attentional differences between these two sets of waveforms would suggest that the attentional focus can be selectively narrowed to include only specific phalanxes.

In the two-location task, tactile stimuli were delivered to the middle phalanx of the right index, middle, ring, or little finger. Here, the task was to direct attention simultaneously to two of these 4 locations, in order to detect infrequent targets presented at these locations. In different blocks, attention was directed either to two adjacent fingers (index finger and middle fingers: Attend IM; ring finger and little finger: Attend RL), or, importantly, to two non-adjacent fingers (index finger and little finger: Attend IL). The crucial question was whether tactile stimuli delivered to the middle and ring finger do or do not receive attentional processing when attention is directed to the two outer (index and little) fingers. To answer this question, ERPs to middle and ring finger stimulation obtained under Attend IL instructions were compared to ERPs elicited by the same stimuli when these were either attended (Attend IM for middle finger; Attend RL for ring finger) or unattended (Attend RL for middle finger; Attend IM for ring finger). If the focus of tactile attention could be divided and allocated to non-adjacent fingers while excluding intervening fingers, ERPs to middle and ring finger stimulation under Attend IL instructions should be indistinguishable from ERPs observed when these fingers are genuinely unattended. In contrast, if the spatial focus of tactile attention was unitary, and thus necessarily included spatially and anatomically intervening fingers when attention is directed to non-adjacent fingers, ERPs to middle and ring finger stimulation under Attend IL instructions should be similar to ERPs obtained when these fingers are attended.

2. Methods

2.1. Participants

Thirteen paid volunteers participated in the experiment. One participant had to be excluded due to excessive eye blink activity contaminating more than 70% of all trials. Thus 12 participants (5 females, 7 males, aged 21–42 years) remained in the sample. All participants gave written informed consent. The experiment was approved by the Ethics Committee, School of Psychology, Birkbeck College.

2.2. 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 V 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. Four tactile stimulators were used, and these were attached with adhesive medical tape to fingers of the right hand. In one experimental part (one-location task), the 4 possible stimulation locations were the middle and bottom phalanx of the right index and middle fingers, respectively. In the other experimental part (two-location task), stimulators were attached to the middle phalanx of the right index, middle, ring, and little finger, respectively. Tactile stimuli were always delivered on the radial side of the respective finger. Participants were instructed to place their left and right hands on a table in their usual position, in order to adopt and maintain a comfortable hand and body posture. The right hand (which received tactile stimulation) was resting on a piece of foam. In the one-location-task, the index finger was resting in a slightly lower position than the other fingers, thus preventing any contact between the stimulators attached to the middle and index fingers. In the two-location task, participants had to slightly spread the fingers of the right hand, with each fingertip resting on an additional small piece of foam, in order to prevent contact between adjacent stimulators and fingers. Throughout the experimental blocks, a fixation cross was present at the centre of the computer screen, and white noise (62 dB SPL) was continuously delivered to mask any sounds made by the tactile stimulators.

Each vibratory tactile stimulus consisted of a sequence of 20 brief pulses. The stimulus onset asynchrony between successive pulses was 17 ms, corresponding to a stimulation frequency of 58.8 Hz, and a stimulation duration (i.e. interval between the onset of the first pulse and the offset of the last pulse) of 325 ms. Two stimulus intensities were employed. To present 'weak' vibrations, the contact time between rod and skin was set to 2 ms, followed by a 15 ms interpulse interval. To present 'strong' vibrations, contact time was set to 3 ms, followed by a 14 ms interpulse interval. Subjectively, these manipulations resulted in perceived vibrations with identical frequency, but noticeably different intensity. On each trial, a single vibratory tactile stimulus was presented at one of the 4 possible stimulation locations. The intertrial interval between successive stimuli varied randomly between 650 and 950 ms, with a mean interval of 800 ms.

2.3. Procedure

The experiments consisted of two parts (one-location task and two-location task). Six participants completed the one-location task prior to the two-location task, and this order was reversed for the other 6 participants. In both experimental parts, participants were instructed to keep their gaze focused on the central fixation cross, to respond vocally (by saying 'yes') whenever an infrequent weak vibratory stimulus was detected at relevant/attended locations, and to ignore all strong vibrations there, as well as all tactile stimuli at irrelevant/unattended locations. The latency of vocal responses was measured with a voice key. Attended locations were specified in advance of each experimental block, and remained constant throughout this block.

2.3.1. One-location task

The one-location task consisted of 12 blocks. Here, one stimulation location was relevant, and the other 3 locations were to be ignored. Attention was directed to each of the 4 possible stimulation locations (middle or bottom phalanx of index or middle finger) in 3 blocks. The order in which these blocks were delivered was randomised for each participant. Each block consisted of 181 trials. In 160 trials, non-target stimuli (strong vibrations) were delivered equiprobably to one of the 4 possible stimulus locations. In the remaining 21 trials, weak vibratory stimuli were delivered. On 12 trials, these stimuli were delivered to the currently relevant location, and thus required a response. On the remaining 9 trials, they were presented equiprobably to one of the 3 irrelevant locations, and thus had to be ignored.

2.3.2. Two-location task

The two-location task, where stimuli could be delivered to the middle phalanx of the right index, middle, ring, or little finger, consisted of 9 blocks. Here, two locations had to be monitored for potential targets in each block. In 3 successively presented blocks (Attend IM), index and middle finger were relevant. In 3 other successive blocks (Attend RL), ring and little fingers were relevant. Finally, in 3 further successive blocks (Attend IL), attention had to be directed simultaneously to two non-adjacent fingers (index and little finger). The order in which these 3 attention conditions were delivered was balanced across participants.[1] Each block consisted of 180 trials. In 160 trials, non-target stimuli (strong vibrations) were delivered equiprobably to one of the 4 possible stimulus locations. In the remaining 20 trials, weak vibratory stimuli were delivered. On 12 trials, these stimuli were delivered with equal probability to one of the two currently relevant locations, and thus required a response. On the remaining 8 trials, they were presented equiprobably to one of the two irrelevant locations, and thus had to be ignored.

2.4. Recording and data analysis

Electroencephalography (EEG) was recorded with Ag–AgCl electrodes and linked-earlobe reference from 56 scalp electrodes. Horizontal electrooculogram (EOG) was recorded bipolarly from the outer canthi of both eyes. Electrode impedance was kept below 5 kΩ, amplifier bandpass was 0.1–40 Hz, and digitisation rate was 200 Hz. Trials with eyeblinks, horizontal eye movements, or muscle artefacts were excluded. ERPs to non-target stimuli (strong vibrations) were averaged relative to a 100 ms pre-stimulus baseline for all combinations of task (one-location vs. two-location), attentional instruction, and stimulation location. ERP mean amplitudes were computed within a measurement windows centered on the latency of the somatosensory P100 component (90–130 ms post-stimulus). To investigate longer-latency effects of spatial attention, mean amplitudes were also computed between 170 and 250 ms post-stimulus.

Statistical analyses of ERP data were restricted to the left hemisphere contralateral to stimulated hand, and to electrode sites located close to primary somatosensory cortex (C3, C1, FC3, CP3), where early somatosensory evoked potentials (SEP) components are maximal. Mean amplitude values were analysed with repeated measures analysis of variances (ANOVAs), separately for the one-location and two-location task.

For the one-location task, the initial overall analysis included the factors attended location (attend to middle vs. bottom phalanx of index vs. middle finger), stimulus location (middle vs. bottom phalanx of index vs. middle finger) and electrode site. Follow-up analyses then compared ERPs to attended-location stimulation to ERPs elicited by unattended stimuli presented either to the finger containing the relevant location, or to the other finger.

For the two-location task, the initial analysis only included data from the Attend IM and Attend RI conditions, where attention was directed to two adjacent fingers. This analysis included the factors attention (stimulus at one of the two attended vs. unattended location), stimulus location (index vs. ring vs. middle vs. little finger) and electrode site. The critical follow-up analyses compared ERPs to stimulation delivered at attended and unattended locations under Attend IM and Attend RL instructions to ERPs obtained under Attend IL instructions (where attention had to be directed to non-adjacent locations), separately for outer (index, little) fingers and inner (middle, ring) fingers. For all analyses, Greenhouse–Geisser adjustments to the degrees of freedom were performed when appropriate. For vocal response times (RTs; measured relative to the onset of each vibratory stimulus) and error rates, repeated measures ANOVAs were performed for the factors task (one-location vs. two-location task) and stimulus location.

3. Results

3.1. Behavioural performance

Responses to correctly detected weak target vibrations were significantly faster in the one-location task than in the two location-task (692 vs. 721 ms; $F(1,11) = 12.4$; $P < 0.005$). In contrast, stimulation location did not affect response latency in either task. Participants missed 9.4% of all relevant targets in the one-location task, and 10.7% of all relevant targets in the two-location task. This difference was not significant. The rate of False Alarms to weak vibrations at currently irrelevant locations and to non-target stimuli was below 1% for both tasks.

3.2. Effects of spatial attention on somatosensory ERP components

3.2.1. One-location task

Fig. 1 shows ERPs elicited at left-hemisphere sites close to somatosensory cortex in response to tactile non-target stimuli at task-relevant attended locations (black solid lines), and at unattended (irrelevant) locations. Unattended-location ERPs are displayed separately for stimuli presented to the irrelevant phalanx of the finger containing the attended location (Unattended/Same Finger; grey solid lines), and for stimuli presented to the currently irrelevant finger (Unattended/Different Finger; black dashed lines). As can be seen from Fig. 1, tactile–spatial attention modulated

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[1] Note that while relevant stimulus locations changed randomly across blocks in the one-location task, attentional instructions remained constant for 3 successive blocks in the two-location task. This difference was introduced to account for the fact that the attentional two-location task was more demanding than the one-location task, as two stimulation location had to be monitored simultaneously.

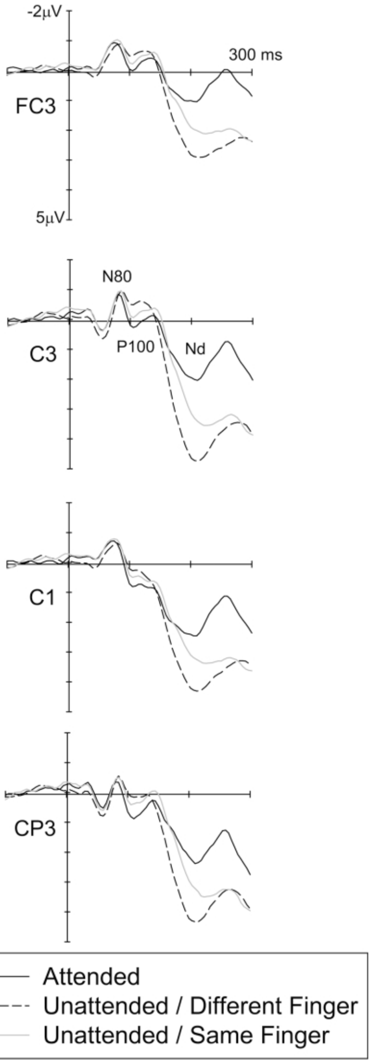

Fig. 1. Grand-averaged somatosensory ERPs elicited in the one-location task by tactile non-target stimuli in the 300 ms interval following stimulus onset over the left hemisphere at electrodes close to S1. Displayed are ERPs obtained in response to stimuli delivered to the attended phalanx of the task-relevant finger (attended; black solid lines), to the unattended phalanx of the task-relevant finger (unattended/same finger; grey solid lines), and to either phalanx of the task-irrelevant finger (unattended/different finger; black dashed lines).

the somatosensory P100 component, with larger P100 amplitudes for tactile stimuli delivered to attended locations relative to Unattended/Different Finger stimulation. In addition, an enhanced sustained negativity (Nd) was elicited for stimuli at attended locations as compared to Unattended/Different Finger stimulation, starting at about 160 ms post-stimulus. Importantly, P100 and Nd modulations in response to stimulating the unattended phalanx of the relevant finger (Unattended/Same Finger; grey lines) appear to be intermediate between Attended and Unattended/Different Finger ERP waveforms.

In the overall analyses, main effects of attended location were obtained for both the P100 and Nd measurement windows ($F(3,33) = 3.5$ and 20.9; $P < 0.05$ and 0.001; $\varepsilon = 0.691$ and 0.456, respectively), indicating that the current focus of attention systematically affected SEP waveforms within these time intervals. No interactions between attended location and stimulus location and between attended location and electrode site were obtained. Subsequent analyses directly compared ERPs elicited on Attended, Unattended/Different Finger and Unattended/Same Finger trials. P100 amplitudes differed significantly between Attended and Unattended/Different Finger trials, with larger P100 components on trials where tactile stimuli were presented at attended locations ($F(1,11) = 4.9$; $P < 0.05$). In contrast, no statistically reliable P100 amplitude differences were found between Attended and Unattended/Same Finger trials, and between Unattended/Same Finger and Unattended/Different Finger trials. In the Nd time interval (170–250 ms post-stimulus), all comparisons between these 3 conditions were significant (all $F(1,11) > 12.4$; all $P < 0.005$). This latter result demonstrates that a reliable sustained attentional negativity (Nd) was elicited on trials where tactile stimuli were presented to the unattended phalanx of the currently relevant finger relative to Unattended/Different Finger trials, but that this negativity was smaller than on trials where stimuli were delivered to the attended phalanx (see Fig. 1).

3.2.2. Two-location task

Fig. 2 shows ERPs elicited at left-hemisphere sites close to somatosensory cortex, collapsed across all 4 stimulus locations, in response to tactile non-target stimuli at attended locations (black solid lines), and at unattended locations (black dashed lines), when attention was directed to two adjacent locations (Attend IM, Attend RL). Similar to the one-location task, tactile–spatial attention resulted in a modulation of the P100 component, with larger P100 amplitudes for tactile stimuli at attended locations. This was reflected in a significant effect of attention in the P100 measurement window ($F(1,11) = 23.5$; $P < 0.001$), without any attention × stimulus location or attention × electrode site interactions. The subsequent attentional Nd modulation was considerably smaller than in the one-location task, and the main effect of attention failed to reach significance in the Nd measurement window. However, an attention × electrode location interaction was obtained ($F(3,33) = 3.5$; $P < 0.05$; $\varepsilon = 0.947$), and subsequent analyses revealed significantly enhanced attentional negativities at CP3 and C3 (both $F(1,11) > 5.0$; both $P < 0.05$), but not at FC3 and C1.

Fig. 3 shows ERPs in response to tactile stimuli delivered to the middle and ring finger (left panel: inner fingers), and to the index and little finger (right panel: Outer Fingers). These panels include ERPs to stimuli at attended and unattended locations under Attend IM and Attend RL instructions (black solid and dashed lines) together with ERPs elicited in the crucial Attend IL condition, where attention had to be directed to two non-adjacent fingers (grey solid lines). For both inner and outer fingers,

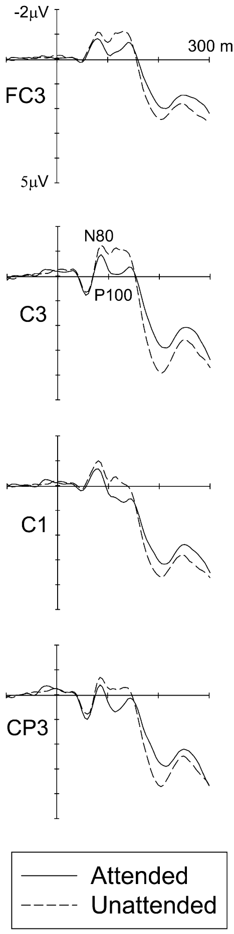

Fig. 2. Grand-averaged somatosensory ERPs elicited in the two-location task by tactile non-target stimuli in the 300 ms interval following stimulus onset over the left hemisphere at electrodes close to S1. ERPs obtained in response to stimuli delivered to the index, middle, ring, and little fingers under conditions where attention was directed to two adjacent fingers (index and middle fingers; ring and little fingers) are displayed separately for stimuli at attended locations (solid lines) and unattended locations (dashed lines).

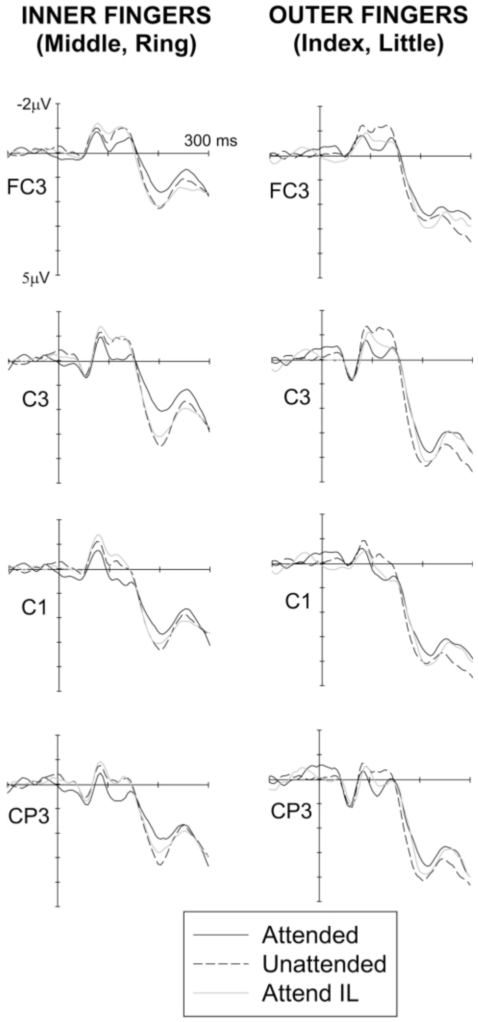

Fig. 3. Left panel: grand-averaged somatosensory ERPs elicited in the two-location task by tactile non-target stimuli in response to stimuli delivered to the middle and ring fingers. Waveforms are displayed separately for stimuli at attended locations (Attend IM for middle finger; Attend RL for ring finger; black solid lines), for stimuli at unattended locations (Attend RL for middle finger; attend IM for ring finger; black dashed lines), and for stimuli presented when attention was directed to the index and little finger (Attend IL; grey solid lines). Right panel: ERPs in response to stimuli delivered to the index and little finger. Waveforms are displayed separately for stimuli at attended locations (Attend IM for index finger; Attend RL for little finger; black solid lines), for stimuli at unattended locations (Attend RL for index finger; Attend IM for little finger; black dashed lines), and for stimuli presented when attention was directed to the index and little finger (Attend IL; grey solid lines).

attentional enhancements of the P100 component for tactile stimuli at attended as compared to unattended locations are clearly visible, in line with the overall pattern of effects shown in Fig. 2. This was reflected in significant attended-unattended differences for P100 amplitudes for inner as well as for outer fingers ($F(1,11) = 11.1$ and 15.1; $P < 0.007$ and 0.003, respectively).[2]

Crucially, P100 components elicited when attention had to be directed simultaneously to the non-adjacent outer fingers (Attend IL, grey lines) appeared to differ systematically for stimulation of the inner fingers (Fig. 3, left panel) and the outer fingers (Fig. 3, right panel). For middle-finger stimulation, the P100 triggered under Attend IL instructions closely resembled the P100 observed for unattended locations, and was clearly smaller than on attended-location trials. This was confirmed by statistical analyses, which revealed significant P100 amplitude differences between attended-location and Attend IL trials ($F(1,11) = 20.1$; $P < 0.001$). In contrast, there was no difference whatsoever between Attend IL and unattended-location trials ($F < 1$).

A different pattern of results was found for outer-finger stimulation (Fig. 3, right panel). Here, P100 amplitudes were enhanced under Attend IL instructions relative to unattended-location trials, and this difference was statistically

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[2] In the Nd time interval, the only significant difference between tactile stimuli presented at attended versus unattended locations was observed for inner fingers at C3 ($F(1,11) = 6.2$; $P < 0.03$). No other Nd differences between the conditions shown in Fig. 3 were significant.

significant ($F(1, 11) = 4.9$; $P < 0.05$). Although Fig. 3 also suggests that attentional P100 enhancements for outer finger stimulation were somewhat less pronounced under Attend IL instructions than when attention could be directed to two adjacent locations (black solid lines), this difference was not statistically reliable ($F < 1.5$).

4. Discussion

The aim of the present ERP study was to investigate the spatial distribution of attentional selectivity in touch by delivering vibratory tactile stimuli to 4 possible locations on the right hand, and instructing participants to direct attention to one or two relevant locations in order to detect and respond to infrequent targets presented there. Unlike previous ERP investigations of tactile–spatial attention, where attention was allocated to one hand versus the other, the present experiment studied electrophysiological correlates of within-hand attentional selectivity in touch. In the one-location task, stimuli were delivered to the middle or bottom phalanx of the index and middle finger, and one of these 4 locations was relevant in each block. In the two-location task, stimuli were presented to the middle phalanx of the index, middle, ring, or little finger, and two of these locations were relevant in each block (index and middle finger; ring and little finger; index and little finger). These task conditions were designed to find out (i) whether tactile attention can be allocated selectively to single fingers, (ii) whether the attentional focus can be effectively narrowed to include just one phalanx of a specific finger (one-location task), and (iii) whether tactile attention can be directed simultaneously to two non-adjacent digits while excluding intervening digits (two-location task).

In both experimental parts, enhanced P100 components were elicited in response to tactile stimuli presented to a currently relevant finger, as compared to tactile stimulation of an unattended finger. This attentional modulation of an early sensory-specific somatosensory ERP component clearly demonstrates that tactile attention can be selectively allocated to single fingers, and that this attentional focus affects early, modality-specific stages of somatosensory processing. Previous ERP studies of between-hands attentional selectivity in touch (cf. Desmedt and Robertson, 1977; Josiassen et al., 1982; Michie, 1984; Michie et al., 1987; García-Larrea et al., 1995; Eimer and Driver, 2000) have also observed attentional modulations of early somatosensory ERP components. The fact that early attentional effects were restricted to the P100 in the present study, while other somatosensory ERP components known to be sensitive to spatial attention (N80, N140) were not affected, may reflect genuine differences between within-hand attentional selectivity (studied here) and the selection of one hand versus the other (as studied in earlier ERP investigations).

In addition to these effects of spatial attention on the P100 component, a sustained negativity for attended-finger as compared to unattended-finger stimulation ('Nd') was observed beyond 160 ms post-stimulus, again analogous to earlier findings (Michie, 1984). The Nd effect was much more pronounced in the one-location task (Fig. 1) than in the two-location task (Fig. 2), where it failed to reach overall statistical significance. This fact is most likely due to the differences in the attentional demands posed by these two tasks, as it is more difficult to simultaneously monitor two locations for potential targets than to focus attention on just one relevant location.[3]

The central question investigated in the one-location task was whether the focus of tactile attention can be restricted to the level of single finger phalanxes, or whether whole fingers constitute the smallest possible unit of attentional selectivity in touch. If the first alternative was correct, within-finger attentional selectivity should be as effective as between-finger selectivity. Therefore, ERPs elicited on Unattended/Same Finger trials should be equivalent to ERPs observed for Unattended/Different Finger trials. The results shown in Fig. 1 are not in line with this prediction. The P100 elicited on Unattended/Same Finger trials was numerically (although not significantly) larger than the P100 observed for Unattended/Different Finger stimuli, and there was a significantly increased attentional negativity (Nd) in response to Unattended/Same Finger stimulation relative to Unattended/Different Finger trials. This latter fact suggests that stimuli delivered to an irrelevant phalanx of the currently attended hand are not completely excluded from attentional processing, as would be predicted by the hypothesis that whole fingers constitute the smallest possible unit for selective attention in touch. However, according to this account, ERPs delivered to the currently relevant finger should be completely unaffected by whether attention was to be directed to the middle or bottom phalanx of this finger. This prediction was also not confirmed: Attentional ERP modulations were more pronounced in response to attended tactile stimuli as compared to Unattended/Same Finger trials, although this difference was statistically reliable only for the Nd effect, but not for the P100 component. This observation indicates that fingers do not represent the basic unit in tactile–spatial attention, but that attentional processing in touch can operate at least to some degree on a smaller scale.

Overall, the results obtained in the-one location task indicate that attentional selectivity within fingers is less effective than selectivity between fingers, suggesting that cortical somatotopic representations of individual digits may constrain the allocation of tactile–spatial attention. More generally, the decrease in attentional ERP modulations as a function of the distance of a tactile stimulus from the current focus of attention strongly suggests the existence

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[3] This difference in the attentional demands posed by the two tasks was also reflected in the fact that vocal response times were significantly faster in the one-location task.

of 'attentional gradients' in touch. This is in line with interpretations of results from earlier behavioural and electrophysiological studies investigating the distribution of spatial attention in vision (Downing and Pinker, 1985; Mangun and Hillyard, 1988; Eimer, 1997) and in audition (Mondor and Zatorre, 1995; Rorden and Driver, 2001; Teder-Sälejärvi and Hillyard, 1998), as well as with observations in patients with left visual hemineglect or extinction (Smania et al., 1998).

The central question studied in the two-location task was whether the focus of tactile attention can be split and directed to two non-adjacent fingers (index and little finger), without simultaneously also including task-irrelevant fingers (middle and ring finger), even though these are intermediate both in terms of external space and of somatotopic cortical representation. The ERP results shown in Fig. 3 (left panel) in response to stimulation of the middle and ring fingers strongly suggest that tactile attention can be divided in this way. ERP amplitudes in the P100 time window observed under Attend IL instructions (attention directed to index and little finger) were virtually identical to ERPs elicited when middle and ring finger were unattended (with attention directed to two other adjacent fingers). In addition, the P100 component in response to attended middle and ring finger stimuli was significantly larger than the P100 observed in Attend IL blocks. This pattern of results demonstrates that fingers located between two non-adjacent attended locations can be excluded from attentional processing, which is at odds with the hypothesis that the focus of tactile–spatial attention necessarily forms a unitary, and spatially contiguous spotlight.

There may, however, be other explanations for the fact that P100 amplitudes in response to middle and ring fingers stimulation in the Attend IL condition were indistinguishable from P100 amplitudes elicited when these fingers were unattended. It could be argued that since the attentional focus is unitary, it is simply impossible to direct tactile attention simultaneously to non-adjacent fingers, and that participants had therefore been unable to focus attention at all under Attend IL instructions. If this was the case, P100 components elicited in this condition in response to outer (index and little) finger stimulation should also be equivalent to ERPs observed when these fingers were task-irrelevant. As can be seen from Fig. 3 (right panel), this was clearly not observed. P100 amplitudes elicited by outer finger stimulation were significantly larger under Attend IL instructions than when outer stimuli were irrelevant, indicating that attention was focused on these two non-adjacent locations. Alternatively, and perhaps more plausibly, one could argue that the unitary focus of tactile–spatial attention is wider under Attend IL instructions (where it includes all 4 possible stimulus locations) than under Attend IM and Attend RL instructions (where only two positions are included), and that attentional effects decrease with increasing focus width. While this hypothesis may be consistent with the observation that attentional P100 amplitude modulations for outer finger stimulation were somewhat (though not significantly) reduced in the Attend IL condition (Fig. 3, right panel), it cannot account for the effects observed in response to stimulation of the middle fingers (Fig. 3, left panel). If these fingers were included within a wide attentional focus under Attend IL instructions, this should have been reflected in systematic (albeit perhaps reduced) attentional ERP modulations relative to unattended ERPs.

Overall, the results from the two-location task suggest that the focus of tactile–spatial attention is not necessarily unitary. It appears to be possible to direct tactile attention simultaneously to two non-adjacent digits, so that other digits, which are located at intermediate positions both in terms of external space and cortical somatotopic representational space, are excluded from attentional processing. This finding is intriguing, since it suggests that the allocation of tactile–spatial attention may be fundamentally different from attentional focusing in the visual domain. In vision, both behavioural and electrophysiological data clearly suggest that spatial attention cannot be divided between non-contiguous areas of visual space (Heinze et al., 1994). The focus of visual–spatial attention is thus assumed to be unitary, and to include regions located between currently task-relevant locations. The present results strongly suggest that the allocation of spatial attention in touch is more flexible that the allocation of visual–spatial attention, and demonstrate that the focus of tactile attention is not closely linked to somatotopic boundaries in primary somatosensory cortex (see also Behrmann and Moscovitch, 1994; Aglioti et al., 1999, for neuropsychological evidence for multiple spatial frames involved in the mapping of tactile events within a single hand).

In summary, the present experiment has provided several new insights into the spatial distribution of tactile–spatial attention. Results have shown that attention can be selectively allocated to one finger versus another of the same hand, as reflected by attentional modulations of an early sensory-specific ERP component (P100). When attention is directed to specific finger phalanxes, attentional ERP modulations decrease as a function of the distance of a tactile stimulus from the current attentional focus, suggesting the existence of spatial gradients in tactile attention. Finally, and perhaps most importantly, results strongly suggest that the focus of tactile attention can be split, with attention allocated simultaneously to non-adjacent parts of the body surface, thus excluding intermediate regions from attentional processing. Overall, these results demonstrate how somatosensory ERPs can provide detailed insights into spatial distribution of attentional selectivity in touch.

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