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RESEARCH ARTICLE

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Modulations of early somatosensory ERP components by transient and sustained spatial attention

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Abstract To investigate when and how spatial attention affects somatosensory processing, event-related brain potentials (ERPs) were recorded in response to mechanical tactile stimuli delivered to the left and right hand while attention was directed to one of these hands. The attended hand either remained constant throughout an experimental block (sustained attention), or was changed across successive trials (transient attention). Attentional modulations of the N140 component and a sustained 'processing negativity' for attended stimuli were observed in both attention conditions. However, attentional effects on earlier somatosensory components differed systematically. Sustained attention resulted in a contralateral negativity overlapping with the N80 component, while transient attention was reflected by a bilateral positivity overlapping with the P100 component. This dissociation indicates that sustained and transient attention affect different somatosensory areas. It is suggested that sustained attention can modulate tactile processing within primary somatosensory cortex (S1), while effects of transient attention are located beyond S1. Overall, results demonstrate that spatial selectivity in touch is mediated by activity modulations in modality-specific somatosensory cortex.

Keywords Spatial attention · Somatosensory processing · Event-related brain potentials · Transient spatial attention · Sustained spatial attention · Mechanical tactile stimuli

Introduction

Spatial attention has a profound impact on the perceptual processing of visual and auditory stimuli, and this is reflected in behavioural and electrophysiological measures. Performance is faster and more accurate in response to stimuli at currently attended locations, both for vision (cf. Posner et al. 1978) and audition (cf. Spence and Driver 1994). Spatial attention also modulates the amplitudes of early sensory-specific ERP components elicited by visual or auditory stimuli (cf. Mangun and Hillyard 1991; Woldorff et al. 1992), demonstrating that attention affects early perceptual processes in visual and auditory cortex. In contrast, less is known about the behavioural effects and neural basis of *tactile*-spatial attention. While Posner (1978) failed to find any effect of spatial attention on response latencies in a tactile detection task, more recent studies have shown that tactile attention can facilitate both accuracy (Sathian and Burton 1991) and speed (Spence et al. 2000) of responses to tactile stimuli.

The fact that tactile-spatial attention can improve performance raises the important question which stages of somatosensory processing are modulated by attention. Mechanical tactile stimulation of the body surface is transmitted from peripheral mechanoreceptors via dorsal columns and ventroposterior thalamic nuclei to somatosensory cortex. It is received in the contralateral primary somatosensory cortex (S1), and then passed on to the second somatosensory area (S2) and somatosensory regions in posterior parietal cortex (cf. Pons et al. 1992). While the functional role of different somatosensory cortical areas is still poorly understood, some studies have begun to investigate which of these areas can be affected by attention. Single-cell recordings from monkeys (Hsioa et al. 1993; Hyvärinen et al. 1980) observed strong effects of attention on the activity of S2 neurons, but much smaller effects in S1. Magnetoencephalographic (MEG) studies (Mauguière et al. 1997; Mima et al. 1998) found attentional modulations of bilateral S2 responses beyond 100 ms, but no effects of active attention on earlier contralateral MEG components thought to originate from S1. In contrast, two functional imaging studies (Johansen-Berg et al. 2000; Meyer et al. 1991) have observed attentional effects in S2 as well as in S1. Given the limited temporal resolution of hemodynamic measures, it is possible that activity mod-

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ulations within S1 occur not during initial sensory processing, but at longer latencies, and are mediated by re-entrant signals from higher-order areas. It should also be noted that in most of the studies cited above, attentional effects were measured by comparing a condition where participants were attending to the location of tactile stimulation to a condition when their attention was actively engaged elsewhere (e.g. by watching a movie). In other words, spatial attention was manipulated together with *intermodal attention* (directing attention to one modality versus another), thus making it difficult to assess effects specifically due to spatial selectivity.

Other experiments have used somatosensory event-related brain potentials (SEPs) to investigate when spatial attention starts to affect the processing of tactile information. In most of these studies, electrical stimuli were delivered to one hand or the other, with attention focused on one designated hand (Desmedt and Robertson 1977; García-Larrea et al. 1995; Michie 1984; Michie et al. 1987). A consistent finding from these experiments is that tactile-spatial attention modulates the somatosensory N140 component, with increased N140 amplitudes for tactile stimuli delivered to the attended hand. The N140 is elicited bilaterally and is thought to be generated in secondary somatosensory cortex (SII; Frot et al. 1999). Following this N140 effect, a sustained negativity for stimuli at attended locations (‘processing negativity’) was also observed (cf. Michie 1984), which is assumed to reflect in-depth processing of task-relevant features of attended stimuli. There is some evidence that spatial attention may also affect somatosensory ERPs prior to the N140, although these findings are less consistent. For example, Michie et al. (1987) observed attentional modulations of the N80 component recorded from somatosensory areas contralateral to the stimulated hand. An enhanced positivity (P105) in response to tactile stimuli delivered to the attended hand has also been reported (Josiassen et al. 1982; Michie et al. 1987). However, these early effects were not observed in other SEP studies (García-Larrea et al. 1995; Michie 1984). In several recent ERP experiments, effects of spatial attention on somatosensory ERPs were investigated from a crossmodal perspective (Eimer and Driver 2000; Eimer et al. 2001, 2002; Van Velzen et al. 2002; Hötting et al. 2003). In these studies, tactile stimuli were interspersed with visual or auditory stimuli, and participants were instructed to attend to one location for one relevant modality only, while ignoring all irrelevant-modality stimuli, regardless of their location. When touch was relevant, enhanced N140 components were observed in response to tactile stimuli delivered to the attended hand, thereby confirming findings from earlier unimodal experiments.[1]

In summary, while there is consistent evidence that spatial attention can affect somatosensory processing in S2 at latencies beyond 120 ms poststimulus, it is not yet known whether attentional effects can occur even earlier, such as in S1. The present study aimed to clarify this issue by investigating the latencies and scalp distributions of attentional modulations of early SEP components. Based on comparisons of intracranial and scalp ERP recordings, Allison et al. (1992) have suggested that somatosensory ERP components elicited within 100 ms after stimulus onset originate in S1.[2] S1 receives information from the contralateral side of the body, and the hand area of S1 has few direct commissural connections to the ipsilateral hemisphere (Powell 1977). In contrast, S2 and posterior parietal somatosensory cortex contain a large percentage of somatosensory neurons with bilateral receptive fields (Iwamura et al. 1994). In line with these anatomical facts, early MEG responses originating from S1 are only evoked by contralateral stimulation, while S2 responses are elicited by both contra- and ipsilateral tactile stimuli (Hari et al. 1984), and SEPs have been recorded intracranially from both contralateral and ipsilateral S2 (Frot and Maguière 1999; Frot et al. 1999). Given these findings, any observation that early effects of spatial attention on SEP waveforms are confined to electrodes contralateral to the stimulated body side would be consistent with a locus of attentional selectivity within S1. In contrast, bilaterally distributed attentional effects are more likely to be generated in higher-order somatosensory areas.

The objective of the present ERP experiment was to further investigate the locus of spatial selectivity in touch, and to study whether attentional modulations of sensory processing may be affected by the characteristics of an attention task. Previous ERP studies on tactile-spatial attention differed considerably in terms of the nature of the attentional task, the type of tactile stimulation used (electrical vs. mechanical), as well as with respect to stimulation loci, and stimulus intensity (see Michie et al. 1987 for effects of intensity on the latency of attentional ERP modulations). In addition, effects of spatial attention on SEP waveforms may also be influenced by differences in the way that attention is allocated. In most previous ERP studies, participants were instructed to attend to their left or right hand, and to maintain attention at this location for an entire experimental block. In contrast to this *sustained attention* manipulation, other experiments (Eimer et al. 2001, 2002) have cued the to-be-attended hand on a trial-by-trial basis. Under such *transient attention* conditions, tactile attention has to be frequently shifted from one hand to the other on successive trials. While it has been shown that transient and sustained spatial attention can have differential effects on visual ERPs (Eimer 1996), it is not yet known whether this factor also affects attentional modulations of tactile ERPs.

To investigate the locus of spatial selectivity in touch, and any differential impact of sustained and transient

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[1] In these studies, attentional modulations of the somatosensory N140 component were also found when attention was directed to one side for a visual or auditory task, thus demonstrating crossmodal links in spatial attention (cf. Eimer 2001; Eimer and Driver 2001 for reviews).

[2] However, note that recent intracranial SEP recordings (Barba et al. 2002; Frot and Maguière 1999) have suggested that some S2 sources may already be active between 60 ms and 90 ms poststimulus.

spatial attention on attentional SEP modulations, single mechanical tactile stimuli were delivered to the left or right hand, while participants attended to one hand in order to detect infrequent target (‘gap’) stimuli at that hand. In one experimental half (transient attention), the relevant hand was indicated by a visual precue presented on a computer screen at the beginning of each trial. In the other half (sustained attention), the relevant hand was specified prior to the start of each block, remained constant for this block, and was switched to the opposite hand in the next block. Based on the results of our earlier crossmodal ERP studies (Eimer et al. 2001, 2002), which used identical tactile stimulators, mechanical finger stimulation was expected to trigger successive sensory-specific ERP components at frontocentral and centroparietal sites close to somatosensory cortex. Two early components (P45, N80) were expected to be elicited contralateral to the stimulated hand, while subsequent P100 and N140 components should be observed bilaterally. We compared SEPs elicited by tactile non-target stimuli delivered to the attended hand to SEPs in response to unattended-hand stimulation, separately for the transient and the sustained attention condition, to find out (1) when and how tactile-spatial attention modulates SEP waveforms, and (2) whether there are any systematic differences in the effects of transient and sustained spatial attention on somatosensory ERPs.

Materials and methods

Participants

Twelve paid volunteers participated in the experiment. One participant had to be excluded due to excessive α-wave activity, and another participant was excluded because of insufficient eye fixation control in the cue-target interval of the transient attention condition. Thus ten participants (six females, four males, aged 20–39 years) remained in the sample. All participants gave written informed consent. The experiment was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and was granted ethical approval by the Ethics Committee, School of Psychology, Birkbeck College.

Material and procedure

Participants sat in a dimly lit experimental chamber, wearing a head-mounted microphone. Tactile stimuli were presented using 12-V solenoids, driving a metal rod with a blunt conical tip to the outside of the middle segment of the index fingers, making contact with the fingers whenever a current was passed through the solenoid. Rods and fingertips were occluded to prevent visibility of the rod movements. Two tactile stimulators were placed on a table in close spatial register 25° to the left and right of fixation. White noise (62 dB SPL) was continuously present to mask any sounds made by the tactile stimulators. In the transient attention condition, two adjacent triangles, presented centrally on a computer screen at a viewing distance of 55 cm (visual angle: 3.5×2.5°), served as cue stimuli. One triangle was red, the other blue, and they always pointed in opposite directions (‘><’ or ‘<>’). A central fixation cross, located between both triangles, was continuously present throughout the experimental blocks. In the sustained attention condition, no cues were presented, and only the fixation cross was visible throughout each block. Tactile non-target stimuli consisted of one rod contacting a finger for 200 ms. Tactile target stimuli had a gap, where this contact was interrupted for 10 ms after a duration of 95 ms.

Two task conditions were run (transient and sustained attention), each consisting of six experimental blocks. The order in which these two conditions were delivered was balanced across participants. In the transient attention condition, blocks consisted of 64 trials. Each trial started with a 100-ms presentation of the cue, and 600 ms after cue offset a tactile stimulus (200 ms duration) was presented to the left or right hand. Intertrial interval was 1000 ms. Participants had to respond vocally (“yes”) whenever a target (gap) stimulus was detected at the cued hand. The attended hand was cued by the direction of one of the triangles. For half of the participants, blue triangles were relevant, and red triangles were relevant for the other half. Relevant left-pointing or right-pointing triangles were presented with equal probability to the left or right of fixation. In 48 trials, non-target stimuli were presented with equal probability to the left or right hand, and were preceded with equal probability by a left or right cue, resulting in 12 trials for each of the four combinations of cued location and stimulus location. The remaining 16 trials contained gap targets, and these were equally likely to be delivered to the left or right hand, and to be preceded by a left or right cue. Thus, eight targets were delivered to the cued hand and thus required a vocal response, and eight targets were delivered to the uncued hand.

In the sustained attention condition, blocks consisted of 80 trials, and intertrial interval was again 1000 ms. Here, participants were instructed prior to the start of each block to direct attention to the left or right hand, and to respond vocally to targets delivered to the attended hand. Three attend-left and attend-right blocks were presented, and the attended hand was switched after each block. Half of the participants started with an attend-left block, and the other half with an attend-right block. In 64 trials, non-target stimuli were presented with equal probability to the left or right hand. The remaining 16 trials contained gap stimuli, and these were equally likely to be delivered to the left or right hand. Thus, eight targets were delivered to the attended hand and thus required a vocal response, and eight targets were delivered to the unattended hand.

EEG recording and data analyses

EEG was recorded with Ag-AgCl electrodes and linked-earlobe reference from 23 scalp electrodes. Horizontal 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 digitization rate was 200 Hz. No additional filters were applied to the EEG data, and all ERP analyses were based on these unfiltered data. Trials with eyeblinks, horizontal eye movements, or muscle artifacts were excluded. Averaged HEOG waveforms obtained in the cue-target interval for the transient attention condition in response to cues directing attention to the left versus right hand were scored for systematic deviations of eye position. One participant was disqualified due to residual HEOG deflections exceeding ±3 μV.

ERPs to non-targets (tactile stimuli without gaps) were averaged relative to a 100-ms prestimulus baseline for all combinations of task condition (transient vs. sustained attention), attention (stimulus at attended vs. unattended hand), and stimulated hand (left vs. right). ERP mean amplitudes were computed for each participant within successive measurement windows centred on the latencies (in ms poststimulus) of early SEP components: P45 (40–60 ms), N80 (70–95 ms), P100 (100–125 ms), P140 (130–160 ms). To investigate longer-latency effects of attention, mean amplitudes were also computed between 200 ms and 300 ms poststimulus.

Statistical analyses were conducted for recording sites close to somatosensory areas (C3/4, FC5/6, CP5/6), as well as for electrodes F3/4, Fz, and Cz. Because SEPs differ systematically between recording sites contralateral and ipsilateral to the stimulated hand, separate analyses were conducted for contralateral, ipsilateral, and midline ERPs. Mean amplitude values were analysed with repeated measures ANOVAs, for the factors task condition, attention, stimulated hand, and electrode site (frontal vs. frontocentral vs. central vs. centroparietal, for contralateral and ipsilateral electrodes; Fz vs. Cz, for midline sites). When appropriate, Greenhouse-Geisser adjustments to the degrees of freedom were performed. For vocal response times (RTs) and arcsin-transformed error rates, repeated measures ANOVAs were performed for the factors task condition and stimulated hand.

Results

Behavioural data

Mean vocal RTs to infrequent gap targets at attended locations were faster when attention was cued on a trial-by-trial basis (557±25 ms) than for sustained attention (602±24 ms), resulting in a main effect of task condition ($F_{(1,9)}=8.2$; $p<0.02$). Participants missed 3.5% (±2.3%) and 0.6% (±0.4%) of all relevant target stimuli in the transient and sustained attention condition, respectively, and this difference was not significant. False alarms to targets presented to the unattended hand or to non-target stimuli occurred on less than 0.2% of all trials.

Somatosensory event-related brain potentials

Figure 1 shows ERPs elicited in response to tactile stimuli delivered to the attended hand (solid lines) and to the

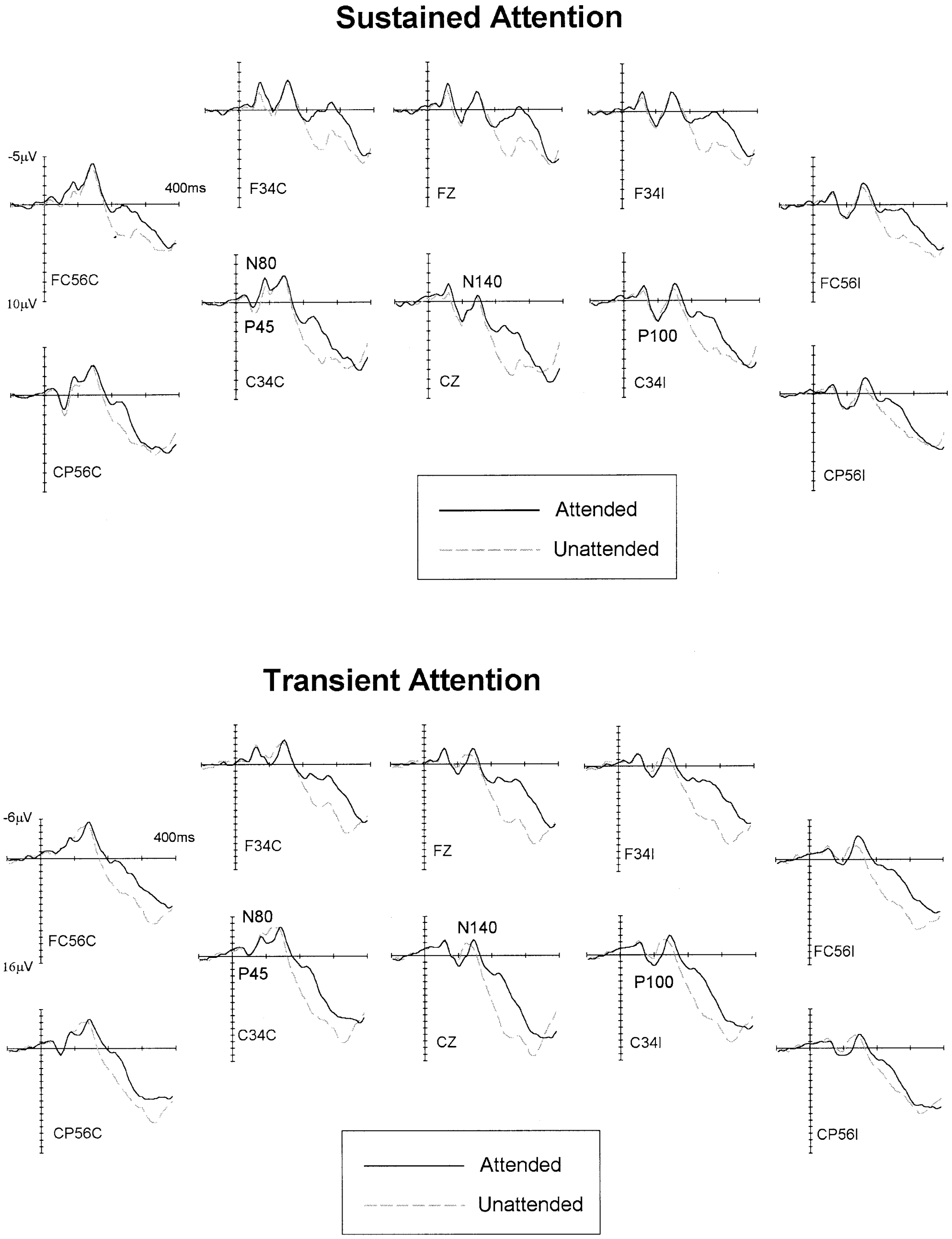

Fig. 1 Grand-averaged somatosensory ERPs elicited in the 400-ms interval following stimulus onset by tactile non-target stimuli delivered to the attended hand (*black solid lines*) and to the unattended hand (*grey dashed lines*) at frontocentral, central, and centroparietal electrodes contralateral (*C*) and ipsilateral (*I*) to the stimulated hand, and at midline electrodes Fz and Cz. Waveforms are displayed separately for the sustained attention condition (*top*) and the transient attention condition (*bottom*)

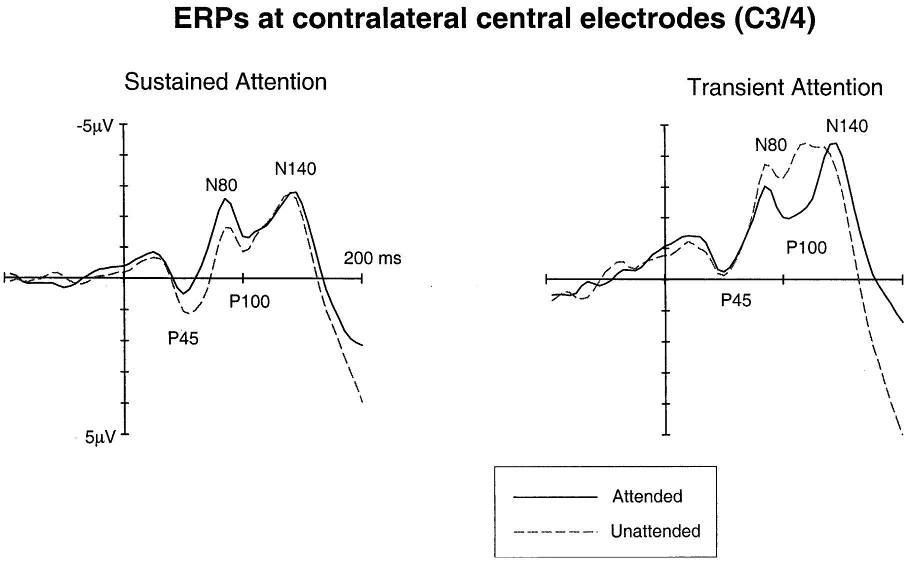

Fig. 2 Grand-averaged somatosensory ERPs elicited in the 200-ms interval following stimulus onset by tactile non-target stimuli delivered to the attended hand (*black solid lines*) and to the unattended hand (*grey dashed lines*) at central electrodes C3/C4 contralateral to the stimulated hand for the sustained attention condition (*left panel*) and the transient attention condition (*right panel*)

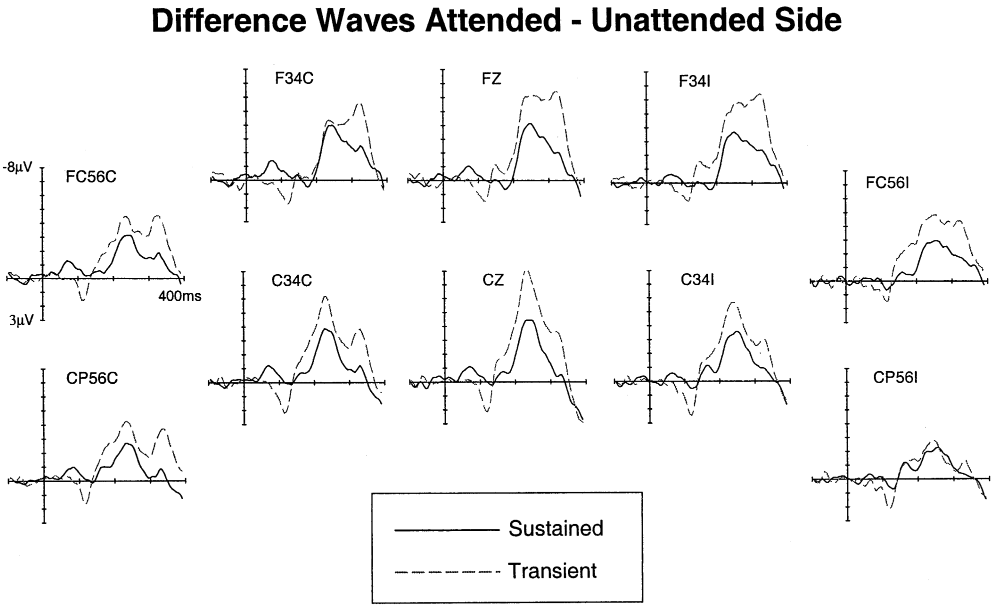

Fig. 3 Difference waveforms obtained at contralateral (*C*), midline, and ipsilateral (*I*) electrodes by subtracting ERPs elicited by tactile non-target stimuli delivered to the unattended hand from ERPs elicited by stimuli presented to the attended hand, in the sustained attention condition (*black solid lines*), and in the transient attention condition (*grey dashed lines*)

unattended hand (dashed lines) in the sustained attention condition (top) and the transient attention condition (bottom). ERPs are displayed separately for electrodes contralateral (C) to the stimulated hand (left side of panels), for ipsilateral (I) electrodes (right side), and for midline electrodes Fz and Cz. ERP waveforms were characterized by contralateral P45 and N80 components, followed by P100 and N140, which were present at contralateral as well as at ipsilateral and midline sites. These early ERP components can be seen more clearly in Fig. 2, where ERPs at contralateral central electrodes located over primary somatosensory cortex (C3/4) are shown separately for the sustained and transient attention conditions. As can be seen from these figures, both sustained and transient attention resulted in systematic modulations of early SEP components, and these effects were followed by a sustained negativity for attended versus unattended stimuli. While this late ‘processing negativity’ was present for both attention conditions, transient and sustained attention appeared to affect early SEP components differentially: Sustained attention was reflected by an early negativity for attended relative to unattended stimuli, resulting in an enhanced contralateral N80 component (Fig. 1, top; Fig. 2, left). In contrast, transient spatial attention resulted in an enhanced positivity, with larger P100 amplitudes elicited in response to stimuli at cued locations (Fig. 1, bottom; Fig. 2, right). These differential effects of transient and sustained tactile-spatial attention are further illustrated in Fig. 3, which shows difference waveforms computed by subtracting ERPs for stimuli presented to the unattended hand from ERPs in response to attended-hand stimuli, displayed separately for sustained attention (solid lines) and transient attention (dashed lines). In these difference waveforms, enhanced negativities for attended stimuli are reflected by negative values (upward-going deflections), and enhanced positivities by positive values (downward-going deflections). As can be seen from this figure, an enhanced positivity for attended-hand versus unattended-hand stimuli (reflecting an attentional modulation of the P100) was elicited exclusively when attention was cued on a trial-by-trial basis. In contrast, an earlier enhanced negativity for attended stimuli in the N80 time range was present only in the sustained attention condition.

These observations were substantiated by statistical analyses. No significant main effects of attention or attention × task condition interactions were present in the P45 time range (40–60 ms poststimulus). In the N80 time window (70–95 ms poststimulus), an attention × task condition interaction ($F_{(1,9)}$=7.0; p<0.03) was present at contralateral electrodes. While no significant effect of attention was obtained contralaterally for transient attention, reliable contralateral effects were present in the sustained attention condition ($F_{(1,9)}$=5.9; p<0.04), reflecting an enhanced N80 component for tactile stimuli at attended locations (see also Fig. 2, left). No main effects or interactions involving attention were present ipsilaterally or at midline electrodes in the N80 time window.

In the subsequent P100 time window (100–125 ms poststimulus), an attention × task condition interaction was again obtained at contralateral recording sites ($F_{(1,9)}$=11.1; p<0.01). However, attention now affected SEP amplitudes in the transient attention condition ($F_{(1,9)}$=10.7; p<0.01), with increased P100 amplitudes for stimuli delivered to the cued hand. In contrast, no significant contralateral attentional effects were present in the sustained attention condition. In addition to this differential effect at contralateral sites, attention × task condition interactions were also found at midline electrodes ($F_{(1,9)}$=6.1; p<0.04). Again, attentional effects were significant for transient attention ($F_{(1,9)}$=5.6; p<0.05), but not for sustained attention. A similar picture emerged at electrodes ipsilateral to the stimulated hand. Here, an electrode site × attention × task condition interaction was observed ($F_{(3,27)}$=4.3; p<0.04; ε=0.638). To further explore this interaction, follow-up analyses were conducted separately for single electrode sites. With transient attention, significant effects of attention were present at C3/4 and C5/6 (both $F_{(1,9)}$>7.0; both p<0.03), while no such effects were observed with sustained attention.

In the N140 time window (130–160 ms poststimulus), enhanced N140 amplitudes were elicited by stimuli presented to the attended hand. This was reflected in a main effect of attention at ipsilateral electrodes ($F_{(1,9)}$=10.5; p<0.01), and this effect approached significance at contralateral sites ($F_{(1,9)}$=3.8; p<0.09). Although Fig. 1 suggests that this attentional N140 modulation was more pronounced in the transient attention condition, this difference was not substantiated by attention × task condition interactions.

A sustained ‘processing negativity’ for attended-hand versus unattended-hand stimuli elicited beyond 200 ms poststimulus was reflected by main effects of attention at contralateral, ipsilateral, and midline sites in the 200–300 ms poststimulus measurement window (all $F_{(1,9)}$>14.7; all p<0.005). Attention × task condition interactions were absent at lateral electrodes, but present at midline sites ($F_{(1,9)}$=5.3; p<0.05), indicating that the attentional negativity at Fz and Cz was larger under transient than under sustained attention conditions (see Fig. 3).

Discussion

The aim of the present ERP study was to investigate the locus of spatial selectivity in the processing of tactile information by measuring when and how somatosensory ERPs elicited by mechanical tactile stimuli delivered to the left and right index finger were affected by the current focus of spatial attention. Participants directed attention to their left or right hand in order to detect infrequent tactile ‘gap’ targets delivered to the attended hand. To find out whether transient and sustained spatial attention result in differential modulations of somatosensory ERPs, the attended hand was either defined prior to each block, and remained constant throughout this block (sustained attention condition), or was signalled by a visual cue presented at the start of each trial, and thus changed unpredictably across trials (transient attention condition).

Some results obtained in this study confirmed findings from previous ERP experiments (cf. Eimer et al. 2001; García-Larrea et al. 1995; Michie et al. 1987). We observed attentional modulations of the sensory-specific N140 component, which is assumed to be generated in S2 (Frot et al. 1999), and a subsequent sustained ‘processing negativity’ for stimuli delivered to the attended hand. One central question of the present research was whether tactile-spatial attention would also affect SEP components elicited prior to the N140. Such early attentional modulations were indeed found, but these effects showed a markedly different pattern in the transient and the sustained attention conditions. When attention was maintained at a specific location for an entire block, an enhanced contralateral negativity was elicited for attended-hand as compared to unattended-hand stimuli, resulting in a significant effect of attention in the N80 latency window (70–95 ms poststimulus). This effect was entirely absent with transient attention.[3] When the relevant hand was cued on a trial-by-trial basis, an enhanced attentional positivity was observed in the P100 interval (100–125 ms poststimulus), resulting in larger P100 amplitudes in response to stimulation of the attended hand. This attentional positivity was not restricted to contralateral sites, but was also observed at midline and

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[3] Note that this result is in line with informal observations from our previous study investigating crossmodal links in spatial attention (Eimer et al. 2001), where attentional modulations of the contralateral N80 component were present for sustained attention (Experiment 1; see also Hötting et al. 2003), but not for transient attention (Experiment 2).

ipsilateral sites (Fig. 1, bottom), and was absent in the sustained attention condition.

These findings demonstrate that tactile-spatial attention results in systematic modulations of SEPs elicited by mechanical stimuli delivered to currently attended versus unattended hands, and that the earliest manifestations of spatially selective processing clearly precede the somatosensory N140 component. Perhaps the most striking aspect of the present findings is the fact that the onset latency, polarity, and laterality of these early effects differed systematically between sustained and transient attention. While sustained tactile-spatial attention resulted in a *contralateral negativity* overlapping with the contralateral N80 component, transient attention was reflected by a *bilateral positivity* overlapping with the bilateral P100 component. This obvious dissociation strongly suggests that sustained and transient modes of spatial attention affect different brain areas involved in the processing of tactile information.

As outlined in the "Introduction", short-latency effects of tactile-spatial attention elicited exclusively at electrodes contralateral to the stimulated hand are consistent with attentional modulations of primary somatosensory cortex, while bilateral effects suggest modulations of secondary somatosensory areas, such as S2. In the light of these assumptions, it is tempting to interpret the early contralateral negativity observed exclusively for sustained attention as a reflection of spatially selective processing in S1. In contrast, the subsequent bilateral positivity found only for transient attention might result from attentional modulations in S2. Spatially selective effects on tactile information processing might occur at an earlier stage with sustained attention than with transient attention because tactile attention may be focused more efficiently when it can be maintained at one location for an extended period of time, as compared to a situation where the attentional focus has to be frequently shifted and reallocated on successive trials.[4] The fact that the direction of these transient attentional shifts was indicated by symbolic visual cues may also have contributed to the observed difference in the onset of transient and sustained attention effects, as visual information had to be translated into somatosensory spatial codes in the transient attention condition.

According to this interpretation, sustained tactile attention results in a 'sensory gating' of activity in primary somatosensory cortex, while transient shifts of tactile attention in response to visual spatial cues primarily affect subsequent somatosensory stages (such as S2). While this hypothesis is consistent with the pattern of results obtained in the current study, it is of course merely based on differences in the onset latency and scalp distribution of SEP modulations between transient and sustained spatial attention, and thus needs to be further substantiated in future experiments using MEG measures, or dipole source analyses based on high-density SEP recordings.[5]

In summary, the present experiment demonstrated that tactile-spatial attention has systematic effects on sensory-specific somatosensory ERP components in the first 100 ms after stimulus onset. Moreover, transient and sustained spatial attention resulted in distinct early modulations of SEP waveforms, suggesting that early loci of attentional selectivity in somatosensory processing are strongly affected by the way in which attention is manipulated. Sustained attention may modulate tactile processing within primary somatosensory cortex, whereas effects of transient attention are more likely to be restricted to somatosensory areas beyond S1. While these hypotheses need to be confirmed by further research, the current results demonstrate that, analogous to vision and audition, spatially selective processing in touch is mediated by attentional modulations of sensory-perceptual processes in modality-specific somatosensory cortex.

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[4] One finding which may appear inconsistent with this hypothesis is that vocal RTs were faster with trial-by-trial cueing than with sustained attention. However, this difference is presumably due to a spatially unspecific alerting effect of precues. Visual stimuli presented at the start of each trial act as warning signals, and thus increase overall response readiness. This will speed up responses, especially if targets are infrequent, as in the present study.

[5] Another issue that may be resolved in future high-density SEP studies is whether tactile-spatial attention modulates the amplitudes of early exogenous SEP components (N80, P100), or whether the effects of attention observed in the N80 and P100 time range are primarily due to an overlap of these components with an endogenous attentional negativity (or positivity). Figure 2 suggests that early attentional modulations only partially overlapped with the N80 and P100, which seems more in line with the overlap idea than with a pure amplitude modulation account.

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