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**Adverse effects of viewing the hand on tactile-spatial selection
between fingers depend on finger posture**

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Abstract

Primary somatosensory cortex (S1) is known to rapidly adapt to task demands and to intermodal information (e.g. from vision). Here we show that also intramodal information (i.e. posture) can affect tactile attentional selection processes and the intermodal effects of vision on those processes at S1 stages of processing. We manipulated the spatial separation between adjacent fingers; that is, thumb and index finger where either close, far apart or touching. Participants directed their attention to either the index finger or thumb to detect infrequent tactile targets at that location while they either saw their fingers or these were covered from view. In line with previous results we found that attentional selection affected early somatosensory processing (P45, N80) when fingers were near and this attention effect was abolished when fingers were viewed. When fingers were far or touching, attentional modulations appeared reliably only from the P100, and furthermore, enhanced tactile spatial selection was found when touching fingers were viewed. Taken together, these results show for the first time a profound effect of finger posture on attentional selection between fingers and its modulations by vision at early cortical stages of processing. They suggest that the adverse effects of vision on tactile attention are not driven by a conflict between the selected information in vision (two fingers) and touch (one finger), and imply that external spatial information (i.e. finger posture) rapidly affects the organisation of primary somatosensory finger representations and that this further affects vision and tactile spatial selection effects on S1.

Introduction

Tactile-spatial selection between the hands is improved when the hands are spatially distant compared to close together (Driver and Grossenbacher 1996; Eimer, Forster, Fieger and Harbich 2004; Gillmeister, Adler and Forster 2010). Furthermore, viewing one of the hands can ameliorate deficits in tactile-spatial selection between the hands (di Pellegrino and Frassinetti 2000; Làdavas, Farnè, Zeloni and di Pellegrino 2000); while viewing both hands facilitates tactile between-hand spatial selection (Sambo, Gillmeister and Forster 2009). Thus, tactile-spatial selection may be enhanced by the availability of additional (visual) spatial information about the relative distance of the hands in external space, possibly by reinforcing the remapping of tactile information into reference frames based on external spatial coordinates (see Röder et al. 2004).

Comparably little is known, however, about the effects of posture and vision on the spatial representation of touch *within* the hand. While some researchers have suggested that fingers are represented in a purely somatotopic spatial framework (Röder et al. 2002; Haggard, Kitadono, Press and Taylor-Clarke 2006), others (Craig 2003; Overvliet, Anema, Brenner, Dijkerman and Smeets 2011; Riemer, Trojan, Kleinböhl and Hölzl 2011; Roberts and Humphreys 2010; Shibuya, Takahashi and Kitazawa 2007) have more recently argued for an influence of external visual-spatial frameworks on finger representation. For example, Overvliet et al. (2011) found that tactile localization to one of three possible locations on each of the fingertips was more accurate when fingers were spread out than when they were together and touching. Interestingly, it was also found that, when tactile stimuli were mislocalized to another finger, they were not mislocalized to an adjacent finger any more often than to a non-adjacent finger, suggesting that improved localization accuracy when fingers

are spread is not driven by decreases in the overlap between tactile receptive fields for neighboring fingers. The authors suggested that, similar to the effects of stimulus intensity (e.g., Johansson 1976), some tactile receptive fields may be affected by finger posture such that greater spatial separations between the fingers lead to less skin surface falling within such a receptive field, and that this in turn leads to greater tactile sensitivity.

In studies of attentional selection between the hands, it has been shown that vision of the hands facilitates selection (di Pellegrino and Frassinetti 2000; Làdavas et al. 2000; Sambo et al. 2009). Vision, therefore, may act as one source of information that relays spatial information in external coordinates. Together with the external spatial framework provided by proprioception, visual-spatial information may be integrated with tactile information and guide its remapping into external coordinates. When selecting one finger over another on the *same* hand, however, the picture is less straightforward. We have recently shown that vision of adjacent fingers of the same hand can have detrimental effects on tactile-spatial selection between the fingers (Gillmeister, Sambo and Forster 2010). Rather than assist in providing relative locational information about the fingers, vision appears to have played one or more different roles. First, viewing the fingers may have reorganised and partially merged their representations in primary somatosensory cortex, akin to the effects of temporally correlated tactile exposure (Rockstroh et al. 1998; Sterr et al. 1998). Second, vision may have provided conflicting information (both fingers were viewed) compared to touch (only one finger was selected), and the resolution of this conflict between visual and tactile spatial information may have delayed effects of selection. It may be that vision did not contribute to the remapping of touch into external spatial coordinates because, unlike all previous investigations of this kind, our earlier study

did not specifically manipulate the relative locations between body parts. However, it is difficult to see why this would have lead to *detriments*, rather than simply an absence of vision effects on selection. It may be more plausibly assumed that viewing adjacent fingers has several, more complex effects on tactile selection.

The present study was designed to further investigate the putative involvement of external spatial frameworks provided by proprioception and vision on the mechanisms of between-finger selection. A second aim was to disentangle the different roles that vision may play over and above providing such an external-spatial framework for touch. To this end, we manipulated the effects of finger posture (near, far versus touching at the finger tips) and of viewing the fingers (vision of fingers versus covered) on early somatosensory ERPs effects of tactile attentional selection between fingers. There are two strands of hypotheses. First, if vision either reorganises somatosensory cortical finger representations or provides conflicting spatial information to touch, we should replicate the findings from our earlier study (Gillmeister et al. 2010): early effects of attentional selection (attentional differentiations at P45 and N80 components) should be absent when the fingers are viewed. If the adverse effects of vision on between-finger selection are driven by a conflict between visual and tactile spatial information specifically, then these adverse effects should not differ across posture conditions. This is because the same conflict between what is selected by touch (one finger) and what is selected by vision (both fingers) is present for all finger postures. Second, if external spatial frameworks play a role in between-finger selection, attentional selection should be superior at greater distances between fingers, similar to the superior localisation found for spread than touching fingers in Overvliet et al.'s (2011) study. If vision contributes to these external spatial frameworks, it would reinforce the assumption that each finger

represents a separate source of tactile input and thus ameliorate the detrimental effects it has on cortical organisation when adjacent fingers are viewed. Specifically, the detrimental effects of vision should be less pronounced over P45 and N80, or arise later in cortical processing (P100, N140 or Nd), when fingers are far than when they are near.

Method

Participants

Fourteen right-handed participants (ten men; mean age = 28.14 years) gave informed written consent and were paid for their participation. The study was approved by the local ethics committee and conducted in accordance with the 1964 Declaration of Helsinki.

Stimuli and Materials

Tactile stimuli were presented using two 12-volt solenoids (M & E Solve, Rochester, UK; <http://www.me-solve.co.uk>), masked by white noise (65 dB SPL), which were secured with medical tape to the finger pads of the left index finger and the left thumb. The left rather than the right hand was chosen based on Summers and Lederman's (1990) meta analysis that showed a left hand advantage for tasks involving spatial mediation. To present tactile non-targets the rod of the solenoid contacted the fingertip for 200ms (single tap), and to present tactile targets the 200 ms contact was interrupted for 30 ms half-way through presentation (double tap). Participants' hand(s) were covered by a black wooden board with a small viewing window, which was either open (vision conditions) or closed (no vision conditions) (see Figure 1). Vocal responses were recorded with a free-standing microphone.

Figure 1 about here

Procedure

Participants placed their left hand on the tabletop in front of their body midline, with the fingertips of their index finger and thumb above and below a central fixation point (see Figure 1). In separate conditions, fingertips were placed about 2 cm apart (near condition), about 12 cm apart (far condition), or touching (touching condition). They were instructed to continually attend to either their index finger or, in separate blocks, their thumb in order to detect and vocally respond (“pa”) to infrequent tactile targets (double taps) at that finger, while ignoring tactile stimuli at the other finger. When they viewed their fingers (vision), they were instructed to fixate their gaze on a white marker located between the tips of the attended and unattended fingers (near and far condition) or on the point where index finger and thumb were touching (touching condition). When they did not view their fingers (no vision), they were instructed to fixate on a white marker placed in an equivalent location on the closed viewing window.

Each trial consisted of a blank interval of 300 ms, followed by the 200-ms presentation of a tactile stimulus at either attended or unattended finger, followed by a blank interval of 800 ms, such that there was a total 1000-ms time window during which a vocal response to a target could be made. This was followed by a random intertrial interval between 0 and 400ms. Each participant completed two blocks of 72 trials of each combination of attended finger (index finger and thumb), finger posture (near, far, and touching), and vision (vision and no vision) in counterbalanced order. All three different posture blocks were completed in one of the vision conditions

before being repeated in the other vision condition. Attended finger alternated from one block to the next, and half the participants started with an attend-index finger block while the other half started with an attend-thumb block. Each block was composed of 60 non-target trials (30 non-targets at the attended and 30 at the unattended finger), and twelve target trials (8 targets at the attended finger, requiring a vocal response, and 4 at the unattended finger).

EEG recording and ERP analysis

EEG was recorded (BrainAmp amplifier and BrainVision Recorder software, version 1.02; Brain Products GmbH, Gilching, Germany; <http://www.brainproducts.com>) with Ag/AgCl electrodes from Fp1, Fp2, F3, Fz, F4, FC5, FC1, FCz, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, O1 and O2 (subset of the international 10-10 system), referenced to the earlobes (off-line). Vertical EOG was recorded bipolarly from above and below the right eye. EEG and EOG were amplified, band-pass filtered at 0.01 – 100 Hz, digitised at 500 Hz, and filtered off-line with a low pass filter of 30 Hz. EEG and VEOG were epoched for a period from 100 ms before to 400 ms after the onset of the tactile stimulus. Trials with vertical eye movements (VEOG exceeding $\pm 30 \mu\text{V}$ relative to the 100-ms pre-stimulus baseline), eye blinks or other artefacts (a voltage exceeding $\pm 60 \mu\text{V}$ at any electrode relative to baseline) measured in this interval were excluded from analysis. ERPs to non-targets were averaged relative to baseline for all combinations of attention (attended vs. unattended finger), finger posture (near vs. far vs. touching), vision (vision vs. no vision), and stimulated finger (index finger or thumb). ERP mean amplitudes were computed within successive 30-ms measurement windows from 35 ms to 155 ms post-stimulus onset, each covering one of the successive somatosensory components

P45 (35-65 ms), N80 (65-95 ms), P100 (95-125 ms), and N140 (125-155 ms). ERP mean amplitudes were further computed within two successive 90-ms time windows, covering early and late aspects of the late negative difference (Nd1: 185-275 ms; Nd2: 275-365 ms). Within each of those measurement windows statistical analyses of ERP mean amplitudes were conducted separately for lateral electrodes F3/4, F7/8, FC1/2, FC5/6, C3/4, T7/8, CP1/2, CP5/6, P3/4, P7/8 and midline electrodes Fz, FCz, Cz, Pz. To test whether attention was affected by task and vision conditions, initial repeated-measures ANOVAs were conducted on the within-subject factors attention (attended vs. unattended finger), finger posture (near vs. far vs. touching), vision (vision vs. no vision), hemisphere (ipsilateral vs. contralateral electrode sites), and electrode (see above) for lateral electrodes, and on the factors attention, posture, vision and electrode for midline electrodes. Follow-up ANOVAs separate for each posture were conducted for each time window in which effects of posture or vision on attention were found and for time windows showing a main effect of attention to confirm its presence across postures and vision conditions. When appropriate, Greenhouse-Geisser adjustments to the degrees of freedom were applied.

Results

Behavioral performance

Participants responded vocally upon detection of infrequent target stimuli only at the currently attended finger. Few responses in those trials were missed (2.43 %), and few incorrect responses were made to targets at currently unattended fingers (< 1 %), or to non-targets at any location (< 1 %). Correct responses were subjected to a repeated-measures ANOVA for the within-subject factors finger posture (near vs. far vs. touching) and vision (vision vs. no vision). RTs were slightly faster when fingers were

not viewed (524.5 ms) than when they were viewed (528.6 ms), but this difference did not reach significance (vision: $F(1,13) = .63$, $p = .441$, $\eta_p^2 = .05$). RTs were faster when fingers were near (517.5 ms) than far (530.1 ms), and slowest when fingers were touching (532.0 ms; finger posture: $F(2,26) = 5.05$, $p = .014$, $\eta_p^2 = .28$), irrespective of whether fingers were viewed or not (finger posture x vision: $F(2,26) = 1.93$, $p = .166$, $\eta_p^2 = .13$). Pairwise comparisons of the estimated marginal means of RTs for each combination of finger postures (with p-values adjusted for multiple comparisons) showed that RTs were significantly faster when fingers were near compared to when they were touching ($t(13) = 3.28$, $p = .018$), but not compared to when they were far ($t(13) = 2.36$, $p = .105$), while RTs in far and touching postures did not differ ($t(13) < 1$, $p = 1.0$).

Somatosensory ERPs

Figure 2 shows somatosensory ERPs at attended and unattended fingers for each vision condition in the three different finger postures.

Figure 2 about here

It can be seen that early (65-125ms) effects of spatial attention (differences between attended and unattended waveforms) were larger when selecting between fingers placed close together that were not viewed (near, no vision, see Fig.2A) than when they were viewed (near, vision), and larger when selecting between fingers that were touching when they were viewed (touching, vision, see Fig.2C) than when they were

not viewed (touching, no vision), while there were no vision-related differences when selecting between fingers placed further apart (far, see Fig.2B). Later effects of attention look similar for vision and no vision conditions when fingers were near, larger for no vision than vision conditions when fingers were far, and more prolonged for no vision than vision conditions when fingers were touching. These patterns of attentional effects were confirmed with repeated measures ANOVAs for different time windows. Given previous findings, modulations of early somatosensory components (P45, N80) were of specific interest in this study. Analyses also investigated mid (P100, N140) and later (Nd1, Nd2) latency components which are typically modulated by attention (in endogenous between hand selection studies). Table 1 provides an overview of the present results. As this study tested whether tactile attention may be modulated by finger posture and by vision of the fingers, we were particularly interested in overall main effects of attention and in any interactions between attention and posture, attention and vision, and attention, posture and vision. Planned follow-up ANOVAs for each finger posture then tested for main effects of attention and whether this was modulated by vision. If such interactions between attention and vision were found, further follow-up ANOVAs tested for attentional effects in vision and no vision conditions separately.

Table 1 about here

Attentional modulations at P45

For the time window of the *P45* component (35-65ms), there were no overall effects of attention or interactions with posture or vision (attention: $F(1,13) < 1$, $p \geq .862$, $\eta_p^2 < .01$; attention x posture: $F(2,26) \leq 1.20$, $p \geq .312$, $\eta_p^2 \leq .09$; attention x vision: $F(1,13) < 1$, $p \geq .714$, $\eta_p^2 \leq .01$; attention x posture x vision: $F(2,26) \leq 1.19$, $p \geq .315$, $\eta_p^2 \leq .08$; for lateral and midline electrodes), except for an interaction between attention, posture, vision, and electrode ($F(6,78) = 3.78$, $p = .041$, $\eta_p^2 = .23$, for midline electrodes). Bonferroni-corrected pairwise comparisons of the estimated marginal means of attended and unattended ERP amplitudes for each combination of posture, vision and electrode revealed that there were significant effects of attention for frontal electrodes Fz ($F(1,13) = 5.42$, $p = .037$, $\eta_p^2 = .29$) and FCz ($F(1,13) = 5.88$, $p = .031$, $\eta_p^2 = .31$) when fingers were near and not viewed, but not for any other comparison ($F(1,13) \leq 2.45$, $p \geq .141$, $\eta_p^2 \leq .16$). Planned follow-up analyses separate for each posture showed for the **near** posture no effects of, or interactions with, attention for lateral electrodes ($F \leq 3.16$, $p \geq .067$, $\eta_p^2 \leq .20$). For midline electrodes there was a significant interaction between attention, vision, and electrode ($F(3,39) = 5.44$, $p = .033$, $\eta_p^2 = .30$) and pairwise comparison revealed a significant attention effect at Fz and FCz (as above). Further follow-up analyses for the near posture revealed no overall effect of attention in either vision condition ($F(1,13) \leq 2.31$, $p \geq .153$, $\eta_p^2 \leq .15$). In contrast to the near posture, follow-up analyses for the **far** and **touching** postures showed no effects of, or interactions with, attention (Far: $F \leq 2.75$, $p \geq .111$, $\eta_p^2 \leq .18$, and touching: $F \leq 1.36$, $p \geq .273$, $\eta_p^2 \leq .10$, for lateral and midline electrodes).

Attentional modulations at N80

For the time window of the *N80* component (65-95 ms), there were no overall effects of attention or interactions with posture or vision (attention: $F(1,13) \leq 2.00$, $p \geq .181$, $\eta_p^2 \leq .13$; attention x posture: $F(2,26) < 1$, $p \geq .913$, $\eta_p^2 < .01$; attention x vision: $F(1,13) < 1$, $p \geq .416$, $\eta_p^2 \leq .05$; for lateral and midline electrodes; attention x posture x vision: $F(2,26) = 2.48$, $p = .108$, $\eta_p^2 = .16$; for midline electrodes). There was, however, a three-way interaction between attention, posture, and vision for lateral electrodes ($F(2,26) = 3.72$, $p = .039$, $\eta_p^2 = .22$). Bonferroni-corrected pairwise comparisons of the estimated marginal means of attended and unattended ERP amplitudes for each combination of posture and vision showed that there were significant effects of attention when fingers were near and not viewed ($F(1,13) = 5.87$, $p = .031$, $\eta_p^2 = .31$) and when fingers were touching and viewed ($F(1,13) = 5.68$, $p = .033$, $\eta_p^2 = .30$), but not for any other condition ($F(1,13) \leq 1.06$, $p \geq .322$, $\eta_p^2 \leq .08$). Planned follow-up analysis of the **near** posture there were no overall effects of attention ($F(1,13) < 1$, $p \geq .340$, $\eta_p^2 \leq .07$; for lateral and midline electrodes), but an interaction between attention and vision for lateral ($F(1,13) = 4.91$, $p = .045$, $\eta_p^2 = .27$) but not for midline electrodes ($F(1,13) = 4.06$, $p = .065$, $\eta_p^2 = .24$). Follow-up analyses for each vision condition confirmed that there were no effects of attention when fingers were viewed ($F(1,13) \leq 1.16$, $p \geq .301$, $\eta_p^2 \leq .08$; for lateral and midline electrodes). When fingers were not viewed, attentional effects were present for lateral electrodes ($F(1,13) = 5.87$, $p = .031$, $\eta_p^2 = .31$) and marginal for midline electrodes ($F(1,13) = 4.47$, $p = .054$, $\eta_p^2 = .26$). In contrast, for the **far** and **touching** postures no effects of, or interactions with, attention (far: $F \leq 2.13$, $p \geq .106$, $\eta_p^2 \leq .14$, and touching: $F \leq 2.03$, $p \geq .177$, $\eta_p^2 \leq .14$, for lateral and midline electrodes) were present. Surprisingly, in the touching posture there was also no reliable interaction

between attention and vision ($F(1,13) \leq 2.03$, $p \geq .177$, $\eta_p^2 \leq .14$, for lateral and midline electrodes).

Attentional modulations at P100

For the time window of the *P100* component (95-125 ms), there were overall effects of attention ($F(1,13) \geq 8.57$, $p \leq .012$, $\eta_p^2 \geq .40$, for lateral and midline electrodes), but no interactions with posture or vision (attention x posture: $F(2,26) < 1$, $p \geq .451$, $\eta_p^2 \leq .05$; attention x vision: $F(1,13) < 1$, $p \geq .633$, $\eta_p^2 \leq .02$; attention x posture x vision: $F(2,26) \leq 1.34$, $p \geq .280$, $\eta_p^2 \leq .09$; for lateral and midline electrodes). Planned follow-up analysis of the **near** posture effects of attention ($F(1,13) \geq 5.91$, $p \leq .030$, $\eta_p^2 \geq .31$, for lateral and midline electrodes) did not differ across vision conditions ($F(1,13) \leq 1.12$, $p \geq .312$, $\eta_p^2 \leq .08$, for lateral and midline electrodes). For the **far** posture effects of attention were only present as an interaction between attention and hemisphere for lateral electrodes ($F(1,13) = 6.67$, $p = .023$, $\eta_p^2 = .34$). Bonferroni-corrected pairwise comparisons of the estimated marginal means of attended and unattended ERP amplitudes for each hemisphere showed only a contralateral attention effect ($F(1,13) = 9.21$, $p = .010$, $\eta_p^2 = .42$). There were no attentional effects for midline electrodes ($F(1,13) < 1$, $p = .586$, $\eta_p^2 = .02$), and there were no interactions between attention and vision ($F(1,13) < 1$, $p \geq .552$, $\eta_p^2 \leq .03$, for lateral and midline electrodes). Analysis of the **touching** posture showed that effects of attention were present for lateral electrodes ($F(1,13) = 15.15$, $p = .002$, $\eta_p^2 = .54$), but only marginal for midline electrodes, ($F(1,13) = 4.41$, $p = .056$, $\eta_p^2 = .25$). Attentional effects differed across vision conditions as an interaction with hemisphere for lateral electrodes ($F(1,13) = 5.96$, $p = .030$, $\eta_p^2 = .31$), but did not differ across vision conditions for midline electrodes ($F(1,13) = 1.24$, $p = .286$, $\eta_p^2 = .09$). Further

follow-up analyses revealed that in this posture effects of attention were present only when fingers were viewed ($F(1,13) \geq 7.98$, $p \leq .014$, $\eta_p^2 \geq .38$; for lateral and midline electrodes), and not when fingers were not viewed ($F(1,13) \leq 1.56$, $p \geq .233$, $\eta_p^2 \leq .11$; for lateral and midline electrodes).

Attentional modulations at N140

For the time window of the *N140* component (125-155 ms), there were significant effects of attention for lateral electrodes ($F(1,13) = 21.37$, $p < .001$, $\eta_p^2 = .62$), but no attentional effects for midline electrodes ($F(1,13) = 4.15$, $p = .063$, $\eta_p^2 = .24$), in the absence of interactions between attention and posture or vision (attention x posture: $F(2,26) \leq 1.89$, $p \geq .177$, $\eta_p^2 \leq .13$; attention x vision: $F(1,13) < 1$, $p \geq .698$, $\eta_p^2 \leq .01$; attention x posture x vision: $F(2,26) \leq 1.44$, $p \geq .255$, $\eta_p^2 \leq .10$; for lateral and midline electrodes). Planned follow-up analysis of the **near** posture showed that effects of attention ($F(1,13) \geq 6.42$, $p \leq .025$, $\eta_p^2 \geq .32$, for lateral and midline electrodes) did not differ across vision conditions ($F(1,13) \leq 1$, $p \geq .395$, $\eta_p^2 \leq .06$, for lateral and midline electrodes). Analyses of the **far** and **touching** postures showed that there were effects of attention for lateral (far: $F(1,13) = 5.16$, $p = .041$, $\eta_p^2 = .28$, and touching: $F(1,13) = 6.67$, $p = .023$, $\eta_p^2 = .34$) but not for midline electrodes ($F(1,13) < 1$, $p > .473$, $\eta_p^2 = .04$), which were independent of vision (far: $F(1,13) \leq 2.26$, $p \geq .156$, $\eta_p^2 \leq .15$; and touching: $F(1,13) < 1$, $p \geq .807$, $\eta_p^2 < .01$ for lateral and midline electrodes).

Attentional modulations at Nd1

For the time window of the *Nd1* (185-275 ms), there were overall effects of attention ($F(1,13) \geq 15.58$, $p \leq .002$, $\eta_p^2 \geq .55$, for lateral and midline electrodes),

which did not reliably differ across posture or vision conditions (attention x posture: $F(2,26) \leq 2.98$, $p \geq .074$, $\eta_p^2 \leq .19$; attention x vision: $F(1,13) \leq 2.90$, $p \geq .112$, $\eta_p^2 \leq .18$; attention x posture x vision: $F(2,26) \leq 2.69$, $p \geq .090$, $\eta_p^2 \leq .17$; for lateral and midline electrodes). Planned follow-up analysis of the **near** posture showed that attentional effects ($F(1,13) \geq 10.74$, $p \leq .006$, $\eta_p^2 \geq .45$, for lateral and midline electrodes) did not differ as a function of vision ($F(1,13) < 1$, $p \geq .854$, $\eta_p^2 < .01$, for lateral and midline electrodes). Analysis of the **far** posture showed that attentional effects ($F(1,13) \geq 21.57$, $p < .001$, $\eta_p^2 \geq .62$, for lateral and midline electrodes) differed as a function of vision ($F(1,13) \geq 8.92$, $p \leq .011$, $\eta_p^2 \leq .41$, for lateral and midline electrodes), as attentional effects were stronger when fingers were not viewed (Figure 2). However, attentional effects were present in both vision conditions ($F(1,13) \geq 18.18$, $p \leq .001$, $\eta_p^2 \geq .58$, for lateral and midline electrodes). Analysis of the **touching** posture showed that attentional effects ($F(1,13) \geq 8.50$, $p \leq .012$, $\eta_p^2 \geq .40$, for lateral and midline electrodes) did not differ as a function of vision ($F(1,13) < 1$, $p \geq .953$, $\eta_p^2 < .01$, for lateral and midline electrodes).

Attentional modulations at Nd2

In the time window of the Nd2 (275-365 ms), there were overall effects of attention for lateral electrodes ($F(1,13) = 7.36$, $p = .018$, $\eta_p^2 = .36$), but not for midline electrodes ($F(1,13) = 3.21$, $p = .097$, $\eta_p^2 = .20$), which did not significantly differ across posture or vision conditions (attention x posture: $F(2,26) \leq 2.55$, $p \geq .107$, $\eta_p^2 \leq .16$; attention x vision: $F(1,13) < 1$, $p \geq .454$, $\eta_p^2 \leq .04$; attention x posture x vision: $F(2,26) < 1$, $p \geq .409$, $\eta_p^2 \leq .07$; for lateral and midline electrodes). Planned follow-up analyses separately for the **near** and **far** postures showed that attentional effects (near: $F(1,13) \geq 4.41$, $p \leq .037$, $\eta_p^2 \geq .29$, and far: $F(1,13) \geq 6.66$, $p \leq .023$, $\eta_p^2 \geq .34$, for

lateral and midline electrodes) did not differ as a function of vision (near: $F(1,13) < 1$, $p \geq .532$, $\eta_p^2 \leq .03$, and far: $F(1,13) \leq 1.87$, $p \geq .194$, $\eta_p^2 \leq .13$, for lateral and midline electrodes). In contrast, in the **touching** posture there were no effects of, or interactions with, attention ($F \leq 3.02$, $p \geq .072$, $\eta_p^2 \leq .19$, for lateral and midline electrodes).

General Discussion

This study has shown that, similar to our earlier study (Gillmeister et al. 2010), vision can have adverse effects on the tactile-spatial selection between adjacent parts of the body. When adjacent fingers compete for attentional selection, viewing them simultaneously hinders the otherwise efficient process of filtering tactile inputs at the attended finger over those at the unattended finger. This study extends our earlier findings to show that adverse effects arise only when fingers are near together and are not touching. When fingers were near, attentional differentiations were first clearly present in the time range of the N80 component, with some attentional modulations already present for the P45 component, but crucially, this was only the case when fingers were not viewed. Although they were present also over the P100, attentional differentiations for this, near posture did not differ reliably across vision conditions for this or for any subsequent analysis windows (i.e. N140, Nd1 and Nd2). In contrast, when fingers were far or touching, attentional differences were first present reliably over the P100 component. This shows that posture, like vision, can abolish early attentional modulations of tactile processing and, crucially, that vision effects on attentional selection are dependent on finger posture.

Similar to our previous study (Gillmeister et al. 2010), in the present study we found attentional modulations at the N80 component when fingers were near and not

viewed, with some evidence that such modulations may already arise over P45. This early attentional modulation is in line with previous reports of primary somatosensory cortex (S1) instantaneously adapting to spatial attentional demands (Braun et al. 2002; Iguchi et al. 2001; Noppeney et al. 1999) by sharpening of the contrast between finger representations of attended and unattended fingers through lateral inhibitory processes in S1. However, this process is abolished when viewing the fingers, and one of the aims of the present study was to investigate whether those vision effects on tactile selection may be due to a conflict between visual and tactile spatial information. We hypothesised that the same conflict between viewing both fingers while attending only to one of those fingers would need to be resolved irrespective of finger posture, and therefore, effects of tactile selection should be delayed by vision in the same way for each posture condition. This is not what was found, however. Viewing the fingers abolished early cortical (P45-N80) effects of tactile selection only when the fingers were near, but not when the fingers were far or touching. When fingers were far, viewing them reduced, but did not eliminate, effects of selection compared to not viewing them at much later stages (Nd1). When fingers were touching, there was even some evidence that vision gave rise to earlier cortical (N80-P100) effects of selection compared to not viewing the fingers (N140). These findings suggest that visual-tactile conflict alone cannot be responsible for the abolishment of early tactile selection effects; other factors clearly have important influences.

As described earlier, vision provides spatial information that may facilitate the remapping of tactile event locations into an external spatial coordinate system (e.g., Röder et al. 2004; Sambo et al. 2009). If this is the case for selection between touches, not only on different hands, but also on different fingers of the same hand, this hypothesis would predict that attentional selection is facilitated when fingers are

placed further apart than when they are near. In our study, there were generally no earlier or larger effects of attentional selection for far compared to near fingers at any time window. Instead, we found that tactile selection was reduced (or eliminated) by viewing the fingers at much later stages when fingers were far (Nd1) than when fingers were near (N80). In other words, we found that increasing the spatial separation between fingers ameliorated the detrimental effects of viewing the fingers. This may be because vision reinforces the representation of the two fingers as distinct sources of tactile information, which may restore some of the attentional sharpening of S1 representations prevented by simultaneously viewing both fingers. Our findings thus support the hypothesis that external spatial frameworks do play a role in guiding tactile-spatial selection within the hand, and add to the growing body of evidence that suggests that fingers are not represented within purely somatotopic coordinates (Craig 2003; Overvliet et al. 2011; Riemer et al. 2011; Roberts and Humphreys 2010; Shibuya et al. 2007).

Further, if tactile selection were solely guided by an external spatial coordinate system, very similar attention and vision effects should have been evident in the fingers near and touching conditions. This is because both are ‘near’ in the sense of a purely (visual-)spatial framework for determining tactile localisation. On the contrary, we found that vision adversely affected the selection between near fingers but had no such effects on the selection between touching fingers. If anything, vision effects on attentional modulations of tactile processing were reversed under touching compared to fingers near conditions. That is, when fingers were touching, overall attentional differences were first reliably present over P100, with some evidence for attentional differences already over N80 that were only present when fingers were viewed, but not when fingers were not viewed. A reliable interaction between attention, posture

and vision was present at the N80, based on opposite vision effects in the near and touching conditions; although, follow-up analysis for the touching conditions did not show a reliable attention by vision interaction for this analysis window. At the P100 there was no interaction supporting opposite effects in near and touching postures, but follow-up analyses found that effects of attention when fingers were touching were in fact restricted to conditions when touching fingers were viewed. Taken together, these findings suggest that vision may aid tactile-spatial selection between touching fingers, in contrast to an adverse effect of vision on tactile selection when fingers are near and non-touching. This effect of posture on tactile selection is unlikely to be solely due to the effects of the perceptual system adapting to the constant tactile input present in the touching but not in near or far conditions. Overvliet et al. (2011) ruled out tactile adaptation as a potential explanation of their finger posture effects by showing that localisation was superior for spread than close fingers even when foam pads provided constant tactile input to the sides of the fingers. While the design of our study cannot rule out potential contributions from tactile adaptation, the substantially different effects of vision on tactile selection in all three postures, rather than only in touching compared to non-touching (near or far) postures, suggest that tactile adaptation cannot be the sole explanation for those effects. Instead, our findings are better accounted for by changes in the somatotopic mapping of finger representations when these are near and touching compared to when they are near but non-touching. Likewise, a recent study (Schütz-Bosbach et al. 2009) has suggested that somatosensory organisation for touching body parts is remapped. In addition, skin-to-skin contact between body parts has been reported to lead to activation of neurons in superior parietal cortex (Sakata et al. 1973) suggesting that also higher order processes may differ when body parts are in contact with each other. This might be reflected in an absence of attentional

modulations at later processing stages (Nd2) under touching compared to non-touching (near and far) conditions in the current study. Overvliet et al. (2011) proposed that with (unseen) touching fingers increased amounts of skin surface fall within the receptive fields of posture-sensitive neurons, and this may reduce tactile localisation accuracy compared to non-touching fingers. Our findings suggest that this disadvantage may be reversed by vision of touching compared to non-touching fingers. Viewing the fingers might be helpful in representing the locations of touching fingers as distinct from one another, and thus lead to effects of attentional selection at earlier somatosensory components (N80-P100) than when fingers are not viewed (P100-N140), as indicated by some of the present findings. Vision may similarly improve the accuracy of localising tactile stimuli at touching fingers, and thus counteract the adverse effects of increasing potential locations within a given receptive field.

Taken together, this study has shown that both vision of the fingers and finger posture can abolish early attentional effects within S1, and that this effect is most likely based on changes in somatosensory finger representations rather than a conflict between visual and tactile spatial information. Firstly, vision of fingers may abolish ERP correlates of early attentional selection between closely placed fingers due to effects of visual exposure of the hand on S1 finger representations; that is, changes in the lateral inhibitory processes between finger representations. Similarly, Cardini et al. (2011) recently showed that vision of the hand leads to improved acuity at the finger tip, which correlated with suppression of early somatosensory potentials (P50) when adjacent fingers were simultaneously stimulated, suggesting that activity of interneuronal circuits in S1 are modulated by vision. Secondly, finger posture may also abolish ERP correlates of early attentional selection, suggesting changes in the

primary somatosensory mapping of fingers which may not necessitate attentional modulations to segregate tactile input (into attended and unattended locations) at this early stage of processing. A recent MEG study has shown that hand posture modulates cortical finger representation (Hamada and Suzuki; 2005); however, they reported changes only for secondary somatosensory cortex (S2). Posture may modulate processing within S1 through feedback loops from S2 but since generally sequential processing within somatosensory areas is assumed (e.g. Inui et al. 2004) our results are more adequately explained as effects on the organisation of finger representations in S1. However, future research will need to clarify the precise underlying mechanisms of posture changes of S1 organization and tactile selection.

In sum, finger representations within S1 are not statically fixed but are dynamically modulated by top-down mechanisms like attention (e.g. Braun et al. 2002). Furthermore, we showed that these modulations are dependent on intramodal (i.e. posture) and intermodal (i.e. vision) influences on S1 representations.

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Conflict of interest

The authors declare that they have no conflict of interest.

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Figure legends:

Fig. 1 Images of the near (a), far (b) and touching (c) finger postures including fixation dot located half way between index finger and thumb in the near and far postures. The images are taken from the view of the participant in the vision condition. In the no vision condition the same finger postures were adopted by the fingers was covered from view

Fig. 2 Grand-averaged ERP waveforms to tactile stimuli at attended (black lines) and unattended (grey lines) fingers in the near (left panels), far (middle panels) and touching (right panels) condition when participants' fingers were covered (no vision; top panels) and when participants viewed their fingers (vision; bottom panel). Waveforms are shown for one representative electrode located over somatosensory cortex contralateral to the stimulated hand (C3/4c). The top left panel shows somatosensory components and the measurement windows for which analyses were conducted in ms