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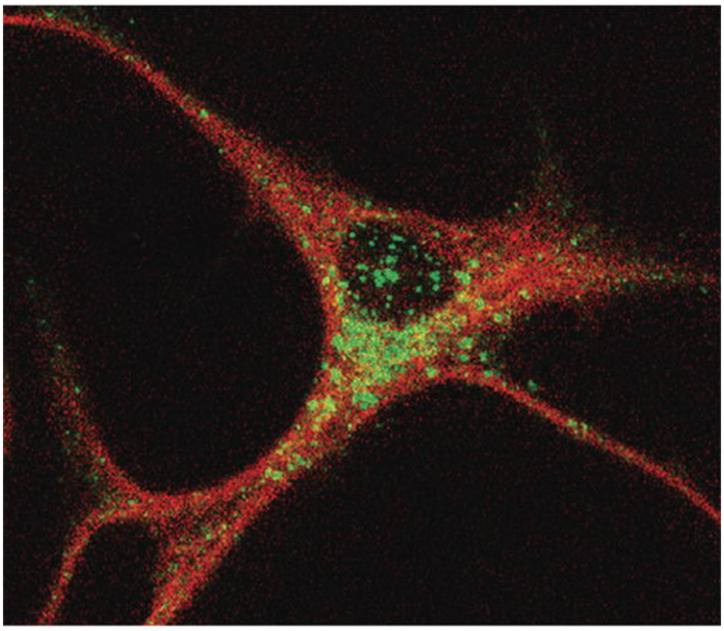

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Research Report

Altered tactile spatial attention in the early blind

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ABSTRACT

To investigate whether superior tactile acuity in the blind is due to alterations of attentional selection mechanisms, event-related brain potentials (ERPs) were measured in a group of early blind and a group of sighted individuals who performed a difficult tactile spatial selection task. We found systematic differences in the attentional processing of tactile events between early blind and sighted individuals. The blind not only responded faster to tactile targets, but also showed attentional modulations of early somatosensory ERP components (P100 and N140). In contrast, ERP effects of spatial attention in the sighted only emerged at longer-latencies (about 200 ms post-stimulus). Our findings suggest that increased use of one sense due to sensory deprivation, such as touch in blind people, leads to alterations of attentional selection mechanism within modality-specific cortex.

1. Introduction

Blind individuals commonly utilize tactual and auditory cues for information and orientation (e.g. auditory pedestrian signals, tactual walking stones or Braille reading). Increased reliance on touch and audition, together with more practice in using these modalities to guide behavior, is often reflected in better performance of blind relative to sighted participants in tactile or auditory discrimination tasks (see Röder and Neville, 2003 for review). For example, early blind individuals perform better than sighted people in tactile tasks measuring two-point threshold (Axelrod, 1959) and pattern discrimination (Goldreich and Kanics, 2003; Grant et al., 2000; Van Boven et al., 2000). Electrophysiological studies have shown changes in the latency (Feinsod et al., 1973; Röder et al., 1996) and topographic distribution (Pascual-Leone and Torres, 1993) of ERP components. Such findings are often interpreted as evidence for compensatory plasticity based on reorganization of cortical functions (cf. Bavelier and Neville, 2002; Röder and Rösler, 2004). However, enhanced performance in the blind could also be due to modulations of sensory processing at low-level sensory stages or improved attentional selectivity developed through continuous practice. Support for the latter hypothesis comes from an ERP study (Röder et al., 1999) demonstrating that the superior spatial selection of tones presented in peripheral space in the blind is linked to a better spatial tuning of early auditory attention (see also Kujala et al., 1995 and Hötting et al., 2004, for further ERP evidence for altered mechanisms of auditory attentional selection in the blind).

However, there is as yet no evidence for similar compensatory changes of *tactile* attention in the blind. In fact, two previous studies (Kujala et al., 1995; Hötting et al., 2004) have failed to find electrophysiological evidence for differences in the spatial tuning of tactile attention between blind and sighted participants. This is surprising, given that the ability to allocate attention to specific regions of the hand and fingers is essential for the blind when relying on touch during haptic exploration and the discrimination of fine patterns, as in

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Table 1 – Participants' details

Description of blind participants						
Age	**Gender**	**Handedness**	**Visual perception**	**Braille reading hand**	**Age of onset**	**Cause of blindness**
60	Male	Right	None	Left	18 months	Eye glass damage
54	Female	Right	None	Right	Birth	Retinopathy of prematurity
63	Male	Right	Diffuse light	Right	Birth	Nervus opticus atrophy
54	Male	Right	None	Right	Birth	Retinopathy of prematurity
52	Female	Right	None	Right	Birth	Retinopathy of prematurity
60	Female	Right	None	Right	16 months	Detached retina
29	Female	Right	None	Left	2 years	Detached retina
52	Female	Right	None	Right	Birth	Retinopathy of prematurity
55	Male	Right	None	Left	Birth	Retinopathy of prematurity
50	Male	Right	None	Right	13 months	Detached retina

Blind participants: mean age of 53 years (range 29–60). Sighted participants: mean age of 57 years (range 30–69), 5 female and 5 male, all right handed. Sighted participants were blindfolded.

Braille reading. The tactile attention tasks used in previous electrophysiological investigations (attending to one finger or hand while ignoring tactile events at other fingers or the other hand) were relatively easy and thus not ideally suited to reveal systematic differences between the blind and the sighted. In the present experiment, a difficult spatial selection task, which also relates to everyday activities of the blind, was used to uncover altered tactile attention mechanisms in the early blind.

Behavioral and ERP correlates of tactile spatial attention were assessed for 10 functionally totally blind Braille readers who lost their sight in infancy, and 10 blindfolded sighted individuals matched for age, gender and handedness (Table 1). Tactile vibrations were presented, in random sequence, by three closely placed tactile mechanical stimulators located at the top and middle phalanx of the index finger (Fig. 1; see Experimental procedures for details). These locations were chosen because they involved the distal part of the index fingers used by blind people to scan tactile surfaces when reading Braille characters. All participants had to attend to one location and to respond vocally when they detected infrequent tactile targets (weak vibrations) at this location, while ignoring stronger non-target tactile vibrations at the attended location, and all tactile events presented to the two unattended locations. Left or right hands were stimulated in different experimental blocks, and attended locations changed across blocks. In a previous study with sighted participants (Eimer and Forster, 2003a), where a similar procedure was used, an attentional enhancement of the somatosensory P100 component was observed, although only when attended and ignored locations were located on different fingers. Importantly, this effect disappeared when both locations were on the same finger, indicating limitations to the spatial tuning of early tactile attention for sighted people. The present study investigated whether tactile attentional selectivity is more finely tuned in the early blind, when focused on those parts of the finger that are constantly used during Braille reading.

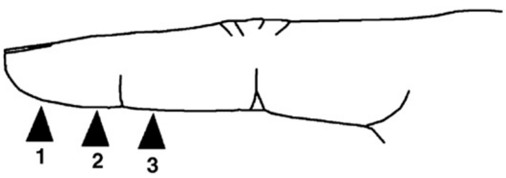

Fig. 1 – Schematic drawing of the placement of the tactile stimulators (▲). Mechanical tactile stimuli were delivered to one of three locations along the midline axes of the left or right index finger. The tip of the stimulators was set 1 cm apart and was placed on the fingers' palm sides with the crease between the top and middle phalanx located half way between the middle stimulator 2 and the outer stimulator 3.

2. Results

Table 2 shows the behavioral performance of both participant groups in detecting task relevant tactile stimuli at attended locations. As expected, blind participants responded faster than sighted participants to tactile targets at attended locations (561 versus 638 ms ($F(1/18)=3.4$, $P<0.05$), and missed fewer targets than sighted participants (1.3% versus 2.3%; $F(1/18)=3.9$, $P<0.05$). False alarm rates did not differ significantly between both groups (see Table 2).

Peak analyses of early somatosensory components showed that the P100 component at lateral electrode sites was present on average 6 ms earlier in the early blind than the sighted (104 versus 110 ms; $F(1/18)=6.42$, $P<0.03$). There was no significant difference between the two groups in the timing of the following N140 component.

Effects of tactile attention on early somatosensory processing for early blind and sighted participants were contrasted by comparing ERPs in response to tactile non-targets at

Table 2 – Behavioral results

	Average reaction times (ms)	% Missed targets	% False alarms to targets at unattended locations
Sighted participants	637.5 ms (SE 20.3)	2.3% (SE 0.5)	2.8% (SE 1.1)
Blind participants	560.8 ms (SE 36.1)	1.3% (SE 0.5)	2.4% (SE 0.8)

attended versus unattended locations for both groups, separately at lateral and midline electrodes (see Experimental procedures for details). Fig. 2 shows ERPs obtained at midline electrode CZ and at lateral central electrodes (C3/C4) contralateral to the stimulated hand for early blind and sighted participants, averaged across the three stimulation location. To enable a direct comparison of the size of attentional modulations between the two groups, Fig. 3 presents difference waveforms obtained by subtracting ERPs to unattended tactile non-targets from ERPs to tactile non-targets at attended locations, separately for early blind and sighted participants. In the early blind group, the P100 component (measured between 90 and 115 ms after stimulus onset) was enhanced in response to attended versus unattended tactile stimuli at lateral electrodes ($F(1/9)=6.45$, $P<0.04$) as well as at midline sites ($F(1/9)=7.95$, $P<0.02$). In contrast, no such attentional modulation of the P100 was present for sighted participants (both $F(1/9)<1.55$, $P>0.24$), and this difference was reflected by group × attention interactions at lateral and midline sites ($F(1/18)=6.25$, $P<0.03$ and $F(1/18)=5.94$, $P<0.03$, respectively).

A similar pattern was also observed for the subsequent N140 component (measured between 120 and 145 ms after stimulus onset). Significant effects of spatial attention (reflecting an enhanced positivity in response to tactile stimuli at the currently attended location; see Fig. 2) were present at lateral and midline electrodes for the early blind group (both $F(1/9)>5.66$, $P<0.05$), but not for the sighted (both $F(1/9)<1$, $P>0.37$). No overall significant group × attention interactions were observed for the N140 (both $F(1/18)<2.22$, $P>0.15$). However, a group × attention × hemisphere interaction was present for lateral electrodes ($F(1/18)=5.09$, $P<0.04$) with significant effects of spatial attention in the early blind group only present over the right hemisphere ($F(1/9)=12.49$, $P<0.01$). There were no other significant interactions that indicate differences in the scalp distribution of spatial attention effects (see Table 3).

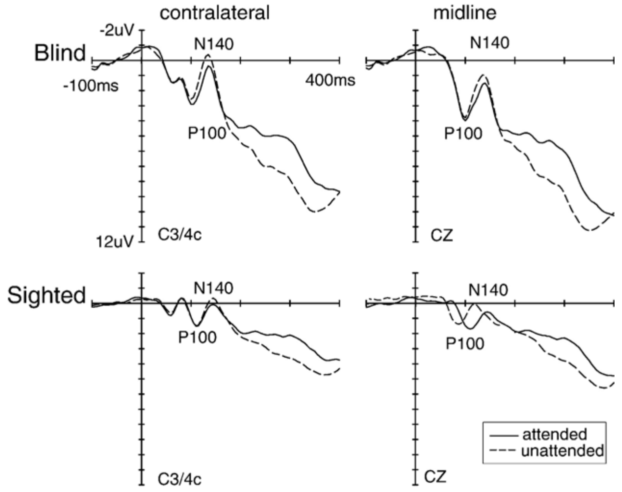

Fig. 2 – ERPs in response to tactile non-target stimuli at attended (solid lines) and unattended (dashed lines) locations obtained at lateral central electrodes over somatosensory cortex contralateral to the stimulated hand (C3/4c) and at midline electrode CZ. ERPs are collapsed across all three stimulation locations, and are shown separately for early blind (top) and sighted (bottom) participants.

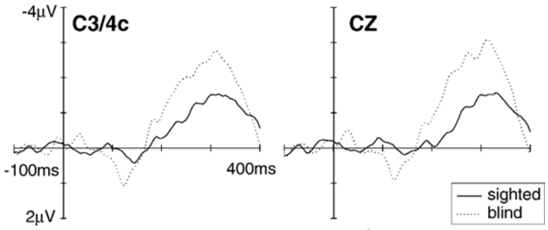

Fig. 3 – Difference waveforms obtained by subtracting ERPs to unattended tactile non-targets from ERPs to tactile non-targets at attended locations at lateral central electrode contralateral to the stimulated hand (C3/4c) and at midline electrode CZ, shown separately for early blind (dotted lines) and sighted (solid lines) participants.

A subsequent sustained attentional negativity (measured between 200 and 300 ms post-stimulus) was present for blind as well as sighted participants (all $F(1/9)>4.29$, $P<0.05$; see Fig. 2). A group × attention interaction that was significant at lateral electrodes ($F(1/18)=4.69$, $P<0.05$) and almost significant at midline electrodes ($F(1/18)=4.02$, $P<0.06$) demonstrated that this late attentional effect was more pronounced in the early blind group. There were no other interactions involving the factors group and attention which would have suggested topographic between-group differences of tactile spatial attention effects (see Table 3).

3. Discussion

Our results demonstrate, for the first time, that the spatial tuning of tactile attention is more precise in early blind than in sighted participants when the area used by the blind during Braille reading is stimulated, and when demands on spatially selective somatosensory processing are high. In line with previous findings showing enhanced tactile discrimination in the blind (Axelrod, 1959; Goldreich and Kanics, 2003; Hötting et al., 2004; Kujala et al., 1995; Röder et al., 1996; Van Boven et al., 2000), the early blind responded faster and were more accurate than the sighted in detecting infrequent tactile targets at currently attended locations, and this was mirrored by an early attentional modulation of the somatosensory P100 component that was absent in the sighted group. Furthermore, the P100 component occurred earlier in the blind than in the sighted, suggesting faster tactile processing speed (see also Feinsod et al., 1973 and Röder et al., 1996). The P100 is a modality-specific somatosensory component that is assumed to be generated within secondary somatosensory cortex (S2). Intracranial recordings from S2 (Frot and Mauguière, 1999) have identified evoked components within time windows comparable to the P100 latency observed in the present study. The fact that the P100 component is elicited bilaterally is consistent with the presence of neurons with bilateral receptive fields in S2 (Iwamura et al., 1994), and with the observation that magnetoencephalographic (MEG) responses originating from S2 can be elicited by both contra- and ipsilateral tactile stimuli (Hari et al., 1984). Our finding that

Table 3 – Results of the statistical analyses of ERP data obtained at lateral recording sites, conducted across both groups and separately for sighted and early blind participants

	90–115 ms		120–145 ms		200–300 ms	
	F-value	P-value	F-value	P-value	F-value	P-value
Overall						
Group	1.20	0.29	0.25	0.62	6.15	0.02
Group × attention	6.25	0.02*	1.85	0.19	4.69	0.04*
Group × electrode × attention	0.81	0.42	0.38	0.70	1.20	0.31
Group × hemisphere × attention	0.08	0.78	5.09	0.04*	0.01	0.98
Group × hand × attention	1.36	0.26	0.66	0.43	0.68	0.42
Group × hemisphere × hand × attention	0.01	0.98	0.84	0.37	0.08	0.78
Sighted						
Attention	1.54	0.25	0.87	0.38	8.95	0.02*
Attention × electrode	0.57	0.57	0.29	0.73	5.15	0.02*
Attention × hemisphere	1.25	0.29	3.87	0.08	21.82	0.01*
Attention × hand	0.02	0.88	1.69	0.23	0.02	0.88
Attention × hemisphere × hand	1.24	0.29	0.97	0.35	1.45	0.26
Blind						
Attention	6.45	0.03*	6.13	0.04*	17.49	0.01*
Attention × electrode	1.05	0.39	1.28	0.30	1.58	0.20
Attention × hemisphere	0.18	0.68	18.82	0.01*	2.39	0.16
Attention × hand	2.30	1.16	0.01	0.91	0.82	0.39
Attention × hemisphere × hand	0.89	0.37	0.02	0.89	3.78	0.08

Results involving the factor attention are shown for three post-stimulus analysis windows: 90–115 ms (P100), 120–145 ms (N140) and 200–300 ms (‘*’ indicates statistical significance).

the P100 occurred earlier and was enhanced by spatial attention for the early blind, but not in the sighted group, thus indicates that compensatory enhancements of spatial selectivity within somatosensory cortical areas such as S2 may occur following visual deprivation from infancy or birth.

Blind individuals commonly use the distal part of their index fingers to explore surfaces and read Braille. The presence of attentional modulations of early somatosensory ERP components (P100, N140) for the early blind, and their absence in the sighted group, suggests that sensory-specific attentional mechanisms are more efficient in the blind during the selection of tactile stimuli within this area. This could be a direct result of the continuous use of this finger region during Braille reading. The blind participants tested in this study all reported reading Braille characters with one index finger while using the other index finger as guidance between lines, thus involving both hands in Braille reading. This may explain why the compensatory enhancement of attentional selectivity for the early blind in the present study was present regardless of which hand was stimulated, and was unaffected by hand dominance. Alternatively, it is possible that the early attentional modulations present in the blind are independent of Braille reading, and instead reflect a general enhancement of discriminating fine spatial patterns. These two alternatives could be tested in future experiments by measuring the spatial tuning of tactile attention in the blind for fingers not involved in Braille reading.

For sighted participants, ERP effects of spatial attention only emerged at about 200 ms post-stimulus as a sustained enhanced negativity triggered by tactile stimuli at attended locations. Such longer-latency attentional negativities are commonly observed in ERP studies of tactile attention (see Michie, 1984; Eimer and Forster, 2003a,b), and are usually interpreted as evidence for the in-depth processing of task-relevant tactile events at post-perceptual stages. The observation that this effect was reliably larger for the early blind group (see Fig. 2) suggests that the superior spatial tuning of attention at early sensory-perceptual stages may result in additional benefits for the subsequent post-perceptual processing of tactile events.

Previous studies investigating tactile spatial attention in sighted participants have reported enhanced negativities for the N80 component (Eimer and Forster, 2003b), the N140 component (Desmedt and Robertson, 1977; Eimer and Forster, 2003b; Forster and Eimer, 2004, 2005; Garcìa-Larrea et al., 1995; Michie et al., 1987) and longer-latencies (Desmedt and Robertson, 1977; Michie et al., 1987; Eimer and Forster, 2003a, b; Forster and Eimer, 2004, 2005). In these studies, participants were typically instructed to attend to one versus the other hand, so that the attentional selection of attended tactile events only required a relatively simple discrimination of left-hand and right-hand stimulation. Early attentional ERP modulations (an enhanced positivity in the time range of the P100 and overlapping with the N140 component) were also observed for sighted participants when attended and unattended tactile stimuli were located on different fingers of the same hand (Eimer and Forster, 2003a). In contrast, when tactile stimuli were delivered to different locations on one finger, and participants were instructed to attend to one of these locations, while ignoring another nearby location on the same finger, no modulations of early somatosensory ERPs were observed, and only longer-latency attentional effects were present (see Eimer and Forster, 2003a). This difference suggests that the increased difficulty of a within-finger selection task can substantially delay the onset of the selective attentional processing of tactile events.

The present study confirmed the absence of any attentional modulations of early somatosensory components in the sighted group when attended and unattended tactile stimulus locations were on the same finger, and within-finger selection was required. In contrast, the early blind showed an enhanced positivity in the time range of the P100 overlapping with N140 component (similar to the effects found previously for between-finger attentional selection in sighted participants; Eimer and Forster, 2003a), thus suggesting that the attentional selection of one location versus another on the same finger can operate faster and more effectively in the blind. This conclusion is also consistent with the results of a recent behavioral study (Collignon et al., 2006) demonstrating superior performance in early blind as compared to sighted subjects during tactile and auditory spatial attention tasks. Furthermore, our results suggest that visual deprivation from a very early age, and the resulting increased usage and dependence on the tactile sense, can alter and improve the spatial tuning of tactile attention within sensory-specific somatosensory cortex. Early blind Braille readers have an enhanced capability to focus attention on small regions of the finger, in order to selectively process relevant information, and to ignore stimuli at nearby irrelevant locations. The superior tactile acuity in blind individuals demonstrated for blind individuals in previous behavioral studies may thus be largely due to altered and more efficient attentional selection mechanisms.

4. Experimental procedures

Twenty paid volunteers participated in the experiment (Table 1). Ten participants were functionally totally blind from infancy and all reported being regular Braille readers from an early age (5 years or below). The other 10 participants were sighted and were matched with the early blind for age, handedness and gender. All participants gave their informed consent prior to the testing.

Participants sat in an experimental chamber, wearing a head-mounted microphone. The sighted participants were blindfolded. Tactile stimuli were presented using three 12 V solenoids, driving a metal rod with a blunt conical tip to one of three possible locations on the index finger, making contact with the skin whenever a current was passed through the solenoid. Tactile stimulators were set into a small wooden block with the solenoids' tips aligned and 1 cm apart. The wooden block was attached with adhesive medical tape to the palm side of the participants' left or right index finger. Two of the solenoids were placed beneath the top phalanx and one beneath the middle phalanx of the index finger (Fig. 1). Participants placed their left and right hands on a table in front of them, and were instructed to adopt and maintain a comfortable hand and body posture. Throughout the experimental blocks, 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 time interval between the onset of successive pulses of a vibratory tactile stimulus was 17 ms, corresponding to a stimulation frequency of 58.8 Hz. The interval between the onset of the first pulse and the offset of the last pulse was 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 with different intensity. On each trial, a single vibratory tactile stimulus was presented at one of the three possible stimulation locations. The intertrial interval between successive stimuli varied randomly between 650 and 950 ms, with a mean interval of 800 ms.

Five blind and five sighted participants performed the task first with their right hand and then with the left hand and this order was reversed for the other five blind and five sighted participants. Participants were instructed to respond vocally (by saying 'yes') whenever an infrequent weak vibratory stimulus was detected at the relevant/attended location, and to ignore all strong vibrations at this location, as well as all tactile stimuli at irrelevant/unattended locations. The latency of vocal responses was measured with a voice key. The to-be-attended location was specified via verbal instruction in advance of each experimental block, and remained constant throughout this block. The experiment consisted of 18 blocks (nine successive blocks with left-hand and right-hand stimulation, respectively). Attention was directed to one of the three possible stimulation locations (location 1 or 2 on the top phalanx or location 3 on the middle phalanx of the index finger) in three blocks. The order in which these blocks were delivered was randomized for each participant. Each block consisted of 140 trials. In 120 trials, non-target stimuli (strong vibrations) were delivered equiprobably to one of the three possible stimulus locations. In the remaining 20 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 8 trials, they were presented equiprobably to one of the two irrelevant locations, and thus had to be ignored. Vocal response times (RTs) were measured relative to the onset of each vibratory stimulus.

Electroencephalography (EEG) was recorded with Ag–AgCl electrodes and linked-earlobe reference from midline electrodes FPZ, Cz, Pz and Oz, from electrodes F3, F7, FC5, T7, C3, CP5, P3, P7 and OL (halfway between O1 and P7) over the left hemisphere and from the homologous electrode sites over the right hemisphere. Horizontal electrooculogram (HEOG) 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. Trials with eyeblinks, horizontal eye movements or muscle artifacts were excluded. ERPs to non-target stimuli (strong vibrations) were averaged relative to a 100 ms pre-stimulus baseline for all combinations of stimulated hand, attended location and stimulation location. ERP mean amplitudes were computed within measurement windows centered on the latency of the somatosensory P100 and N140 components (90–115 and 120–145 ms post-stimulus, respectively), and for a 200–300 ms post-stimulus interval.

Statistical analyses of ERP data were performed separately for midline electrodes (FZ, CZ, PZ), and for lateral electrodes located close to somatosensory cortex over the left and right hemisphere (F3, F4, FC5, FC6, C3, C4, CP5, CP6, P3, P4). Peak values for early somatosensory components (P100 and N140) and mean amplitude values (see above for time ranges) were analyzed with analyses of variance with group (blind/sighted) as a between-subject factor and attention (stimulus at currently attended/unattended location), stimulus location (1/2/3), stimulated hand (left/right), electrode site and hemisphere (left/right, for lateral electrodes only) as within-subject factors. A preliminary statistical analysis performed for the blind group found no main effects or interactions caused by hand dominance (Braille reading hand versus other hand, see Table 1 for participants' handedness), and this factor was therefore not included in the main analyses.

RTs and error rates were analyzed with analyses of variance with group as between-subject factor, and hand and location as within-subject factors. For all analyses, Greenhouse–Geisser adjustments to the degrees of freedom were performed when appropriate.

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