

The Involvement of Occipital Cortex in the Early Blind in Auditory and Tactile Duration Discrimination Tasks

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Abstract

■ Early blind participants outperform controls on several spatially oriented perceptual tasks such as sound localization and tactile orientation discrimination. Previous studies have suggested that the recruitment of occipital cortex in the blind is responsible for this improvement. For example, electroencephalographic studies showed an enlarged posterior negativity for the blind in these tasks compared to controls. In our study, the question was raised whether the early blind are also better at tasks in which the duration of auditory and tactile stimuli must be discriminated. The answer was affirmative. Our electroencephalographic data revealed an enlarged posterior negativity for the blind relative to controls. Source analyses showed comparable solutions in the

case of auditory and tactile targets for the blind. These findings support the interpretation of these negativities in terms of a supramodal rather than a modality-specific process, although confirmation with more spatially sensitive methods seems necessary. We additionally examined whether the early blind are less affected by irrelevant tactile or auditory exogenous cues preceding auditory or tactile targets than controls. No differences in alerting and orienting effects of these cues were found between the blind and the controls. Together, our results support the view that major differences between early blind participants and sighted controls on auditory and tactile duration discrimination tasks relate to a late and likely supramodal process that takes place in occipital areas. ■

INTRODUCTION

Neuroimaging studies of blind participants provide an important source of evidence regarding the plasticity of human cerebral cortex (e.g., see Pascual-Leone, Amedi, Fregini, & Merabet, 2005; Sathian, 2005). Specifically, studies on the early and congenitally blind revealed that occipital cortex is involved when performing tasks ranging from sound localization to the retrieval of information from verbal or episodic memory. This occipital involvement appears to be related to improved abilities for the blind compared to sighted controls on these tasks (see Gougoux, Zatorre, Lassonde, Voss, & Lepore, 2005; Amedi, Raz, Pianka, Malach, & Zohary, 2003). However, the scientific understanding of the specific function(s) reflected by these occipital activities in the blind is limited. Sathian (2005) remarks: "... we are left with the impression that visual cortex may participate in linguistic as well as sensory processing in the blind. Whether these various functions are subserved by the same or segregated sets of neurons, as well as the neural mechanisms that mediate such plasticity, are completely unknown ..." (p. 283).

Several studies have shown that the early blind perform better than sighted controls on a range of auditory and tac-

tile tasks. Blind participants display superior auditory localization abilities when attending to sounds in peripheral space (Röder et al., 1999) and are better able to discriminate pitch (Gougoux et al., 2004). Imaging studies with the blind (Collignon, Lassonde, Lepore, Bastien, & Veraart, 2007; Weaver & Stevens, 2007; Gougoux et al., 2004, 2005; Kujala et al., 2005) point to the crucial involvement of occipital cortex in auditory tasks in these subjects. Similar to the approach of the present study, several studies (e.g., Liotti, Ryder, & Woldorff, 1998; Kujala et al., 1995, 1997; Röder, Rösler, Hennighausen, & Näcker, 1996) employed event-related potentials (ERPs), a measure that can be derived from the electroencephalogram (EEG). These studies showed that the N2b component,¹ or a slow negativity starting simultaneously with the N2b component at about 200 msec after stimulus onset, exhibited a more posterior scalp distribution in the early blind than in sighted controls.

Liotti et al. (1998) examined the congenitally blind and controls in an auditory oddball task with standard and deviant target tones that were either to be attended or to be ignored, with attended target tones requiring a button press. For ignored tones and attended standards, no ERP group differences were found, which suggests no differences in early sensory processes (see also Röder et al., 1996) and no differences in sustained attention between the blind and the sighted (but see Alho, Kujala, Paavilainen, Summala, & Näätänen, 1993). However, target-specific

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processing (attended targets minus attended standards) resulted in an enhanced posterior slow negativity for the blind that spanned 200–400 msec, overlapping in time with the N2b and the P3b components. Liotti et al. additionally observed that the group difference had a left-hemispheric maximum, which might signify that this hemisphere is reorganized to a larger extent than the right hemisphere.

Improved tactile abilities in the blind also appear to be related to processes that occur in occipital areas. Cohen et al. (1997) revealed that transcranial magnetic stimulation (TMS) of occipital cortex of blind participants interfered with Braille reading. Furthermore, Hamilton, Keenan, Catala, and Pascual-Leone (2000) reported Braille alexia in a blind woman who was a proficient Braille reader before a stroke to occipital areas (for other evidence, see Ptito, Fumal, de Noordhout, Schoenen, & Kupers, 2008; Wittenberg, Werhahn, Wassermann, Herscovitch, & Cohen, 2004; Goldreich & Kanics, 2003; Weeks et al., 2000). ERPs elicited by tactile targets showed a comparable group difference (an enhanced posterior negativity for the blind as compared to controls) as ERPs elicited by auditory targets (Röder et al., 1996; Kujala et al., 1995).

Interestingly, Röder et al. (1996) compared the blind and controls in both a tactile and an auditory oddball task. In the tactile oddball task, a device was used for Braille reading that enabled the tactile presentation of lines of different orientations. Participants counted rare targets among rare backgrounds and frequent backgrounds. For the blind, a posterior negativity starting at approximately 200 msec was observed for rare tactile targets as compared to rare backgrounds (a so-called relevance effect); however, this effect was not observed with the controls. A similar but somewhat later effect, starting at approximately 350 msec, was found in the auditory task. Importantly, comparable topographies of these group-dependent relevance effects were observed, which led Röder et al. to conclude that it is unlikely that the occipital cortex of the blind participates in modality-specific information processing (for fMRI support, see Weaver & Stevens, 2007).

An interesting question regarding the nature of cortical reorganization of occipital areas in the blind concerns whether it is supramodal (e.g., see Renier et al., 2005; Wallace, Ramachandran, & Stein, 2004; Rauschecker, 1995) or remains modality-specific. As an extension of this first possibility, specific supramodal functions in the blind may be carried out in separate occipital areas (see Amedi et al., 2007). For example, one region (e.g., the right hemisphere) may be dedicated to more extensive processing of spatial features (e.g., relevant for orientation or shape), irrespective of input modality, whereas another region (e.g., the left hemisphere) may be specialized in temporal, abstract, or other nonspatial features (e.g., see Van der Lubbe, Schölvink, Kenemans, & Postma, 2006). A modality-specific conception, however, might state that separate occipital regions in the blind are engaged in advanced perceptual processing, with one area involved in tactile processing and another area involved in auditory

processing. For example, the similar locus in the occipital lobe for auditory functions (Collignon et al., 2007; Weeks et al., 2000) and verbal memory (Amedi et al., 2003) could be due to a shared process operating on the same type of codes. Namely, verbal memory may employ a rehearsal and/or retrieval mechanism that operates on acoustic-like codes, which is in line with the leading views on working memory (Baddeley, 2003), and these codes may also be involved in auditory localization or pitch discrimination.

In two EEG studies (Röder et al., 1996; Kujala et al., 1995), tactile and auditory oddball tasks were employed, and no support was obtained for the modality-specific conception. An advantage of the use of oddball tasks is that the contribution of motor processes is mostly minimal. Potentially relevant alterations in perception–action links, rather than pure perception-related changes, in the blind may, therefore, also remain unnoticed. For example, changes in occipital cortex of the blind could influence processing along the action-related dorsal path by enabling auditory and/or tactile stimuli to directly affect motor processes, which may be highly beneficial in the case of blindness. In the current study, we focus on tactile and auditory discrimination tasks that require a response on nearly every trial, thereby increasing the load on perception–action links. Several studies have demonstrated that the early blind outperform controls on tasks that emphasize spatial aspects (e.g., see Röder et al., 1999). However, whether this advantage for the early blind is also present in other stimulus features, such as stimulus duration, is unknown. Indeed, apart from space, time is likely to be a crucial dimension, and spatial and temporal features may differentially involve the left and right hemispheres (see above). An additional advantage of this feature is that it can quite easily be compared across the auditory and tactile modalities. Therefore, we examined whether the early blind outperform controls in auditory and tactile duration discrimination tasks, in which a response is required on every trial.

In separate auditory and tactile tasks, target stimuli were presented for either 100 or 175 msec. A first point of interest in our study concerned the possibility that the early blind are better at discriminating the duration of both auditory and tactile stimuli than controls. Second, we explored whether occipital cortex in the blind is involved in these tasks to a greater extent. This extra involvement may be reflected in an enhanced posterior negativity among the blind as compared to the controls in both tasks. Moreover, because the tasks were identical in all aspects (apart from the stimulus modality), the supramodal and modality-specific hypotheses can be examined. To tentatively answer the latter question, we determined the likely sources of recorded activity.

We applied up-to-date correction methods for eye movements and other artifacts (Ille, Berg, & Scherg, 2002), and improved source localization techniques (Frishkoff, Tucker, Davey, & Scherg, 2004). In addition to indicating potentially relevant brain areas, source analyses circumvent the common problem encountered with ERP components

that one component likely reflects several simultaneously active processes (e.g., see Luck, 2005). Decomposition of ERPs into separate source waveforms related to specific brain areas facilitates the interpretation of effects on specific ERP components and enables more straightforward conclusions than a comparison of ERP topographies (as was done in the study by Röder et al., 1996). In the auditory task, we expected to observe the P50, N1, and P2 ERP components (which likely originate from frontal and auditory cortex; Weisser et al., 2001; Tarkka, Stokić, Basile, & Papanicolaou, 1995) in the early blind and controls, followed by N2 and P3b components, with an enhanced posterior slow negativity in the blind (see Liotti et al., 1998). In the tactile task, we expected to observe several early components (P1, N1, P2; originating from primary and secondary somatosensory areas; Thees, Blankenburg, Taskin, Curio, & Villringer, 2003) for both groups, followed by N2 and P3b components, with an enhanced posterior slow negativity in the blind.

Blocking of To-be-ignored Stimuli in the Blind

The sections above highlight that major differences between the blind and the controls in terms of auditory and tactile processing may be related to a relatively late process that is carried out in occipital cortex. Earlier research on neural plasticity (mostly based on animal studies), however, indicates that rewiring might occur in structures that are often related to spatial attention such as superior colliculus, thalamus, and parietal cortex (e.g., see Karlen, Kahn, & Krubitzer, 2006; Bavelier & Neville, 2002).² These structures are thought to play an important role in orienting attention towards sudden changes in the environment, such as stimulus onsets (see Rafal, Posner, Friedman, Inhoff, & Bernstein, 1988). Interestingly, recent studies suggest that the early blind are more efficient at blocking an irrelevant modality (Hötting & Röder, 2004; Hötting, Rösler, & Röder, 2004), which may be related to changes in the aforementioned structures. Typically, a stimulus of a task-irrelevant modality (e.g., a sound) pulls attention to its location, thereby accelerating the processing of a subsequent relevant (e.g., visual) stimulus at a nearby location (so-called cross-modal exogenous orienting effects, e.g., see Van der Lubbe & Postma, 2005). This idea of more efficient blocking of irrelevant stimuli in the early blind might imply a reduction of cross-modal exogenous orienting effects. In our two tasks, this was additionally examined by presenting to-be-ignored left or right cues in one modality before presenting a target to the left or right in another modality on a specific proportion of trials. The position of the cue was unpredictable about the target location, and target modality and cue modality were blocked per task. In one task, tactile cues (or no cues) preceded auditory targets, and in another task, auditory cues (or no cues) preceded tactile targets. This manipulation of cues may result in improved performance when the cue and the target originate from the same location as compared to when they originate from different

locations: a so-called cross-modal exogenous orienting effect (for a review, see Spence, 2002). Thus, we additionally examined whether cross-modal exogenous orienting effects (from the tactile to the auditory modality and vice versa) were reduced in the early blind, which may be due to changes in structures related to spatial attention.

METHODS

Participants

Informed consent was obtained from 24 participants, 12 early blind (for details, see Table 1) and 12 sighted controls (matched on age, education, and sex). The handedness of each participant was assessed with Annet's Handedness Inventory (Annet, 1970). Analyses of variance (ANOVAs) confirmed that no age (36 vs. 35 years) or intelligence differences (scores on the vocabulary subtest of WAIS III, 3rd edition) were present between the groups ($p > .12$). In the control group (all right-handed), six women participated, whereas in the blind group (2 left-handed, 3 ambidextrous, 7 right-handed), seven women were involved. All participants were in good physical health and reported no history of psychiatric or neurological disorder, apart from the disorder that led to blindness. The blind were recruited with the help of Bartimeus Institute for the Blind and Poor Sighted in Utrecht. All participants were paid for their participation of approximately 5 hours. The study was approved by the ethics committee of the Faculty of Social Sciences of the University of Utrecht, and was performed in line with the Declaration of Helsinki.

Stimuli, Procedure, and Design

Tactile vibrations (100 Hz) were applied for 100 or 175 msec to the left and right index fingers by a vibrator normally used in cell phones. Auditory stimuli, bursts of pink noise (70 dB), were presented for either 100 or 175 msec from two boxes at an angle of approximately 30° to the left or right of the participant. The boxes were placed on a table in front of the participant at a distance of 75 cm. The participant's hands were located at a comfortable position on the table at a small distance in front of the boxes. Left or right foot responses were required on separate footpads located on the floor, which were placed roughly 30 cm apart.

Separate tactile and auditory duration discrimination tasks were conducted, with the order of tasks balanced across participants. Each task consisted of three separate equally sized consecutive blocks of 350 trials. In the tactile task, participants were instructed to perform a left or right foot press to tactile targets of 100 or 175 msec, respectively. The intertrial interval for these 1050 trials amounted to 2900 msec. In a subset of 600 trials, tactile targets, presented to the left or right, were preceded by to-be-ignored auditory cues of 100 msec to the left or right (i.e., a cross-modal cue). Each combination of cue and target side was equiprobable; trials in which the cue and target sides were

Table 1. Details of the Early Blind Participants

No.	Sex	Age	Hand	Education	WAIS III	Etiology	Onset
1	F	27	R	University	51	Retinopathy of prematurity	0
2	M	46	R	Higher level	59	Amaurosis congenita von Leber	3 months
3	F	20	R	Medium level	45	Glaucoma	<7 years
4	F	35	R	Higher level	61	Retinopathy of prematurity	0
5	F	32	A	Higher level	54	Retinopathy of prematurity	0
6	M	37	L	University	55	Bilateral anophthalmia	0
7	F	35	R	Higher level	50	Retinopathy of prematurity	0
8	F	38	A	–	58	Amaurosis congenita von Leber	<7 years
9	F	42	R	–	58	Congenital retinitis pigmentosa	<7 years
10	M	40	A	Higher level	55	Amaurosis congenita von Leber	<1 year
11	M	51	L	University	63	Glaucoma	<7 years
12	M	34	R	Higher level	53	Glaucoma	<7 years

Handedness was scored as left-handed, ambidextrous, or right-handed (L/A/R). The educational history of two participants could not be retrieved, but scores on the verbal subtest of the WAIS III indicate that their mental capacities were comparable to the other participants. Several of the blind participants reported that they were able to distinguish between light and dark.

the same are denoted as validly cued targets and trials in which these sides were different are denoted as invalidly cued targets. In validly and invalidly cued trials, the time interval (stimulus onset asynchrony) between the cue and the target amounted to 200 msec. In another subset of 300 trials, left or right tactile targets occurred without a preceding cue (the trials used for EEG analyses). In addition to these 900 target trials, another 150 trials were presented in which only auditory cues were presented to the left or right. All abovementioned trial types (validly/invalidly cued tactile targets, tactile targets without preceding cues, and auditory cues alone) varied randomly from trial to trial within three separate blocks of 350 trials.

In the auditory task, the same procedure was applied as in the tactile discrimination task, but now responses were to auditory targets of 100 or 175 msec. In the subset of 600 target trials with “to-be-ignored” cues and 150 cue-only trials, tactile vibrations were presented to the left or right index finger for a duration of 100 msec.

Before the start of each task, participants performed some practice trials to become acquainted to the task and to check whether performance was in accordance with the instructions.

Apparatus and Data Recording

Participants wore an elastic cap (BrainCap, Brain Products GmbH, Germany) with 64 Ag/AgCl ring electrodes, and were seated in a chair in a silent, darkened chamber. The lights were only on during rest periods or breaks for the electrode impedances to be checked. A cross-modal experimental system controlled stimulus presentation (see Van der Lubbe & Postma, 2005). The “Vision Recorder”

software package (version 1.0b Brain Products GmbH) recorded participants’ EEG, electrooculogram (EOG), and the codes of all relevant events. The EEG electrodes were located at standard sites on the scalp according to the extended 10–20 system. Cz was used as an on-line reference, but off-line, an average reference was employed. The EOG was recorded vertically by electrodes placed above and below the left eye, and horizontally by electrodes located at the outer canthi of both eyes. EEG and EOG signals were amplified using a BrainAmp amplifier (Brain Products GmbH) at a rate of 250 Hz, and were digitally filtered (TC = 5.0 sec, low-pass filter of 100 Hz, notch filter of 50 Hz). Electrode resistance was kept below 10 k Ω .

Data Analyses

Reaction time (RT) was defined as the time interval from target onset until the first response. For each participant, average RTs were computed for each condition and task. Trials containing responses that were not too fast, too slow (RT > 100 msec and RT < 1500 msec), or incorrect were included in the analysis. The proportion of correct responses (PC) was defined as the proportion of trials that fulfilled the previous criteria out of the total number of trials per condition, which was determined for each participant.

EEG analyses were carried out using the BESA (version 5.1.6, MEGIS Software GmbH, Germany) software package. For the ERP analyses, EEG was corrected for EOG artifacts using the adaptive method (Ille et al., 2002). This method employs principal component analyses (PCA) to model brain activity, and has the advantage that brain activity will be retained after artifact correction even when artifact and

brain activity are spatially correlated, unlike procedures based on regression methods. Correction for EOG artifacts was done with the surrogate method (Berg & Scherg, 1994), which uses a source model to account for the eye-movement artifact. Trials with other recording artifacts (amplitude 120 μV , gradient 75 $\mu\text{V}/\text{step}$, low activity for 100 msec) were discarded from the analyses. For tactile targets without preceding cues (150 trials per target location), this procedure retained, on average, 92.6% (min to max: 69–100%) of the trials. For auditory targets without preceding cues, this procedure retained 92.5% (79–100%) of the trials. Individual ERPs were identified from -100 to 500 msec relative to target onset for each target modality and target location. Analyses were restricted to targets without preceding cues to avoid a possible confound resulting from overlap and interactions with the cues. Separate statistical analyses were performed on mean individual activity within 20 msec windows with the within-subject factors electrode (Fp1, AF7, AF3, F7, F5, F3, F1, FT7, FC5, FC3, FC1, T7, C5, C3, C1, CP5, CP3, CP1, P7, P5, P3, P1, PO7, PO3, and O1), hemisphere (left/right; a total of 50 electrodes), stimulus side (left/right), and the between-subjects factor group (early blind vs. controls).

For the source analyses, the four-shell spherical head model (brain, cerebrospinal fluid, skull, and skin) was used, including all 59 EEG electrodes. Regional sources (Frishkoff et al., 2004) were determined for individual ERPs. Source parameters were estimated for symmetrical source pairs with independent source orientations for activity within time intervals from 0 to 400 msec after stimulus onset. In the case of auditory stimuli, there is evidence for the early involvement of generators in temporal and frontal areas (Weisser et al., 2001; Tarkka et al., 1995). Given the probable later involvement of occipital areas, a model with three symmetrical source pairs was expected to be sufficient. A PCA of the grand averages per condition and group checked the validity of this approach. Determination of the time windows for the fitting procedure (see Results) was based on inspection of the global field power (GFP: the sum of squared activity over all channels) of the grand averages, and was chosen from the onset of a peak in the GFP to its maximum. An extension of a sequential fitting procedure was subsequently applied to single-subject averages. One symmetrical source pair was fitted to the first time window, a second pair to the second time window, and so forth. This fitting procedure was repeated until a stable solution was obtained. In the case of tactile ERPs, we also expected a solution with three source pairs to be sufficient (e.g., see Thees et al., 2003), which was examined by a PCA by condition and group.

Source waveforms were further analyzed by computing the root-mean-square across the three orthogonal vectors for contralateral and ipsilateral sources per individual. This measure has been argued to represent an equivalent of neural activity (see Frishkoff et al., 2004).

Statistical analyses were additionally employed on source waveforms for the time windows in which an interaction involving the factors electrode and group on the ERPs was found. Finally, averages of these individual estimated source waveforms per condition and group were computed.

In all statistical analyses, repeated measures ANOVAs were employed, unless otherwise specified, and whenever applicable, the Greenhouse–Geisser ϵ correction was used to correct for violations of the sphericity assumption.

RESULTS

Behavior

Early blind participants responded faster [$F(1, 22) = 8.5, p < .01$] and more accurately [$F(1, 22) = 7.9, p < .011$] than controls, both in the tactile and the auditory tasks (see Table 2). In the tactile task, responses of the blind were 70 msec faster and 10.6% more accurate than those of controls, and in the auditory task, they were 93 msec faster and 5.1% more accurate than controls.

Duration discrimination was more difficult for tactile than for auditory targets; responses to tactile targets were slower [$F(1, 22) = 44.2, p < .001, 826$ vs. 709 msec] and less accurate [$F(1, 22) = 32.6, p < .001, 80.3$ vs. 93.4%] than responses to auditory targets. These effects, however, were unaffected by blindness [$F(1, 22) < 1.4, p > .24$]. Cross-modal cueing (Δ cue, see Table 2) resulted in faster responses for validly than for invalidly cued targets [$F(1, 22) = 43.8, p < .001$]. This cueing effect was of comparable magnitude for both tasks and was unaffected by blindness [$F(1, 22) < 1.1$]. With regard to accuracy, cueing resulted in slightly more accurate behavior for controls (although separate effects per task were small and nonsignificant; see Table 2), whereas no effect was observed for the early blind [$F(1, 22) = 5.7, p < .026, \text{Cue} \times \text{Group}$]. Responses to targets preceded by cues were faster than responses to targets not preceded by cues (a warning effect, Δ warn; see Table 2) [$F(1, 22) = 12.6, p < .002$], and this effect was unaffected by blindness [$F(1, 22) = 2.1, p > .15$]. This effect was larger when tactile targets were preceded by auditory cues than when auditory targets were preceded by tactile cues [$F(1, 22) = 7.2, p < .014$]. The presence of auditory cues resulted in more accurate responses for tactile targets, but the presence of tactile cues resulted in less accurate responses for auditory targets [$F(1, 22) = 11.7, p < .003$].

Event-related Potentials

Auditory Targets

For auditory targets (see Figure 1), an early P50 component, a contralaterally enlarged N1 component, and possibly group-dependent P2 and N2 components were distinguished. An occipital slow negativity seems larger

Table 2. Behavioral Results as a Function of Task and Group (Early Blind vs. Controls) with Mean Reaction Times (RT) and Proportion of Correct Responses (PC) and Their Standard Errors (in Parentheses)

	<i>Tactile Duration Discrimination</i>				<i>Auditory Duration Discrimination</i>			
	<i>Controls</i>		<i>Early Blind</i>		<i>Controls</i>		<i>Early Blind</i>	
	<i>RT (msec)</i>	<i>PC (%)</i>	<i>RT (msec)</i>	<i>PC (%)</i>	<i>RT (msec)</i>	<i>PC (%)</i>	<i>RT (msec)</i>	<i>PC (%)</i>
Validly cued	855 (25)	76.5 (3.6)	766 (25)	85.7 (3.6)	732 (23)	91.2 (1.7)	670 (23)	95.2 (1.7)
Invalidly cued	871 (25)	75.1 (3.3)	780 (25)	86.2 (3.3)	745 (22)	89.5 (1.6)	679 (22)	95.9 (1.6)
No-cue	892 (23)	73.4 (3.2)	794 (23)	84.9 (3.2)	754 (24)	91.8 (1.5)	672 (24)	96.9 (1.5)
Δ cue	16***	-1.4	14***	0.5	14**	-0.7	9*	0.7
Δ warn	29**	-2.4*	21*	-1.1	15*	1.4**	-3	1.3***

Cross-modal cueing effects on RT and PC are reflected in the difference between validly and invalidly cued target locations (Δ cue), whereas no-cue conditions indicate that the target stimulus was not preceded by a cue. A comparison of the no-cue condition with the mean of the cue conditions (Δ warn) indicates whether responses were faster (positive) or more accurate (negative) due to alerting effects of the cue. Results of one-tailed *t* tests [the predicted direction is invalidly cued > validly cued, and no-cue > (validly cued + invalidly cued)/2] are additionally indicated.

**p* < .05.

***p* < .01.

****p* < .005.

for the blind than for controls, which resembles the results of Liotti et al. (1998).

Activity was initially largest above contralateral central areas (C3 and C4), being reflected in an interaction between the factors stimulus side, electrode, and hemisphere from 60 to 160 msec [$F(24, 258) > 5.9, p < .001$], which concerns the lateralized effect on the N1 component. An interaction with the additional factor group (Stimulus side \times Electrode \times Hemisphere \times Group) was found from 120 to 180 msec [$F(24, 528) > 2.7, p < .05$], and was most significant from 160 to 180 msec [$F(24, 528) = 4.4, p < .008$]. The latter effect reflects a reduced P2 component for the early blind as compared to controls above centroparietal areas (see Figures 1 and 2), which was slightly dependent on the side of the auditory stimulus. From 220 to 500 msec, an interaction between stimulus side, electrode, and hemisphere was found [$F(24, 528) > 2.7, p < .05$]. This effect differed between groups from 240 to 500 msec [$F(24, 528) > 3.4, p < .01$], and was most significant from 320 to 340 msec [$F(24, 528) = 7.3, p < .001$]. The latter results reflect an enhanced occipital negativity for the blind as compared to the controls (most clearly visible on the O2 electrode; see Figure 1), which appears largest above the right hemisphere.

Tactile Targets

For tactile targets (see Figure 3), a contralateral P1 component was followed by an occipital P2 component, which appeared to be reduced in the blind as compared to controls. Next, an occipital N2 component (or a slow negativity) peaking at approximately 300 msec was visible, which was larger for the blind than for controls.

Activity was initially largest above the contralateral centro-parietal areas, which resulted in a significant inter-

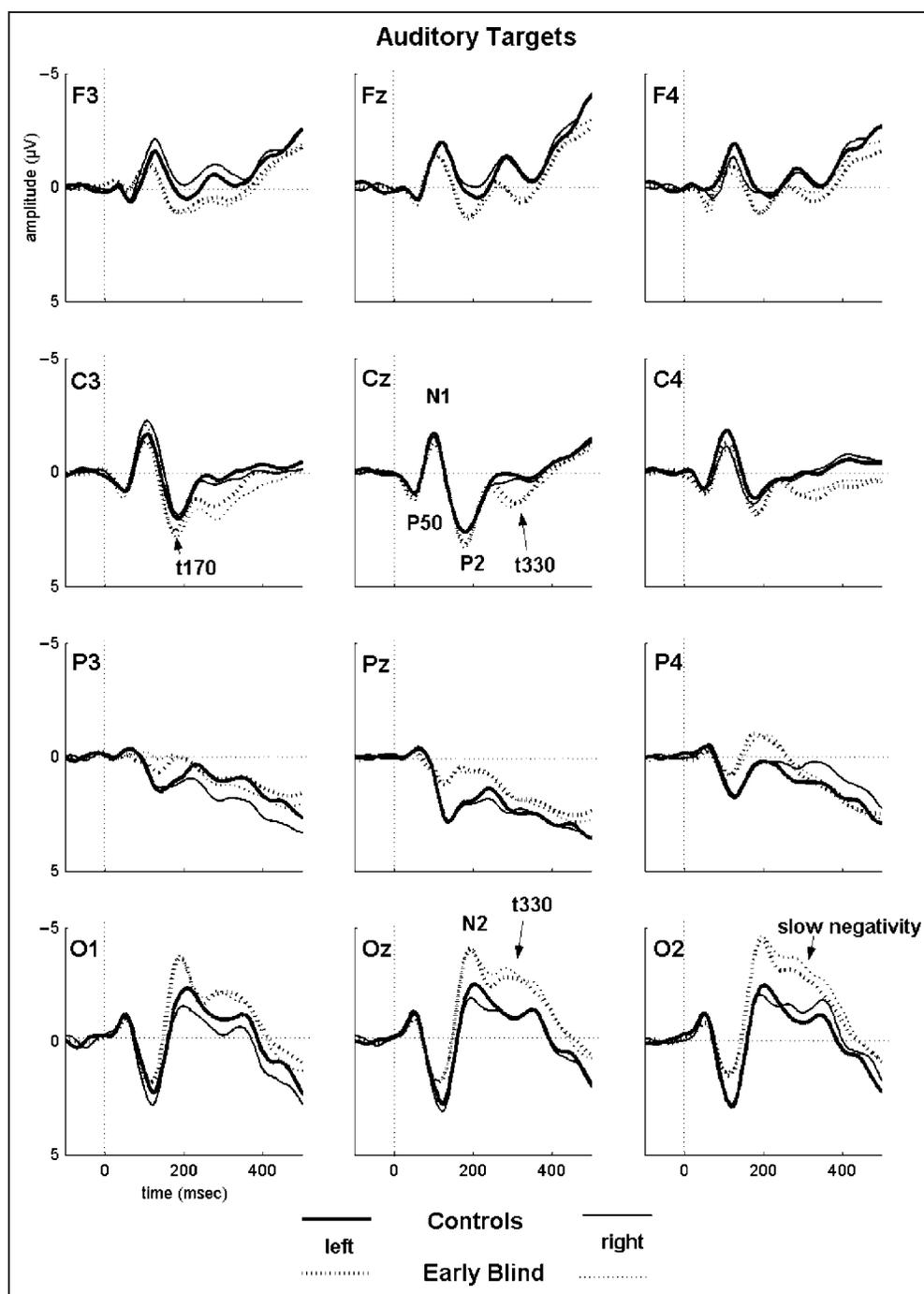
action between stimulus side, hemisphere, and electrode from 60 to 440 msec [$F(24, 528) > 3.3, p < .05$]. This effect not only concerns the contralateral enhanced P1 component but additionally marks the start of stimulus-side dependent differences that continue up to the occipital N2 component. This stimulus-specific effect differed between groups from 380 to 400 msec [$F(24, 528) = 3.3, p < .04$; indicated as t390], with extra involvement of posterior areas in the blind, and was slightly dependent on stimulus side and relevant hemisphere (Figure 4). Apart from this stimulus-specific effect, focal activity from 260 to 320 msec differed between groups [Electrode \times Group: $F(24, 528) > 3.6, p < .05$], and was most significant from 280 to 300 msec [$F(24, 528) = 3.8, p < .015$, indicated as t290]. Inspection of the maps (Figure 4) shows a parietal positivity and increased negativity particularly above right occipital areas for the early blind as compared to controls. This increased negativity reflects the enlarged N2 component for the early blind compared to controls.

Source Analyses

Auditory Targets

A PCA on the grand averages (averaged across stimulus side) revealed that three components (controls: 55.2%, 37.6%, 5.6% for the first, second, and third component, respectively; blind: 85.9%, 6.3%, 4.3%) accounted for at least 96.5% of the variance within the 32–396 msec interval. Inspection of the GFP indicated that three time windows were most appropriate for our fitting procedure: (1) 32–56 msec, (2) 80–192 msec, and (3) 248–396 msec. No stable solution was obtained for one blind participant; therefore, this participant was excluded from further analyses. After finalizing the fitting procedure, the average and standard error (in brackets) of residual variance for controls and

Figure 1. ERPs elicited by auditory targets displayed for frontal, central, parietal, and occipital electrodes. Locations of these electrodes on the scalp are indicated in Figure 2. Negativity is up. The windows of clear significant group differences are indicated as t170 and t330.



the early blind for activity from 32 to 396 msec amounted to 3.3% (0.4) and 3.0% (0.4), respectively.

In Figure 5 (left), the average source locations (averaged across side of target presentation), which account for activity induced by the auditory targets from 32 to 396 msec, are displayed for the early blind (b1, b2, b3) and control groups (c1, c2, c3). The first anterior source (green; b1/c1) accounts for activity within the first time window that contained the P50. The second central source (red; b2/c2) accounts for activity within the second time window that contained the N1 and P2 components and was localized in auditory cortex (see Weisser et al., 2001;

Tarkka et al., 1995). A third posterior source (brown; b3/c3) accounts for activity within the third time window that contained the N2 component and the slow negativity.

A multivariate analysis of variance (MANOVA) on estimates along the x -axis (lateral–medial), the y -axis (anterior–posterior), and the z -axis (superior–inferior) with the factors group, stimulus side, and source (3) on Cartesian head system coordinates, confirmed that sources differed in their estimated locations [$F(6, 16) = 4.3, p < .01$]. However, they revealed neither a group effect [$F(3, 19) = 2.7, p > .07$] nor an interaction with the factor group [$F < 1.7, p > .18$]. Nevertheless, a comparison of the group

effect per axis showed that sources were located more superior for the early blind than for controls [$F(1, 21) = 8.4, p < .01$], although separate analyses per source only revealed a significant difference for the central source [$F(1, 21) = 4.4, p < .05$] and not for the other sources [$F < 0.8$].

The source waveforms for the three different source pairs are displayed in Figure 6. The first source pair displays a peak in activity at approximately 50 msec, the second source pair shows a peak in activity at approximately 110 msec, and the third source pair shows the greatest activity at approximately 300 msec. An analysis on activity from 160 to 180 msec (the P2) with the factors target side, hemisphere, source, and group revealed that the

central source pair (b2/c2), likely located in the auditory cortex, was more active than the anterior and the posterior source pairs [$F(2, 42) = 8.6, p < .002$]. In addition, a nearly significant interaction was observed between target side, hemisphere, and group [$F(1, 21) = 3.9, p < .07$], which might reflect stronger hemispherical differences as a function of target side for controls as compared to the blind (see sources b2/c2). A separate analysis for the central source pair, however, showed no significant interaction between target side, hemisphere, and group [$F(1, 21) = 3.2, p > .085$]. An analysis on activity from 320 to 340 msec (the N2) revealed a main effect of source [$F(2, 42) = 5.1, p < .015$], which

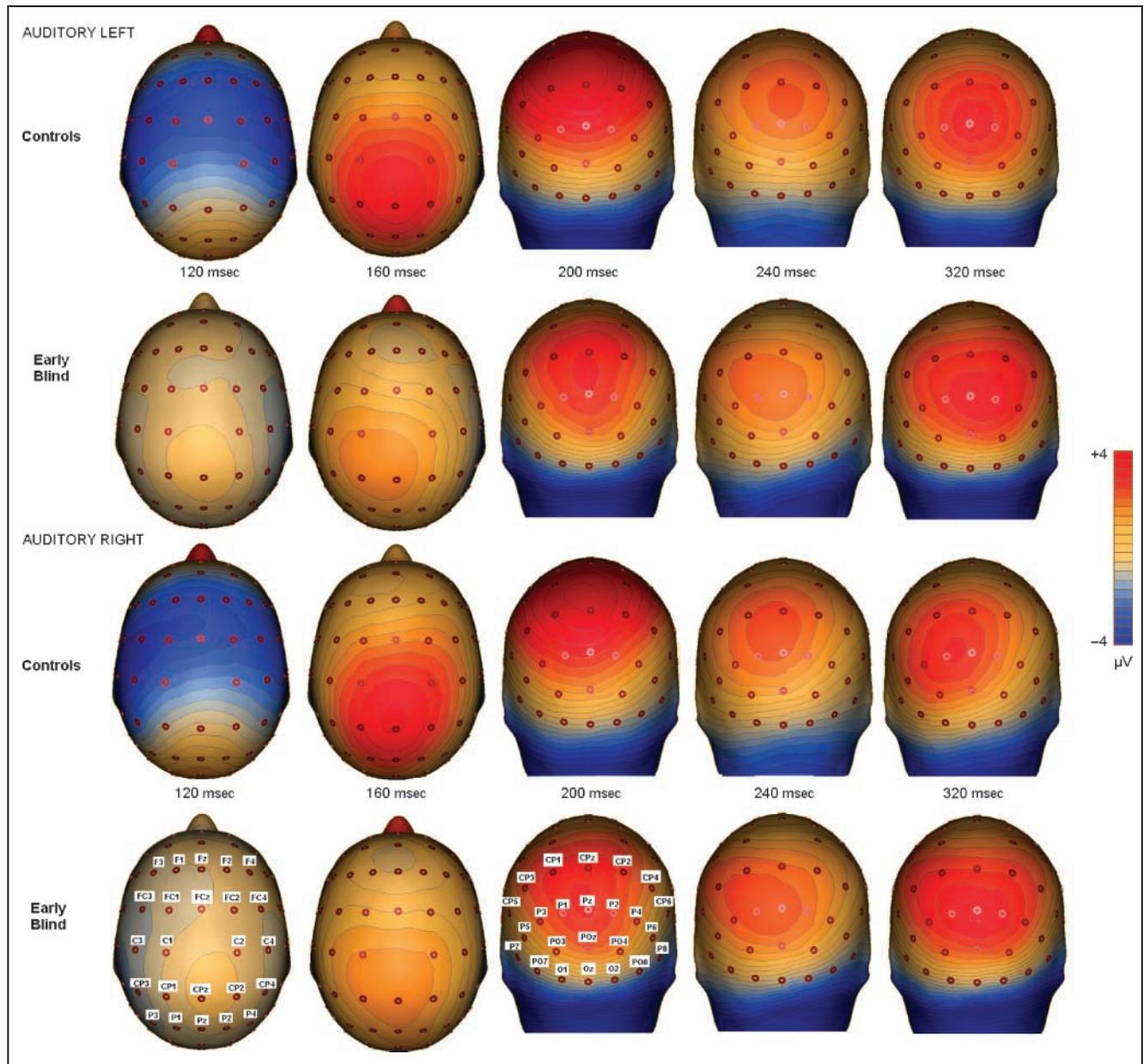
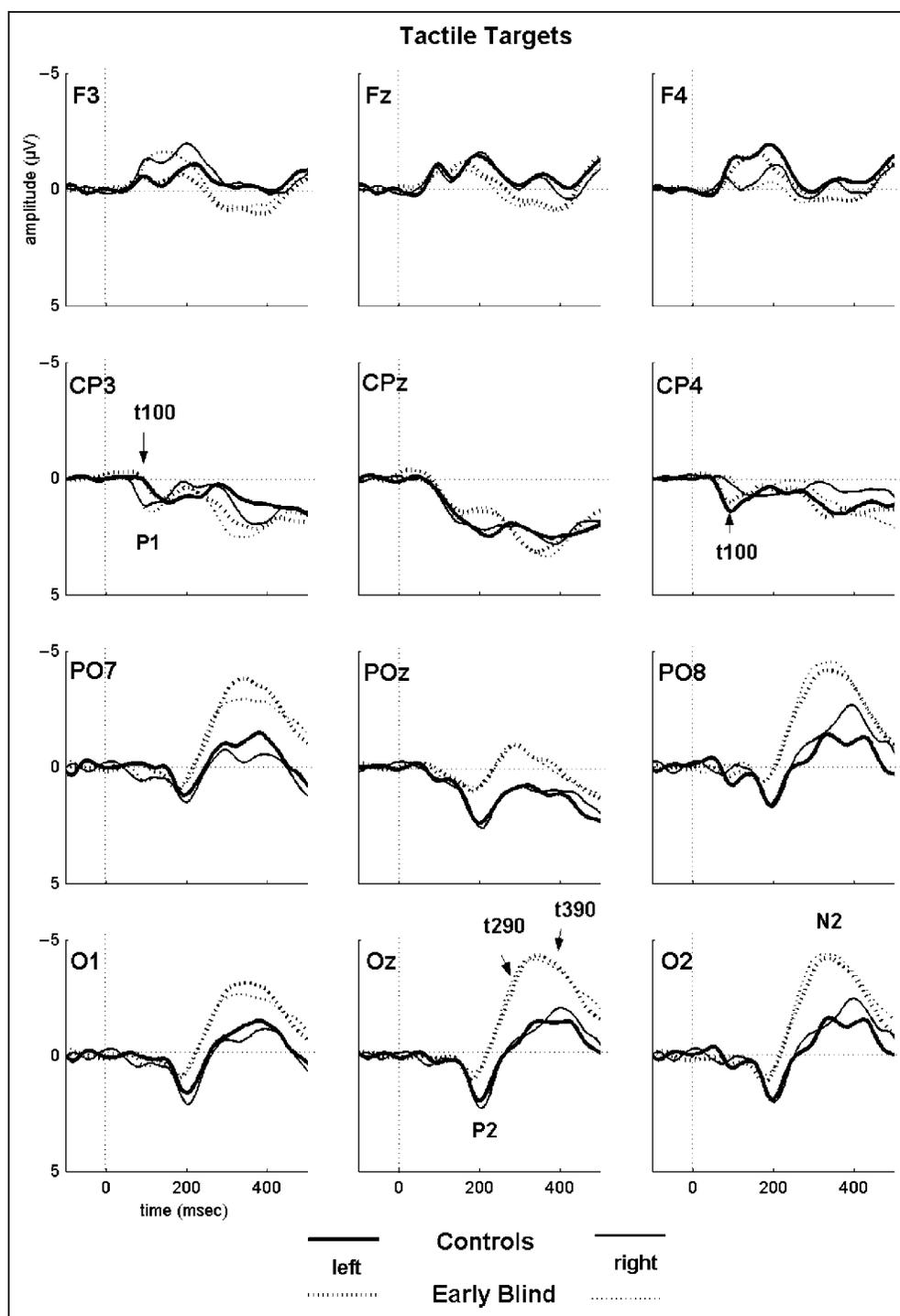


Figure 2. Topographic distributions (isopotential maps) at several relevant moments after onset of the auditory targets are displayed. The two left columns are top views and the three right columns are back views of the head. The upper two rows are the maps for auditory targets presented at the left, and the lower two rows are the maps for auditory targets presented at the right. Electrode labels are indicated in the lower row.

Figure 3. ERPs after tactile targets displayed for frontal, centro-parietal, parieto-occipital, and occipital electrodes. A clear stimulus-side dependent effect was found at 100 msec (t_{100}); group differences were found starting at 260 msec after stimulus onset, and were clearly significant at parieto-occipital and occipital electrodes (indicated as t_{290} and t_{390}).



reflected largest activity of the posterior source pair (b3/c3) and a nearly significant interaction between side of target presentation, hemisphere, and group [$F(1, 21) = 3.6, p < .07$]. The latter interaction may indicate that specifically for the early blind, activity in the right hemisphere (contralateral to stimulus side) increases when a left target is presented. A separate analysis for activity from the posterior source, however, revealed no significant effect involving the factor group [$F(1, 21) < 1.8, p > .19$].

This absence of an occipital group difference may be due to heterogeneity within the blind group.

In the left panel of Figure 7, the individually estimated source locations (b3) for the blind are displayed. These data show that for several individuals, sources were localized in occipital areas; however, this was not observed for all individuals. This pattern indicates that the group of early blind is, indeed, heterogeneous. These results raised the question of whether the absence of a clear

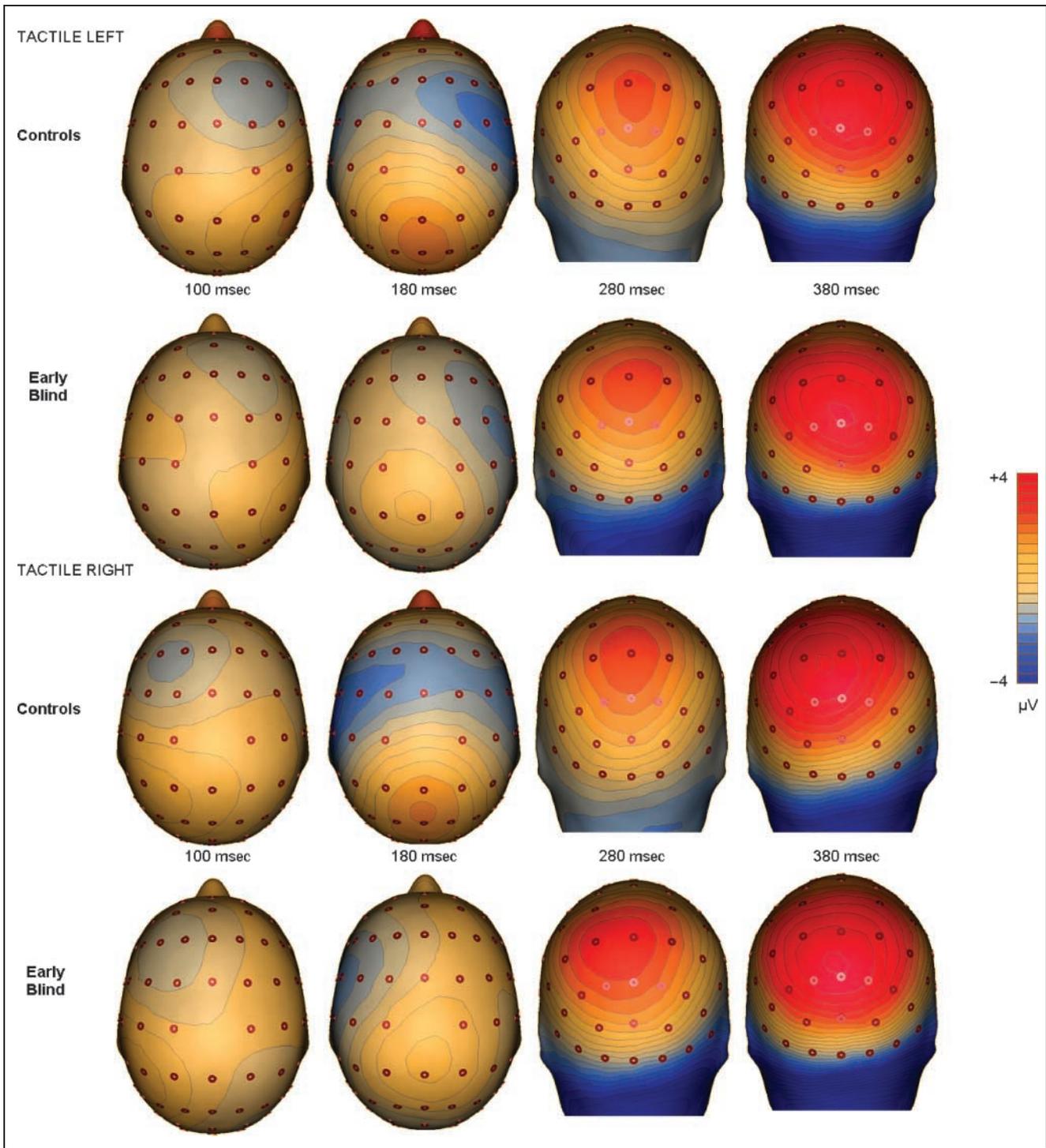


Figure 4. Topographic distributions at several relevant moments after onset of the tactile targets are displayed. The two left columns are top views and the two right columns are back views of the head. The upper two rows are the maps for tactile targets presented at the left, and the lower two rows are the maps for tactile targets presented at the right. Electrode labels are indicated in Figure 2.

recruitment of posterior areas in some of our blind participants was related to their performance. Namely, Gougoux et al. (2005) and Amedi et al. (2003) observed that extra recruitment of posterior areas was related with performance differences between the blind themselves. In line with these observations, a more posterior locus of this third source (the values along the *y*-axis) proved to be related to more

accurate performance on the auditory duration discrimination task ($r = -.77, p < .004$, one-tailed).

Tactile Targets

A PCA on the grand averages revealed that three components (controls: 75.1%, 20.7%, 2.7%; blind: 90.5%, 4.9%,

2.2%) accounted for at least 97.6% of the variance within the 68–396 msec interval. The following time windows were identified: (1) 68–96 msec (b1/c1), (2) 124–192 msec (b2/c2), and (3) 248–396 msec (b3/c3). No stable outcome was obtained for one blind participant (the same participant as in the case of auditory targets). These data were omitted from further analyses. After finalizing the fitting procedure, residual variance for controls and the early blind for the entire time window from 68 to 396 msec amounted to 3.3% (0.6) and 4.2% (0.6), respectively.

Average source locations are displayed in Figure 5 (right). The first (b1/c1) and the second source pairs (b2/c2), which are related to the P1 and P2 ERP components, seem to originate from primary and/or secondary somatosensory areas. In contrast, the third source pair, related to the posterior N2, originates from temporal cortex in controls (c3) and occipital cortex in the blind (b3).

A MANOVA confirmed that sources differed in their estimated locations [$F(6, 16) = 9.2, p < .001$], and revealed

a nearly significant interaction between group and source [$F(6, 16) = 2.5, p < .07$]. Separate analyses for the y -axis showed a significant interaction between source and group [$F(2, 42) = 5.3, p < .011$]. A MANOVA on the source pair related to the posterior N2 component confirmed that the location of this source pair (b3/c3) differed between groups [$F(3, 19) = 4.6, p < .015$]. A separate ANOVA on the y -axis indicated that this source was, indeed, more posterior for the early blind than for controls [$F(1, 21) = 12.2, p < .003$]. A separate MANOVA, including only the first and second source pairs, showed no group differences between estimated source locations [$F(3, 19) = 0.9$], which was additionally confirmed by separate ANOVAs for each axis [$F(1, 19) < 1.3$].

The source waveforms for the different source pairs are displayed in Figure 8. The source pair (b1/c1) that accounts for the rising P1 displayed a peak in activity at approximately 100 msec, and the source pair that accounts for the P2 showed a peak in activity at approximately

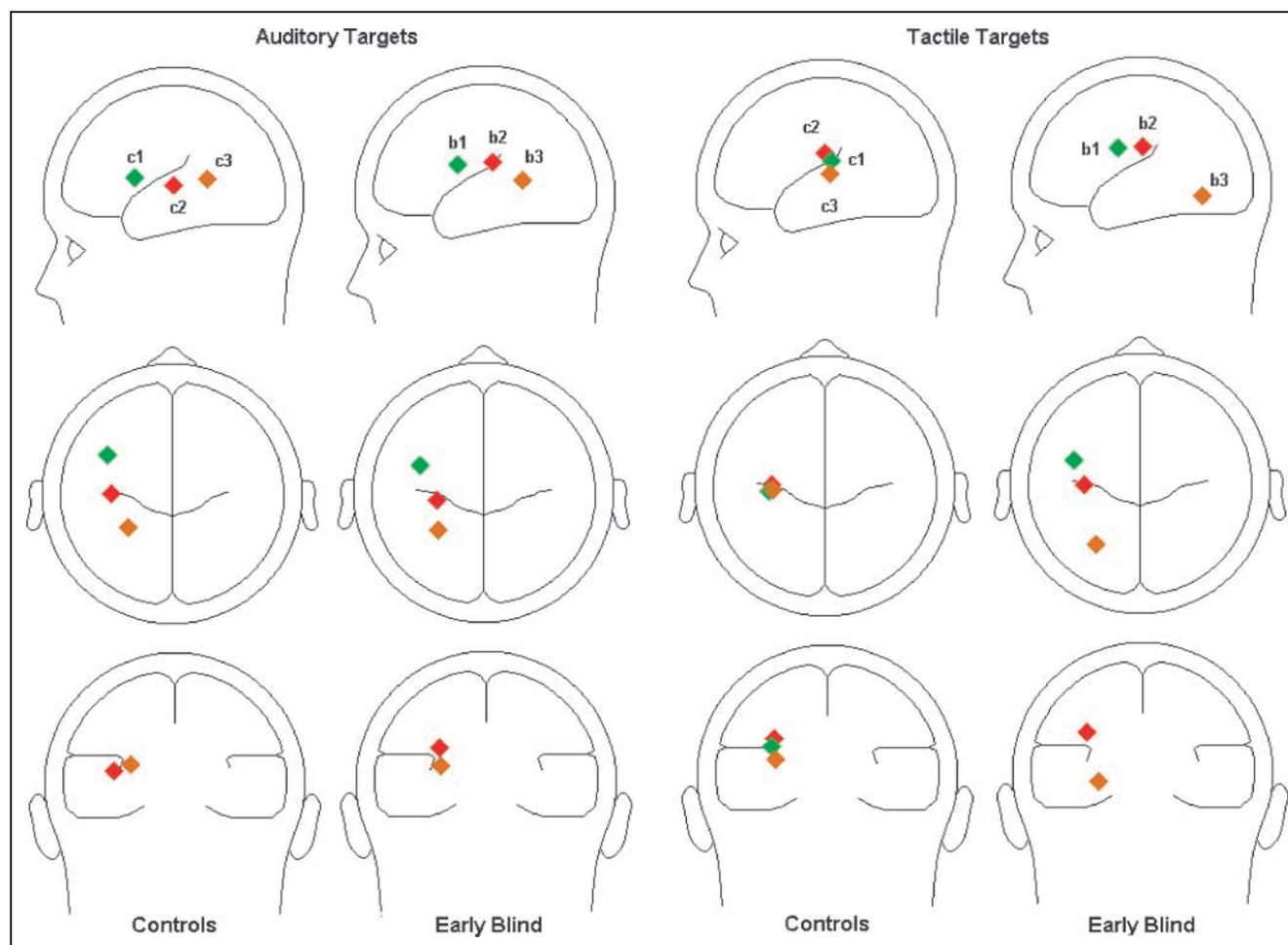


Figure 5. Average estimated source locations for controls and the early blind based on ERPs elicited by auditory (left) and tactile targets (right). The color of each source [green (b1/c1), red (b2/c2) or brown (b3/c3) in the left hemisphere] corresponds with the time window in which a specific source was fitted. For auditory targets, these windows were: (1) 32–56 msec (green), (2) 80–192 msec (red), and (3) 248–396 msec (brown). These time windows correspond with the P50, the N1–P2 interval, and the N2 component, respectively. For the tactile targets, they were set at: (1) 68–96 msec (green), (2) 124–196 msec (red), and (3) 248–396 msec (brown), corresponding with the P1, the N1–P2 interval, and the N2 component, respectively.

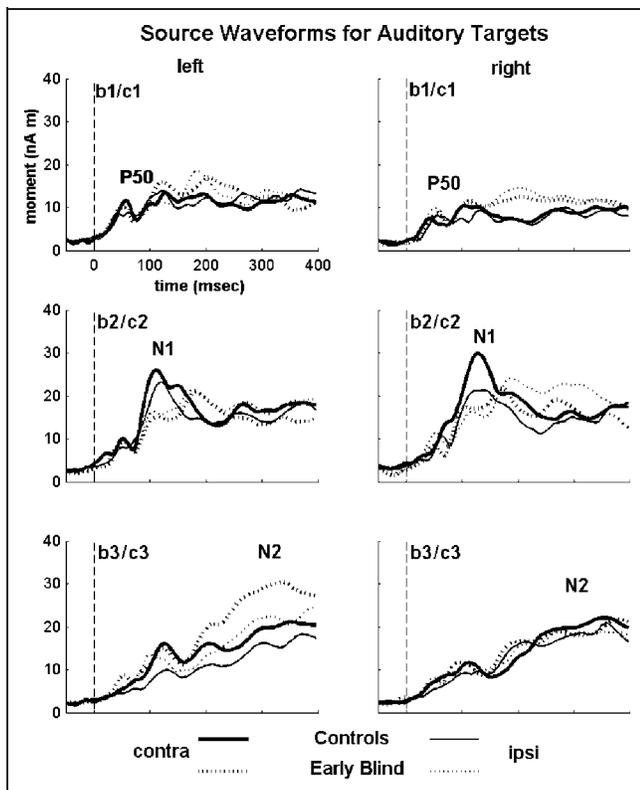


Figure 6. Temporal activity of sources accounting for ERPs produced by auditory targets. Source waveforms were initially determined per individual by computing the root-mean-square across the three orthogonal vectors for contralateral and ipsilateral sources. This was done for each source fitted within each of the three time windows. Contralateral (contra) and ipsilateral (ipsi) averages of these individually estimated source waveforms for left and right auditory targets per condition and group were computed, which are the waveforms displayed. The increased contralateral activity for the early blind in the case of left targets (lower panel) indicates that activity might be larger on the right hemisphere.

200 msec. The source pair that accounts for the posterior N2 showed the largest activity at approximately 300 msec.

Analyses on source waveforms (see Figure 8) with the factors source, hemisphere, target side, and group were performed on activity from 380 to 400 msec. Activity was greatest for the third source pair (b3/c3) [$F(2, 42) = 9.3, p < .004$]. Additionally, interactions were obtained between hemisphere and group [$F(1, 21) = 5.4, p < .031$], and between source, hemisphere, and group [$F(2, 42) = 4.9, p < .02$]. A separate analysis for the third source pair confirmed this interaction between hemisphere and group [$F(1, 21) = 8.3, p < .009$], and points to extra right-hemispheric activity for the blind compared to controls (see Figure 8). With regard to the 280 to 300 msec window, a main effect of source was obtained [$F(2, 42) = 6.8, p < .009$], which indicated that the third source pair was most active. Additionally, a nearly significant interaction between hemisphere and group was found [$F(1, 21) = 3.6, p < .075$], which points to a comparable effect that became signifi-

cant from 380 to 400 msec. Finally, we examined whether there was a relation between performance on the tactile duration discrimination and the locus of the individual b3 sources along the y -axis among the early blind; however, this appeared not to be the case ($p > .11$, one-tailed).

Modality Effects of Posterior Sources

A comparison between the estimated loci of the third source pair in the case of auditory or tactile targets, related to the N2 components or slow negativity, revealed an interaction between group and modality [$F(3, 19) = 3.5, p < .037$]. A separate ANOVA for the y -axis [Group \times Modality; $F(1, 21) = 6.8, p < .017$] confirmed the presence of a group difference in the case of tactile targets, but no effect in the case of auditory stimuli (see previous analyses). Additionally, we examined whether modality differences were present for the individual groups, thereby providing relevant information about the modality specificity of the N2 components. A comparison of the two posterior sources for sighted controls along the y -axis revealed that the source for auditory stimuli was more posterior than the source for tactile stimuli [$F(1, 11) = 4.9, p < .05$], but no effect was found for the blind [$F(1, 10) = 2.3, p > .16$]. Finally, specifically for the blind, we examined whether there was a positive correlation (one-tailed) between the locus of the third source pair for both modalities (see Figure 7) along the y -axis. This correlation failed to reach the level of significance ($r = .52, p < .052$).

DISCUSSION

The current study is the first to demonstrate that the early blind have superior duration discrimination abilities

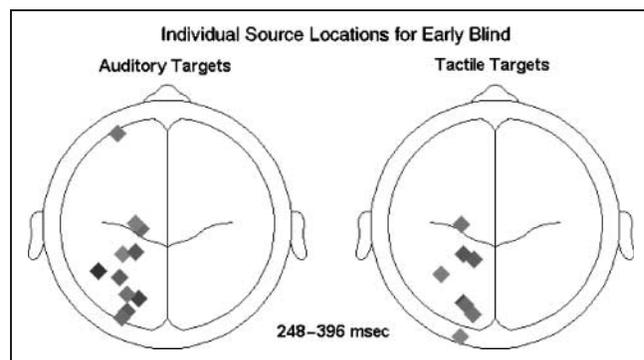


Figure 7. Individually estimated source locations (only indicated for the left hemisphere) for the early blind accounting for activity within the time interval from 248 to 396 msec. In the left panel, the solutions for auditory targets are displayed; in the right panel, the solutions for tactile targets are displayed. Analyses revealed that there was a nearly significant correlation between the individually obtained source locations for both modalities. Furthermore, accuracy of performance in the case of auditory duration discrimination decreased in the case of more anterior source locations.

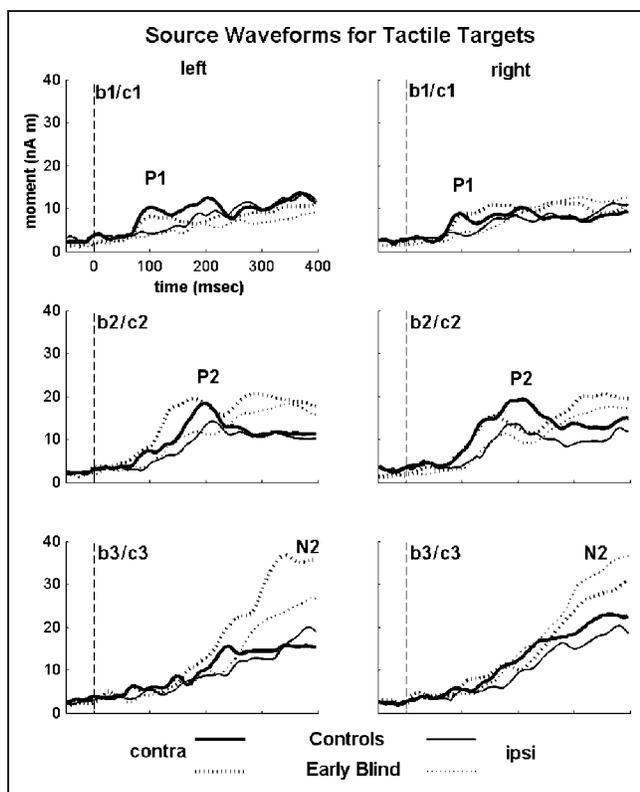


Figure 8. Temporal activity of sources accounting for ERPs produced by tactile targets. Average source waveforms are displayed for left and right tactile targets per group for contralateral and ipsilateral sources (for details, see Figure 6 and Methods). Increased contralateral activity in the case of left targets and increased ipsilateral activity in the case of right targets indicate that posterior sources for the early blind were more active in the right hemisphere.

as compared to sighted controls, which was reflected in the speed and accuracy of their responses. This pattern of results was observed both for auditory and tactile targets. Thus, in addition to superior performance on the spatial dimension (Goldreich & Kanics, 2003; Röder et al., 1999), the early blind outperform sighted controls on tasks contrasting temporal features. These findings underscore the major processing differences between the early blind and sighted controls.

Extra Involvement of Occipital Cortex in the Early Blind

We hypothesized that activity in occipital cortex is related to better performance in the blind. This occipital activation might be visible in an enhanced N2 component or slow negativity for the blind as compared to controls, in accordance with the findings obtained with auditory and tactile oddball tasks (e.g., Liotti et al., 1998; Röder et al., 1996; Kujala et al., 1995).

In line with this hypothesis, our ERP results showed an enlarged occipital slow negativity after auditory targets for

the blind relative to controls, which depended on the side of stimulation and the relevant hemisphere (see Figures 1 and 2). This enlargement was most significant from 320 to 340 msec. Source analyses revealed that this activity may originate from posterior areas (Figure 5, left). Therefore, motor processes, which likely become active much later as responses were rather slow, are unlikely to account for this group difference (e.g., see Lehtokoski, Kujala, Näätänen, & Alho, 1998). Nevertheless, analyses on estimated source activity (c3/b3; Figure 6) from 320 to 340 msec were inconclusive, which we attributed to heterogeneity of the early blind (see Figure 7). To clarify the role of posterior activity in the blind for the auditory modality, we examined whether performance was related to the locus of the estimated source along the anterior–posterior axis. Indeed, more accurate performance was related to a more posterior source location. Hence, increased late posterior activity in the blind as compared to controls appears to be related to improved auditory duration discrimination.

For tactile targets, we observed an enhanced occipital negativity for the blind compared to the controls, peaking at approximately 300 msec (see Figures 3 and 4). Source analyses on this activity revealed a group difference in estimated source locations, with a temporal source for controls and an occipital source for the blind (Figure 5, right). Again, motor processes are unlikely to account for this difference. Analyses of estimated source activity (Figure 8) showed increased activity of the third source pair for the blind, especially for the source located in the right hemisphere. The latter results suggest that improved tactile duration discrimination for the blind relative to controls is related to increased late right posterior activity.

Inspection of topographical changes over time of our occipital negativities (N2 or slow negativity; Figures 2 and 4) revealed that simultaneously with this occipital negativity, a clear parietal positivity is present, which may reflect the rise of the P3b component. This observation corresponds with the results reported by Liotti et al. (1998) in their auditory oddball task (see also Röder et al., 1996). In our study, one source pair was sufficient to account for both this occipital negativity and this parietal positivity. Thus, both effects may have the same origin, although proximity of the sources of the occipital negativity and parietal positivity may hinder their separation.

In our Introduction, we suggested that possible differences between our study and previous studies employing oddball tasks may originate from the employment of more active discrimination tasks, which increase the load on perception–action links. As no major differences were found in our study as compared to previous studies, the increased occipital negativities in the blind are more likely to reflect advanced perceptual processes rather than perception–action links. This issue should be pursued in future studies through a direct comparison between passive and more active tasks.

Supramodal or Modality-specific Involvement of Occipital Cortex in the Early Blind

On the basis of comparable topographies of the N2b/N2 components after auditory and tactile oddball targets, Röder et al. (1996) suggested that occipital involvement in the blind is not modality-specific. In the current study with the early blind, a more direct test was conducted with the N2 and slow negativity observed after auditory and tactile targets by localizing their underlying sources (b3; see Figure 5). Again, no evidence was obtained for a different origin of these activities in the blind. An examination of the individually obtained source locations along the anterior–posterior axis (see Figure 7) additionally showed a nearly significant correlation between the estimated source locations for both modalities. Thus, no support was obtained for a modality-specific involvement of occipital cortex in the blind. One might argue that this null result is to be expected as the accuracy of source localization methods is restricted. However, a recent fMRI study by Weaver and Stevens (2007), in which an oddball paradigm with auditory and tactile stimuli was employed, also identified several areas in occipital cortex of the early blind that responded to both auditory and tactile targets (calcarine sulcus, cuneus, lingual gyrus, and fusiform gyrus). These fMRI findings, combined with the absence of support for a modality-specific hypothesis in our study and previous studies, seem in line with the supramodal hypothesis.

The results for the controls were unexpected as the source (c3; Figure 5) related to the N2 and/or slow negativity had a more posterior locus for auditory targets than for tactile targets. In fact, these results support a modality-specific involvement of posterior areas in controls. A coherent interpretation could be as follows: in sighted participants, a specific (supramodal) area within occipital cortex may, under certain conditions, be recruited for auditory processing, for example, when sitting for an extended time in the dark (e.g., see Lewald, 2007). Direct support for the involvement of occipital cortex in nonvisual tasks in sighted humans has, indeed, been demonstrated by employing TMS (e.g., see Zangaladze, Epstein, Grafton, & Sathian, 1999). In the case of early blindness, this same area may be recruited even more intensively (in line with the ideas of two-step changes by Pascual-Leone et al., 2005). Furthermore, due to its supramodal properties, this area may be recruited for certain aspects of tactile processing in the blind as well, thereby providing an explanation for the modality-specific involvement in controls and the supramodal involvement for the blind. Additional research focusing on the involvement of occipital cortex depending on illumination conditions may allow more definite conclusions.

Interestingly, the topography of the occipital negativity in the blind has a right-hemispheric focus (Figures 1–4). Inspection of the relevant source waveforms (b3/c3; Figures 6 and 8) confirms that, in general, activity in the

blind is enlarged in the right hemisphere. One exception appears to be the condition with auditory targets presented to the right. In this condition, the hemispherical difference appears to be driven by the central sources (b2). Our support for right-hemispheric involvement in early blind contrasts with the results Liotti et al. (1998), who observed that auditory ERPs to targets obtained in an oddball task had a left-hemispheric maximum. TMS research with auditory localization tasks, however, demonstrated a disruptive effect when TMS was applied to right occipital cortex (Collignon et al., 2007; see also Weeks et al., 2000). In the Liotti et al. study, intensity was the relevant feature, and Collignon et al. (2007) additionally reported that TMS to the right occipital areas had no disruptive effect when intensity was relevant. Altogether, these findings accord with a view in which separate supramodal processes are distributed across different parts of occipital cortex in the blind. In the right hemisphere, processes may be involved with spatio-temporal judgments, and in the left hemisphere, they may be related to identity judgments concerning aspects such as intensity or pitch (for somewhat related ideas, see Amedi et al., 2007).

Earlier Modality-specific ERP Effects and Their Estimated Sources

The auditory targets elicited an early P50 component above frontal and central sites (see Figure 1). The source of this activity was localized in anterior areas (see also Weisser et al., 2001), and was highly comparable with regard to its locus and activation strength for both groups. Activity within the interval containing the N1 and P2 components (80–192 msec) was localized in auditory cortex (see also Tarkka et al., 1995). The ERP results suggest that the P2 component from 160 to 180 msec was enlarged for the blind (see also Kujala et al., 1995), but inspection of our results concerning the central source only revealed that this locus was slightly more superior for the early blind than for controls. These somewhat mixed results may be due to the aforementioned heterogeneity of the early blind group.

In the case of tactile targets, the early contralateral P1 component was largest above centro-parietal sites (see Figure 3). Given the results of our source analyses, it may be proposed that this component originates from primary somatosensory areas (see Thees et al., 2003). A later non-lateralized P2 component was visible with a somewhat more posterior locus, which was identified as a separate component from 124 to 192 msec, and which may originate from secondary somatosensory areas (see Thees et al., 2003). Comparable source locations were obtained for the blind and the controls.

The aforementioned results provide no evidence that early auditory and tactile processing in primary and secondary sensory areas differs between the blind and the controls, which contrasts with findings in other mammals

after sensory deprivation (see Bavelier & Neville, 2002). Recently, it was reported that early somatosensory activity at approximately 100 msec after stimulus onset was modulated in the blind, but not in sighted controls (Forster, Eardley, & Eimer, 2007). This effect, however, was specifically related to a manipulation of spatial attention, and not to general changes in somatosensory processing.

Cross-modal Exogenous Orienting Effects

In the Introduction, we considered the idea that cross-modal exogenous orienting effects in the early blind may be reduced due to changes in structures that are crucial for spatial attention. This question was partially based on the observation that blind participants may be more efficient in blocking stimuli that are to be ignored (Hötting & Röder, 2004; Hötting et al., 2004). However, we found no reduced orienting effect of irrelevant tactile cues in the auditory duration discrimination task for the early blind as compared to controls (see Table 2). The same conclusion applies to orienting effects of irrelevant auditory cues; no reduction was found for the early blind in the tactile duration discrimination task.³ Another possible difference between the blind and the controls is that the more general acceleration of processing due to cues (i.e., a warning effect) is reduced in blind participants. A comparison of the influence of presence or absence of to-be-ignored cues on responses to subsequent targets, however, showed no major group differences. How can these results be understood? Apparently, changes in information processing in the early blind participants are not due to modifications in structures relevant for attentional orienting and alertness. Instead, major changes in the early blind appear to be due to a modification at a later more advanced processing level. This is in line with our aforementioned conclusions regarding the supramodal nature of changes in occipital cortex and the absence of a difference in primary and secondary sensory areas.

Conclusion

In conclusion, the early blind are evidently much better at discriminating the duration of both auditory and tactile stimuli than sighted controls, extending their well-known superiority on spatially oriented nonvisual tasks to the temporal domain. This superiority does not seem to be due to gross changes in early perceptual processes in auditory and somatosensory brain areas or to early perceptual processes taken over by occipital cortex. Instead, occipital processes with a supramodal nature appear responsible for this effect.

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Notes

1. The N2b component was thought to be modality-unspecific, and has been associated with a call for focal attention (Näätänen & Gaillard, 1983).
2. It is important to be aware of the multiple meanings of the term attention. Spatial attention refers to the selection of stimuli at a location, whereas attentive processing refers to processing of stimuli after being selected.
3. Our cross-modal exogenous orienting effects are in line with previous reports (Spence, 2002) and extend the generality of these phenomena to duration discrimination tasks.

REFERENCES

- Alho, K., Kujala, T., Paavilainen, P., Summala, H., & Näätänen, R. (1993). Auditory processing in visual brain areas of the early blind: Evidence from event-related potentials. *Electroencephalography and Clinical Neurophysiology*, *86*, 418–427.
- Amedi, A., Raz, N., Pianka, P., Malach, R., & Zohary, E. (2003). Early “visual” cortex activation correlates with superior verbal memory performance in the blind. *Nature Neuroscience*, *6*, 758–766.
- Amedi, A., Stern, W. M., Camprodon, J. A., Bempohl, F., Merabet, L., Rotman, S., et al. (2007). Shape conveyed by visual-to-auditory sensory substitution activates the lateral occipital complex. *Nature Neuroscience*, *10*, 687–689.
- Annet, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology*, *61*, 303–321.
- Baddeley, A. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience*, *4*, 829–839.
- Bavelier, D., & Neville, H. J. (2002). Cross-modal plasticity: Where and how? *Nature Reviews Neuroscience*, *3*, 443–452.
- Berg, P., & Scherg, M. (1994). A multiple source approach to the correction of eye artifacts. *Electroencephalography and Clinical Neurophysiology*, *90*, 229–241.
- Cohen, L. G., Celnik, P., Pascual-Leone, A., Corwell, B., Faiz, L., Dambrosia, J., et al. (1997). Functional relevance of cross-modal plasticity in blind humans. *Nature*, *389*, 180–183.
- Collignon, O., Lassonde, M., Lepore, F., Bastien, D., & Veraart, C. (2007). Functional cerebral reorganization for auditory spatial processing and auditory substitution of vision in early blind subjects. *Cerebral Cortex*, *17*, 457–465.
- Forster, B., Eardley, A. F., & Eimer, M. (2007). Altered tactile spatial attention in early blind. *Brain Research*, *1131*, 149–154.
- Frishkoff, G. A., Tucker, D. M., Davey, C., & Scherg, M. (2004). Frontal and posterior sources of event-related potentials in semantic comprehension. *Cognitive Brain Research*, *20*, 329–354.
- Goldreich, D., & Kanics, I. M. (2003). Tactile acuity is enhanced in blindness. *Journal of Neuroscience*, *23*, 3439–3445.
- Gougoux, F., Lepore, F., Lassonde, M., Voss, P., Zatorre, R. J., & Belin, P. (2004). Pitch discrimination in the early blind. *Nature*, *430*, 309.

- Gougoux, F., Zatorre, R. J., Lassonde, M., Voss, P., & Lepore, F. (2005). A functional neuroimaging study of sound localization: Visual cortex activity predicts performance in early-blind individuals. *PLoS Biology*, *3*, 324–333.
- Hamilton, R., Keenan, J. P., Catala, M., & Pascual-Leone, A. (2000). Alexia for Braille following bilateral occipital stroke in an early blind woman. *NeuroReport*, *11*, 237–240.
- Hötting, K., & Röder, B. (2004). Hearing cheats touch, but less in congenitally blind than in sighted individuals. *Psychological Science*, *15*, 60–64.
- Hötting, K., Rösler, F., & Röder, B. (2004). Altered auditory–tactile interactions in congenitally blind humans: An event-related potential study. *Experimental Brain Research*, *159*, 370–381.
- Ille, N., Berg, P., & Scherg, M. (2002). Artifact correction of the ongoing EEG using spatial filters based on artifact and brain signal topographies. *Journal of Clinical Neurophysiology*, *19*, 113–124.
- Karlen, S. J., Kahn, D. M., & Krubitzer, L. (2006). Early blindness results in abnormal corticocortical and thalamocortical connections. *Neuroscience*, *142*, 843–858.
- Kujala, T., Alho, K., Huottilainen, M., Ilmoniemi, R. J., Lehtokoski, A., Leinonen, A., et al. (1997). Electrophysiological evidence for crossmodal plasticity in humans with early- and late-onset blindness. *Psychophysiology*, *34*, 213–216.
- Kujala, T., Alho, K., Kekoni, J., Hämäläinen, H., Reinikainen, K., Salonen, O., et al. (1995). Auditory and somatosensory event-related brain potentials in early blind humans. *Experimental Brain Research*, *104*, 519–526.
- Kujala, T., Palva, M. J., Salonen, O., Alku, P., Huottilainen, M., Järvinen, A., et al. (2005). The role of blind humans' visual cortex in auditory change detection. *Neuroscience Letters*, *379*, 127–131.
- Lehtokoski, A., Kujala, T., Näätänen, R., & Alho, K. (1998). Enhanced brain activity preceding voluntary movement in early blind humans. *Neuroscience Letters*, *253*, 155–158.
- Lewald, J. (2007). More accurate sound localization induced by short-term light deprivation. *Neuropsychologia*, *45*, 1215–1222.
- Liotti, M., Ryder, K., & Woldorff, M. G. (1998). Auditory attention in the congenitally blind: Where, when and what gets reorganized. *NeuroReport*, *9*, 1007–1012.
- Luck, S. J. (2005). Ten simple rules for designing ERP experiments. In T. C. Handy (Ed.), *Event-related potentials* (pp. 17–32). Cambridge, MA: MIT Press.
- Näätänen, R., & Gaillard, A. W. K. (1983). The orienting reflex and the N2 deflection of the event-related potential (ERP). In A. W. K. Gaillard & W. Ritter (Eds.), *Tutorials in event-related potential research: Endogenous components* (pp. 119–141). Amsterdam: North-Holland.
- Pascual-Leone, A., Amedi, A., Fregini, F., & Merabet, L. B. (2005). The plastic human brain cortex. *Annual Review of Neuroscience*, *28*, 377–401.
- Ptito, M., Fumal, A., de Noordhout, A. M., Schoenen, J., & Kupers, R. (2008). TMS of the occipital cortex induces tactile sensations in the fingers of blind Braille readers. *Experimental Brain Research*, *184*, 193–200.
- Rafal, R. D., Posner, M. I., Friedman, J. H., Inhoff, A. W., & Bernstein, E. (1988). Orienting of visual attention in progressive supranuclear palsy. *Brain*, *111*, 267–280.
- Rauschecker, J. P. (1995). Compensatory plasticity and sensory substitution in the cerebral cortex. *Trends in Neurosciences*, *18*, 36–43.
- Renier, L., Collignon, O., Poirier, C., Tranduy, D., Vankierde, A., Bol, A., et al. (2005). Cross-modal activation of visual cortex during depth perception using auditory substitution of vision. *NeuroImage*, *26*, 573–580.
- Röder, B., Rösler, F., Hennighausen, E., & Näcker, F. (1996). Event-related potentials during auditory and somatosensory discrimination in sighted and blind human subjects. *Cognitive Brain Research*, *4*, 77–93.
- Röder, B., Teder-Sälejärvi, W., Sterr, A., Rösler, F., Hillyard, S. A., & Neville, J. (1999). Improved auditory spatial tuning in blind humans. *Nature*, *400*, 162–166.
- Sathian, K. (2005). Visual cortical activity during tactile perception in the sighted and the visually deprived. *Developmental Psychobiology*, *46*, 279–286.
- Slotnick, S. D. (2005). Source localization of ERP generators. In T. C. Handy (Ed.), *Event-related potentials*. Cambridge, MA: MIT Press.
- Spence, C. (2002). Multisensory attention and tactile information-processing. *Behavioural Brain Research*, *135*, 57–64.
- Tarkka, I. M., Stokić, D. S., Basile, L. F., & Papanicolaou, A. C. (1995). Electric source localization of the auditory P300 agrees with magnetic source localization. *Electroencephalography and Clinical Neurophysiology*, *96*, 538–545.
- Thees, S., Blankenburg, F., Taskin, B., Curio, G., & Villringer, A. (2003). Dipole source localization and fMRI of simultaneously recorded data applied to somatosensory categorization. *NeuroImage*, *18*, 707–719.
- Van der Lubbe, R. H. J., & Postma, A. (2005). Interruption from irrelevant auditory and visual onsets even when attention is in a focused state. *Experimental Brain Research*, *164*, 464–471.
- Van der Lubbe, R. H. J., Schölvinc, M. L., Kenemans, J. L., & Postma, A. (2006). Divergence of categorical and coordinate spatial processing assessed with ERPs. *Neuropsychologia*, *44*, 1547–1559.
- Wallace, M. T., Ramachandran, R., & Stein, B. E. (2004). A revised view of sensory cortical parcellation. *Proceedings of the National Academy of Sciences, U.S.A.*, *101*, 2167–2172.
- Weaver, K. E., & Stevens, A. A. (2007). Attention and sensory interactions within the occipital cortex in the early blind: An fMRI study. *Journal of Cognitive Neuroscience*, *19*, 315–330.
- Weeks, R., Horwitz, B., Aziz-Sultan, A., Tian, B., Wessinger, C. M., Cohen, L. G., et al. (2000). A positron emission tomography study of auditory localization in the congenitally blind. *Journal of Neuroscience*, *20*, 2664–2672.
- Weisser, R., Weisbrod, M., Roehrig, M., Rupp, A., Schroeder, J., & Scherg, M. (2001). Is frontal lobe involved in the generation of auditory evoked P50? *NeuroReport*, *12*, 3303–3307.
- Wittenberg, G. F., Werhahn, K. J., Wassermann, E. M., Herscovitch, P., & Cohen, L. G. (2004). Functional connectivity between somatosensory and visual cortex in early blind humans. *European Journal of Neuroscience*, *20*, 1923–1927.
- Zangaladze, A., Epstein, C. M., Grafton, S. T., & Sathian, K. (1999). Involvement of visual cortex in tactile discrimination of orientation. *Nature*, *401*, 587–590.