Neuropsychologia 47 (2009) 3236–3243

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Early visual deprivation alters multisensory processing in peripersonal space

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ARTICLE INFO

Article history:
Received 29 May 2009
Received in revised form 27 July 2009
Accepted 31 July 2009
Available online 8 August 2009

Keywords:
Blindness
Peripersonal space
Multisensory
Auditory
Somatosensory
Redundant signal effect (RSE)

ABSTRACT

Multisensory peripersonal space develops in a maturational process that is thought to be influenced by early sensory experience. We investigated the role of vision in the effective development of audiotactile interactions in peripersonal space. Early blind (EB), late blind (LB) and sighted control (SC) participants were asked to lateralize auditory, tactile and audiotactile stimuli. The experiment was conducted with the hands uncrossed or crossed over the body midline in order to alter the relationship between personal and peripersonal spatial representations. First, we observed that the crossed posture results in a greater detrimental effect for tactile performance in sighted subjects but a greater deficit in auditory performance in early blind ones. This result is interpreted as evidence for a visually driven developmental process that automatically remaps tactile and proprioceptive spatial representation into an external framework. Second, we demonstrate that improved reaction times observed in the bimodal conditions in SC and LB exceeds that predicted by probability summation in both conditions of postures, indicating neural integration of different sensory information. In EB, nonlinear summation was obtained in the uncrossed but not in the crossed posture. We argue that the default use of an anatomically anchored reference system in EB prevents effective audiotactile interactions in the crossed posture due to the poorly aligned spatial coordinates of these two modalities in such conditions. Altogether, these results provide compelling evidence for the critical role of early vision in the development of multisensory perception and action control in peripersonal space.

1. Introduction

The world around us is made up of events that generally stimulate more than one modality simultaneously, and the neural integration of these different sensory signals offers many benefits, including enhanced discrimination and accelerated reaction to objects (Spence & Driver, 2004; Stein & Meredith, 1993). For example, when acting in peripersonal space, that is, the reachable region immediately surrounding the body (Rizzolatti, Fadiga, Fogassi, & Gallese, 1997), individuals can integrate touch with auditory and visual information in order to strengthen their perception of a multisensory event. However, although we do this intuitively in daily life, it remains a non-trivial problem because the brain must constantly recalibrate the representation of the location of the object acquired in external coordinates (i.e., vision and audition) with the internal representation of the object position relative to the body (Holmes, Sanabria, Calvert, & Spence, 2006; Maravita, Spence, & Driver, 2003). This is particularly critical because the hands move constantly within the peripersonal space as different postures are adopted. Recent studies have suggested that the spatial frames of reference used by our distal senses and the sensory information about our body are aligned because the brain automatically remaps touch and proprioception into extrapersonal coordinates (Azanon & Soto-Faraco, 2008; Kitazawa, 2002; Pavani, Spence, & Driver, 2000; Shore, Spry, & Spence, 2002; Yamamoto & Kitazawa, 2001). This automatic remapping from somatotopic to external space is thought to provide a common framework to coordinate and integrate spatial information obtained through touch with spatial information obtained through other sensory modalities, such as vision and audition, which is coded by default in external spatial coordinates (Eimer, Cockburn, Smedley, & Driver, 2001; Lloyd, Merat, McGlone, & Spence, 2003; Maravita et al., 2003; Sanabria, Soto-Faraco & Spence, 2005; Soto-Faraco, Spence & Kingstone, 2004).

A recent developmental study suggested that this default use of external coordinates for touch and proprioception develops during early infancy (Bremner, Mareschal, Lloyd-Fox, & Spence, 2008), by demonstrating that infants first represent body parts in their normal or typical locations and later develop mechanisms that dynamically remap representations of limb positions with respect to visual and external space (see Bremner, Holmes, & Spence, 2008,

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doi:10.1016/j.neuropsychologia.2009.07.025

for an extended discussion). Recent experiments with blind people have suggested that the default localization of touch and proprioception in external space is in fact dependent on early visual experience (Röder, Rosler, & Spence, 2004; Röder et al., 2007; Röder, Focker, Hotting, & Spence, 2008). Röder et al. (2004) demonstrated that when participants were required to determine the temporal order of two tactile stimuli, one applied to either hand, sighted and late blind subjects' performance was impaired in a crossed when compared to an uncrossed-hand posture but performance of early blind participants remained unchanged across postures changes. The authors argued that the automatic external remapping of touch in sighted and late blind induces a conflict between external and body-centred coordinates which indeed decreases performance. However, in the early blind, an absence of the externalisation process of touch protects them from the detrimental effect of the crossed-hand posture. This explanation was supported by an electroencephalographic study showing that the detection of deviant tactile stimuli at the hand induced event-related potentials that varied in crossed when compared to uncrossed condition of posture in sighted subjects, whereas changing the posture of the hand had no influence on the early blind subjects' brain activity (Röder et al., 2008). Another recent study also reported that sighted subjects profit from the use of an external reference frame when the sound source and the external location of the hand have to be matched whereas this was not the case in congenitally blind people (Röder, Kusmierek, Spence, & Schicke, 2007). These results thus demonstrate that the default remapping of touch/proprioception into external coordinates is acquired during development as a consequence of visual input.

However, an important question which remains open is how this absence of default localization of touch and proprioception in external space in the early blind affects the construction of a common spatial framework for audiotactile stimulus integration. In the present study, we decided to use a crossed-hands paradigm during the lateralization of auditory, tactile and audiotactile stimuli to determine whether the absence of an automatic external remapping of touch and proprioception impairs their ability to use a common "external" spatial frame of reference for the integration of auditory and tactile stimuli across postural changes.

In multisensory paradigms, responses are usually faster when the two stimuli from separate modalities are presented at the same time than when a single target stimulus is presented in isolation (Stein & Meredith, 1993). Raab (1962) proposed an explanation of this redundant-target effect, called the *race model*, in which the redundant-target stimulus response is initiated by the faster of the two separate target detection processes. Thus, faster reaction times (RTs) obtained in bimodal situations occur simply because the two unimodal stimuli set up a "race" for response control, in which the faster process wins. In other words, there is no need to postulate neural interaction between the two stimuli. Thus, this "*race model inequality*" assumes that each sensory modality is detected separately and processed in parallel and one of them is faster than the other (i.e., the *inequality*). On the other hand, if RTs obtained in bimodal condition are faster than those predicted by the race model, it is supposed that information from the two sensory modalities interacts to produce the RTs facilitation. Miller (1982) developed the "co-activation model" and provided a method for testing this "*race model violation*". Testing for the violation of race model inequality (i.e., faster RT than the fastest unimodal response) has recently emerged as a method to assess whether the redundant-target effect (faster RTs in bimodal condition) reflects a true multisensory integrative process or not (Hecht, Reiner, & Karni, 2008; Murray et al., 2005; Neil, Chee-Ruiter, Scheier, Lewkowicz, & Shimojo, 2006; Zampini, Torresan, Spence, & Murray, 2007).

Our hypothesis is that the use of an anatomically anchored reference system for touch and proprioception in subjects visually deprived since birth will impair their ability to integrate audiotactile information across postural changes (assessed by an absence of violation of the RACE model inequality).

2. Methods

2.1. Subjects

One group of sighted and two groups of blind individuals (early blind and late blind) participated in the study. The sighted control group (SC) was composed of 12 adults (3 females) ranging in age from 28 to 56 years with a mean age of 43 years (SD = 10). The early-onset blind group was composed of 10 subjects (2 females) ranging in age from 26 to 56 years with a mean age of 40 years (SD = 10). None of the early blind subjects had ever had functional vision allowing pattern recognition or visually guided behavior. The late-onset blind group was composed of 11 subjects (4 females) ranging in age from 24 to 60 years with a mean age of 44 years (SD = 9). Unlike the early blind group, all subjects in the late blind group had experienced functional vision before sight loss, which allowed them to recognize visual shapes and read printed letters, for instance. The mean age of blindness onset in the late blind group was 17 years (range: 8–27 years) and the mean duration of blindness before participating in the study was 25 years (range: 13–46 years). At the time of testing, the subjects in both blind groups were totally blind or else had only rudimentary sensitivity for brightness differences and no pattern vision. In all cases, blindness was attributed to peripheral deficits with no additional neurological problems (see Table 1 for details). Note that there is no statistical age difference between the three subject groups [EB vs. SC: $t(20) = .93$, $p = .86$; EB vs. LB: $t(19) = -.99$, $p = .33$; SC vs. LB: $t(21) = -.16$, $p = .86$]. All test procedures were approved by the Research Ethics Boards of the Centre for Interdisciplinary Research in Rehabilitation of Greater Montreal (CRIR) and the Université de Montréal. Experiments were undertaken with the understanding and written consent of each subject. None of the subjects reported neurological or psychological problems, and none was taking psychotropic medication at the time of testing. Audiometric thresholds were assessed for all subjects, indicating normal hearing function in both ears. All subjects reported normal tactile perception.

2.2. Stimuli

Tactile stimuli were trains of five 1 ms biphasic square wave pulses delivered every 25 ms (40 Hz for 100 ms). Electrical stimuli were applied to the skin using disposable ring electrodes (Nicolet Biomedical, Madison, USA) placed around the proximal and distal interphalangeal joints of the middle finger of each hand. Stimuli were generated using a Grass S88 dual output stimulator connected to each hand through a PSIU6 isolation unit (Grass, Astro-Med, West Warwick, USA). Due to the very large inter-individual and inter-manual (at the individual level) differences in sensitivity to tactile stimuli, we calibrated stimulus intensity for each hand in order to obtain the most prominent but nonetheless comfortable and not painful sensation. Stimulations were then adjusted between the hands to equate perceived left and right intensity. No between-group differences (using *t*-tests) were observed for the stimuli intensity used [mixed mean for both hands and SD: SC = 23 V (11); EB = 17 V (12); LB = 24 V (11)], reinforcing the idea that ability differences between blind and sighted subjects are more likely to manifest themselves in higher order cognitive tasks than in more basic sensory threshold measurements (Collignon, Renier, Bruyer, Tranduy, & Veraart, 2006).

Auditory stimuli consisted of 100 ms duration pink noise bursts (90% normalized peak value, plateau time 90 ms, rise/fall time 5 ms) produced with Adobe Audition 2.0 (Adobe Systems Inc.) delivered to either the left or right hemispace via stereo speakers (Gigaworks T20, Creative Technology Ltd., USA). For all subjects, stimulus intensity was set at 75 db-SPL in both channels, that is, at least 40 db-SPL above threshold for all subjects.

Bimodal stimuli were obtained by simultaneously presenting auditory and tactile stimuli. The matching was always "congruent," with auditory and tactile stimuli delivered from the same external hemispace.

2.3. Procedure

During testing, subjects sat in a silent room with the head restrained by a chin rest. All subjects were blindfolded during testing. Stimuli were delivered and reaction times were recorded using Presentation software (Neurobehavioral Systems Inc.) running on a Dell XPS computer using a Windows XP operating system. Subjects' hands were placed 30 cm in front of the body, palm side down, 25 cm away from the body midline in the left and right hemispaces. Speakers were placed immediately beside the subject's hands, also 25 cm to either side of the body midline (see Fig. 1 for a schematic diagram of the experimental setup).

Subjects were asked to lateralize auditory, tactile or audiotactile stimuli. Subjects were instructed to respond as quickly and accurately as possible in a forced two-choice discrimination paradigm by pressing the appropriate response key. Subjects performed the task with their hands in either a parallel posture (uncrossed posture) or with the arms crossed over the body midline so that the left hand was in the right hemispace and the right hand was in the left hemispace (crossed posture). In the uncrossed posture, subjects were required to press the right button

Table 1
Characteristics of blind subjects.

Subj.	Age	Sex	Hand.	Residual visual perception	Onset	Cause of blindness	Education
EB1	50	M	R	No	2 months	Medical accident	High school
EB2	43	M	R	No	0	Glaucoma	University
EB3	39	M	R	Diffuse light	0	Leber's congenital amaurosis	University
EB4	55	F	R	No	0	Retinopathy of prematurity	High school
EB5	38	M	R	No	0	Detached retina	High school
EB6	30	F	R	No	0	Bilateral Retinoblastoma	High school
EB7	26	M	R	No	0	Leber's congenital amaurosis	University
EB8	30	M	R	No	2 years	Bilateral retinoblastoma	High School
EB9	46	M	R	No	0	Congenital Cataract	University
EB10	40	M	R	No	0	Retinopathy of prematurity	University
LB1	60	M	R	No	14	Cataract	University
LB2	52	F	R	No	19	Glaucoma, Aniridia	University
LB3	36	M	L	No	16	Glaucoma	High school
LB4	52	F	R	Diffuse light	27	Retinitis pigmentosa	High school
LB5	39	F	R	No	21	Glaucoma	High school
LB6	41	M	L	No	15	Detached retina	High school
LB7	28	M	R	No	15	Section of both optic nerves following accident	High school
LB8	40	M	R	No	17	Section of both optic nerves following accident	University
LB9	53	F	L	No	8	Detached retina following accident	High school
LB10	42	M	R	No	23	Retinitis pigmentosa	High school
LB11	36	M	R	No	15	Glaucoma	University

Note. M: male; F: female; R: right handed; L: left handed; A: ambidextrous. Handedness was evaluated using the Edinburgh inventory (Oldfield, 1971) in sighted subjects and a modified version of the test in early blind subjects.

with their right hand in response to any stimulus coming from the right side (right-sided auditory stimuli and tactile stimulation of the right hand), and conversely for left-sided stimuli. In the crossed posture, subjects were required to press the right button with their left hand in response to any stimulus coming from the right side (right-sided auditory stimuli and tactile stimulation of the left hand), and conversely for left-sided stimuli. In other words, participants press the button in front of the auditory source or under the stimulated hand either in a crossed or uncrossed posture. A total of 300 stimuli were presented in each posture condition (uncrossed or crossed) (2 [sides: left or right] × 3 [Condition: Auditory, Tactile, Bimodal] × 50 [stimuli]), randomly presented with a mean interstimulus interval of 1950 ms (range 1200–2700 ms). Trials for which subjects did not respond were considered as omissions and were rejected. One block of approximately 10 min was used for each posture, and order of posture conditions was counterbalanced across subjects. A 10-min pause was given between two blocks, and subjects completed 21 practice trials before each block.

2.4. Data analysis

Task performance was determined by measuring inverse efficiency (IE) scores to take both response speed and accuracy into account. IE scores are obtained by dividing response times (RT) (150–1000 ms post-stimulus) by correct response rates separately for each condition (higher values indicate lower performance). This standard approach combining RT and accuracy performance measures controls for possible criterion shifts or speed-accuracy tradeoffs effects in the tasks (Collignon et al., 2008; Röder et al., 2007; Spence, Kingstone, Shore, & Gazzaniga, 2001; Townsend & Ashby, 1978, Townsend & Ashby, 1983). IE scores were submitted to repeated measures analysis of variance (ANOVA-RM). Based on significant *F*-values, Bonferroni post hoc analyses were performed when appropriate. As similar results were obtained when submitting accuracy and RT measurements separately to the same ANOVA, as described above, only the results obtained with IE scores are reported here (accuracy and RT data are however illustrated in Supporting figure).

Race Model inequality was analyzed using RMITest software, which implements the algorithm described at length in Ulrich, Miller, & Schroter (2007). This procedure involves several steps. First, empirical cumulative density functions (CDFs) of the reaction time distributions are estimated for every participant and every stimulus condition (i.e., auditory alone, tactile alone and bimodal condition). Second, the bounding sum of the two CDFs obtained in the two unimodal conditions (auditory and tactile) are computed for each participant, thus providing an estimate for each participant of the upper boundary for violation of the RACE model inequality. Third, percentile values are calculated for every stimulus condition and bounding sum (the bound) for each participant. In the present study, bin widths of 10% were used (e.g. Martuzzi et al., 2007; Sperdin, Cappe, Foxe, & Murray, 2009), which gives a good compromise between a sufficient number of bins to observe violation of the Race Model inequality, and a too large number of bins which require a large number of reaction times in each condition for the computation of the Race Model inequality. Fourth, for each percentile, a comparison between the bimodal condition and the bound is carried out using a two-tailed *t*-test. If at any percentile one observes significantly faster RTs in the bimodal condition relative to the bound, it can be concluded that the race model cannot account for the facilitation in the redundant signals condition, thus supporting a multisensory integration process.

3. Results

Performance (see Fig. 2) was analyzed by submitting inverse efficiency (IE) scores (see Section 2.4) to a 3 [Group: EB, LB, SC; between-subjects factor] × [2 (Posture: uncrossed or crossed) × 2

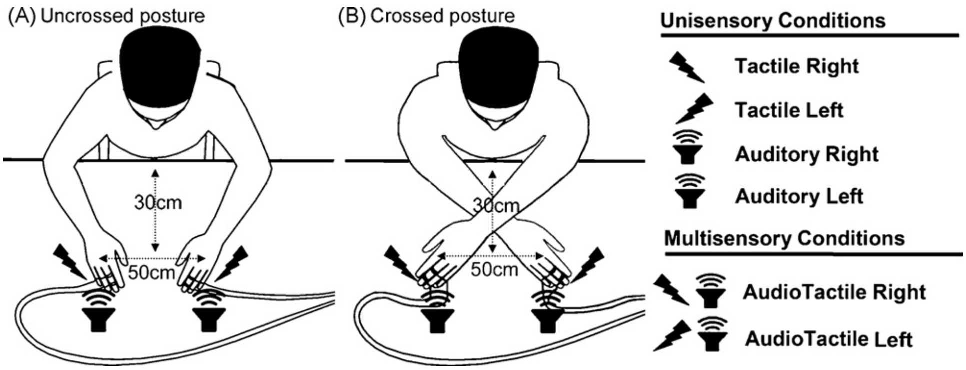

Fig. 1. Schematic representation of the experimental setup (see Section 2.3 for details). Subjects were asked to lateralize auditory, tactile and audiotactile stimuli in either uncrossed (A) or crossed (B) posture condition. In the uncrossed posture, subjects were required to press the right button with their right hand in response to any stimulus coming from the right "external" side, and conversely for left-sided stimuli. In the crossed posture, subjects were required to press the right button with their left hand in response to any stimulus coming from the right "external" side, and conversely for left-sided stimuli.

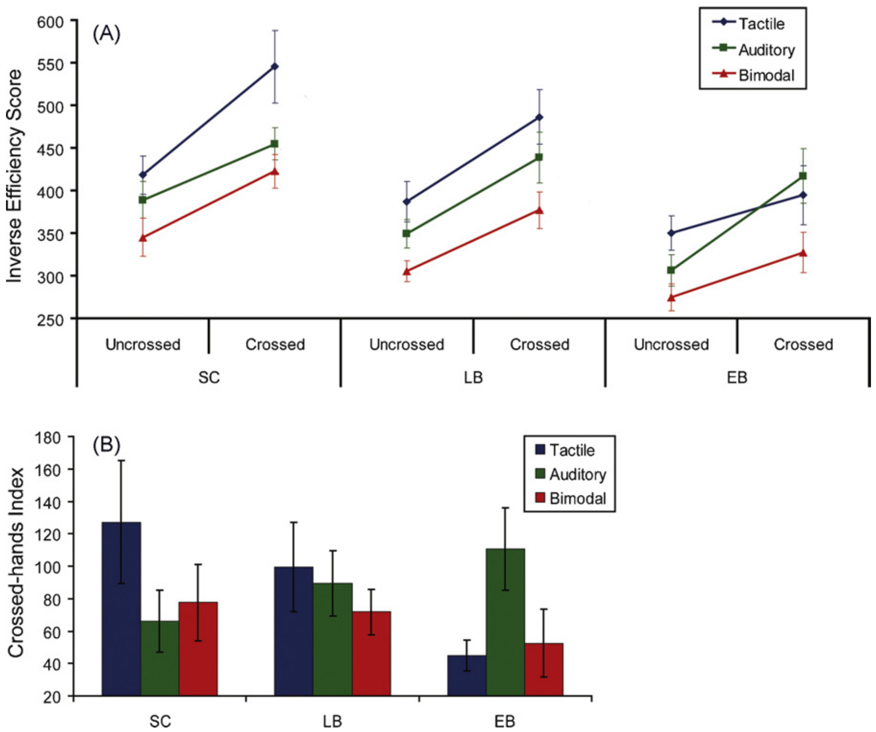

Fig. 2. (A) Mean IE scores and standard errors in sighted (left panel), late blind (centre panel) and early blind (right panel) subjects obtained in uncrossed and crossed postures in the tactile (blue diamonds), auditory (green squares) and bimodal (red triangles) conditions. IE scores were obtained by dividing RTs by correct response rates, thereby eliminating potential speed-accuracy tradeoff effects in the data: the lower the score, the more efficient the performance (Spence et al., 2001; Röder et al., 2007). Data acquired from both left and right stimulation were pooled, as no side effects were observed in the data (see Section 3 for details). EB significantly outperformed SC except in auditory condition with hands crossed. Performances were better in bimodal than unimodal condition. We also observed a significant performance decrease in the crossed posture, except for EB in tactile and bimodal condition. (B) In order to further highlight the detrimental crossed-hand effect, we subtracted IE scores obtained in the uncrossed-posture condition from IE scores obtained in the crossed posture condition. Higher scores represent more disruption in subjects' performance. It can be seen that EB and SC show a reversed pattern of performance disruption between auditory and tactile condition. SC were more disrupted in the tactile than in the auditory condition, whereas EB were more disrupted in audition than in touch. Performance decrease was comparable between auditory and tactile tasks in the LB. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

(Sides: left or right) × 3 (Condition: Auditory, Tactile, Bimodal); within-subject factors] repeated measures ANOVA. For results interpretation, it is important to note that higher level of performance is reflected by lower IE scores (see Fig. 2).

First, we obtained a main effect of the factor "Group" [$F(2,30) = 3.9$, $p = .03$], which showed that EB outperformed SC ($p = .01$). However, we did not observe significant differences in performance between EB and LB ($p = .36$) or between LB and SC ($p = .7$).

We also obtained a main effect of the factor "Posture" [$F(1,30) = 42.19$, $p \leq 10\text{E}{-6}$], which showed an overall substantial decrease in performance with hands crossed compared to uncrossed.

Importantly, we observed a main effect of the factor "Condition" [$F(2,60) = 67.2$, $p \leq 10\text{E}{-6}$], demonstrating much better performance in bimodal stimulation condition than when presenting auditory ($p \leq 10\text{E}{-6}$) or tactile ($p \leq 10\text{E}{-6}$) stimuli alone. As expected, this result demonstrates overall better performance in multisensory situations. We also observed better performance in audition than touch condition ($p \leq 10\text{E}{-4}$).

Finally, we also obtained an interaction effect between the factors "Position," "Condition," and "Group" [$F(4,60) = 4.4$, $p = .003$]. Post hoc analyses revealed that the performances obtained in auditory, tactile and bimodal condition were significantly lower in crossed than uncrossed position in the SC and LB group (range from $p = .01$ to $p \leq 10\text{E}{-6}$). However, in the EB group, although performance in auditory condition was significantly lower in crossed than uncrossed posture ($p \leq 10\text{E}{-6}$), there was no effect of posture in tactile ($p = .67$) or bimodal condition ($p = .15$). Even if the performance of EB also decreased in the crossed-hand posture in the latter two conditions, the statistical analyses demonstrate that the trend is not significant, and therefore the results suggest that the effect of crossing the hands on tactile and multimodal stimuli is at least as much less present for the EB than for the LB and SC.

To further investigate how crossing the hands affected performance differently in the three groups, we subtracted IE scores obtained in uncrossed posture from IE scores obtained in crossed posture (see Fig. 2B). This "crossed-posture effect" index was then submitted to a 3 (Group: EB, LB, SC; between-subjects factor) × 3 (Modalities: auditory, tactile, bimodal; within-subject factors) repeated measures ANOVA. Results showed no main effect of the factor "Group" [$F(2,30) = .16$, $p = .84$] or "Modalities" [$F(2,60) = 2.22$, $p = .12$], but demonstrated a significant interaction effect between the two factors [$F(4,60) = 4.4$, $p = .003$]. Post hoc analyses revealed that crossing the hands in SC disrupted the lateralization of tactile stimuli significantly more than auditory stimuli ($p = .006$), whereas the reverse was found in EB, where the crossed posture had a more detrimental effect on auditory than tactile performance ($p = .003$). Note that, in LB, no differences were observed between the two modalities ($p = .62$).

For all the above analyses, a results pattern similar to that found for the IE scores was observed for both accuracy scores and RTs (see Supporting figure).

To test for the presence of multisensory interactions in our RT data, we investigated whether the gain obtained in bimodal condition exceeded the statistical facilitation predicted by probability summation using Miller's *race model of inequality* [(Miller, 1982); see Section 2.4 for details]. We observed significant violation of

Table 2

Results of follow-up redundancy gain analysis and test for violation of race model inequality (Miller, 1982; Ulrich et al., 2007). *T*-tests were used to estimate in the three groups of subjects whether the fastest 50% of the cumulative RT distributions in bimodal condition were significantly faster than the race model predictions of the redundancy gain obtained when combining RTs recorded in both unimodal conditions, or the Bound (Miller, 1982). We found a statistically significant violation of race model inequality in almost all groups in both posture conditions, except for EB in crossed posture.

Posture	Group	Auditory	Tactile	Bound	Bimodal	t-Value$_{\text{(df)}}$	p-Value
Uncrossed	SC	343	371	327	310	$4{,}4_{(11)}$	0.001*
	LB	289	324	275	259	$4{,}69_{(10)}$	0.0009*
	EB	259	291	247	235	$2{,}75_{(9)}$	0.02*
Crossed	SC	400	439	384	372	$2{,}8_{(11)}$	0.02*
	LB	350	393	330	317	$2{,}51_{(10)}$	0.03*
	EB	310	332	288	277	$1{,}57_{(9)}$	0.15 (ns)

T-tests were used to estimate in the three groups of subjects whether the fastest 50% of the cumulative RT distributions in bimodal condition were significantly faster than the race model predictions of the redundancy gain obtained when combining RTs recorded in both unimodal conditions, or the Bound (Miller, 1982). We found a statistically significant violation of race model inequality in almost all groups in both posture conditions, except for EB in crossed posture.

[*] Asterisk refers to statistically significant values ($p \leq .05$).

the race model prediction in the three groups in both posture conditions, except for EB in the crossed posture (see Fig. 3). In the uncrossed posture, the race model was significantly violated in the three groups over the 10th (EB: $p = .005$; LB: $p = .005$; SC: $p = .00008$), 20th (EB: $p = .002$; LB: $p = .006$; SC: $p = .0002$), 30th (EB: $p = .02$; LB: $p = .0009$; SC: $p = .001$) and 40th (EB: $p = .04$; LB: $p = .001$; SC: $p = .006$) percentiles of the RT distribution and also at 50% in SC ($p = .009$) and LB ($p = .03$) and at 60% in SC ($p = .04$). In the crossed posture, the race model was significantly violated over the 10th ($p = .006$), 20th ($p = .004$) and 30th ($p = .02$) percentiles in SC, and over the 20th ($p = .03$), 40th ($p = .05$) and 50th ($p = .04$) percentiles in LB. No violation of the RACE model was found in EB in the crossed posture (all $p > .05$). To further support these results while avoiding multiple comparisons, we re-tested for race model violation in our data when 10–50% percentiles were pooled, representing the fastest 50% of the RT distribution. Here again, we found a statistically significant violation of the race model in almost all groups in both posture conditions, except for EB in crossed posture (see Table 2 for detailed statistics). These results demonstrate that the auditory and tactile channels are independent in crossed posture condition in EB.

4. Discussion

We first observed that the crossed-hand posture had an overall detrimental effect on performance when stimuli were presented to SC and LB in auditory and tactile condition. In the auditory condition, this crossed-hand effect is thought to be caused by a disruption in the spatial compatibility between the anatomical coordinates of the responding hand and the external sound coordinates such that hemispheric correspondence is reversed (Röder et al., 2007; experiment 2). In the tactile condition, this is thought to be due to a conflict between the internal (somatotopic) and external frames of reference for coding the tactile stimulus location because recent studies have demonstrated that tactile stimuli are automatically remapped into external coordinates beyond an initial somatotopic representation stage (Azanon & Soto-Faraco, 2008; Röder et al., 2004; Shore et al., 2002; Yamamoto & Kitazawa, 2001). However, and of major interest, we observed that crossing the hands did not significantly alter EB performance in tactile stimulus lateralization. This result is in line with recent experiments indicating that the remapping of tactile inputs into external coordinates occurs as a consequence of visual input during ontogeny (Röder et al., 2004, 2008). In other words, we believe that the absence of a crossed-hand effect in our tactile lateralization task in EB is attributable to the lack of automatic external remapping of touch in this population, which would shield them from the detrimental effect of a conflict between internal and external coordinates in the crossed-hand posture.

When further analyzing the detrimental crossed-hand effect, we observed a reversed pattern across modalities between SC and EB, with more impairment for tactile than auditory lateralization in SC and more impairment for auditory than tactile lateralization in EB (see Fig. 2B). As discussed above, when EB lateralize tactile stimuli in a crossed posture, the absence of automatic external remapping of the hand position may prevent the conflict between body-centred and external coordinates that is present in SC (Röder et al., 2004). However, sound lateralization in a crossed position requires an explicit matching of the external sound location with the anatomical coordinate of the responding hand for sending the correct motor command. We might therefore assume that because EB do not use a default external frame of reference to code the position of the responding hand, the conflict created by crossing the hands is more disrupting in EB than in SC in the auditory condition (Röder et al., 2007). Why the crossed-hand effect was more severe for the lateralization of tactile than auditory stimuli in SC is less clear. We may postulate that when SC receive and respond to a touch on the hand, they have to carry out a two-step external coordinate remapping process, once, when receiving the stimulus on the hand (the sensor) and again when producing a response to the stimulation (the effector). Performance decrement in the crossed posture due to a mismatch between the external and anatomical coordinates may therefore be caused by the two processing steps in SC, making them particularly sensitive to a crossed-hand effect.

Our data also demonstrated an overall improvement of performances in EB when compared to SC (see Fig. 2A). The usual interpretation of this recurrent finding in the literature is that sensory compensation in EB arises through an increased use of audition and touch since early childhood in blind when compared to sighted, which may improve their efficiency and trigger cerebral plasticity in absence of visual inputs (Collignon et al., 2006; Forster, Eardley, & Eimer, 2007; Goldreich & Kanics, 2003; Kujala, Lehtokoski, Alho, Kekoni, & Naatanen, 1997; Röder et al., 1999). Another, though not mutually exclusive explanation could be based upon the observation of the qualitative changes in the way EB process non-visual spatial stimuli (Eimer, 2004). As discussed at length above, EB do not use an external spatial reference system for sensory perception and action control (Röder et al., 2004, 2007) whereas SC do it by default, even when the use of a modality-specific reference frame would be sufficient to solve a particular task (Shore et al., 2002; Yamamoto & Kitazawa, 2001). The fact that EB do not make an automatic correspondence between a non-visual frame of reference and a visual one would thus contribute to a faster processing of non-visual spatial information in cases where such correspondence is not required to resolve the task. In fact, in the present study, the only situation where performance of EB was not significantly superior to the one of SC is when auditory stimuli had to be lateralized with the hands crossed (see Supporting Table 1), the only situation

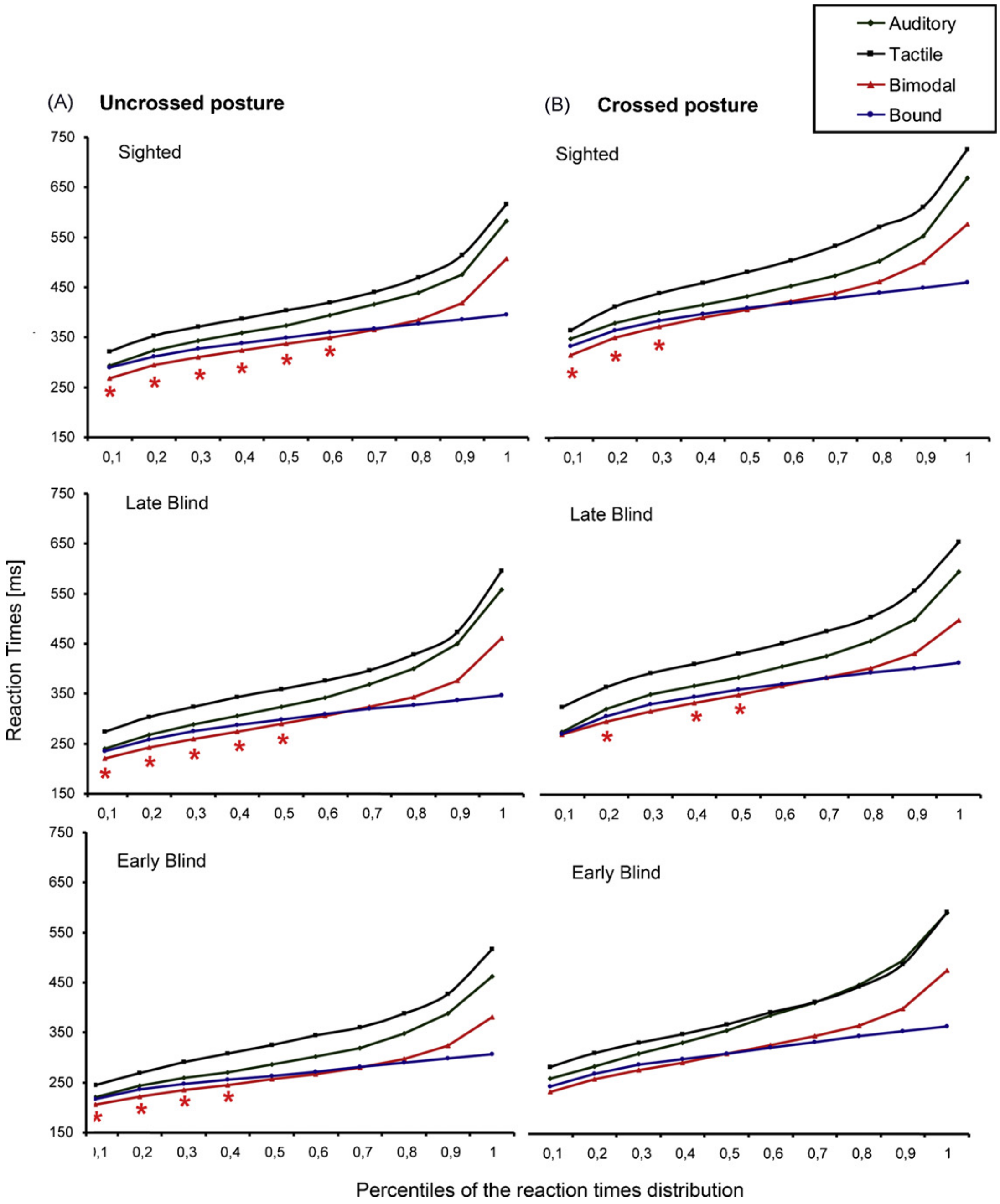

Fig. 3. Redundancy gain analysis and test for violation of race model inequality (Miller, 1982; Ulrich et al., 2007). Reaction times were obtained in either an uncrossed (left panels) or crossed posture (right panels) in sighted controls, late blind and early blind subjects. The graphic represents the cumulative density functions of the reaction times distribution obtained with congruent bimodal stimuli (red triangles) and their unisensory counterparts (tactile: black squares, auditory: grey diamonds) and the race model bound (blue dots) estimated from the unisensory distributions. The bound is obtained by the summation of the cumulative density functions obtained in the two unimodal conditions (auditory and tactile), thus providing an estimate of the upper bound for violation of the RACE model inequality. The *X*-axis refers to the percentiles of the reaction times distribution and the *Y*-axis to the mean reaction times obtained or estimated (in the case of the model bound) in each percentile bin. Bimodal values inferior to the bound indicate race model violation and asterisks refer to statistical significance (two-tailed *t*-test; $p \leq .05$). We observed that the race model inequality was significantly violated over the fastest quantiles of the reaction time distribution, supporting interaction accounts, except in the crossed posture in early blind subjects. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

which requires a voluntary remapping of hands position to efficiently resolve the task. It is thus sensible to assume that faster RTs in EB may be related, at least to some extent, to the absence of a time-consuming remapping process of touch and proprioception into external coordinates.

Interestingly, as for the detrimental crossed-hand effect or the overall performances in our tasks, LB demonstrated an intermediate pattern of performance between the scores obtained in SC and EB (see Fig. 2; no statistical differences between LB and SC or EB however). This may suggest that vision is not only necessary for the establishment but also for the maintenance of the automatic remapping process of touch/proprioception in external coordinates.

As expected, our results also showed better performance overall in bimodal condition compared to either of the constituent unisensory stimuli. This result illustrates the advantages of our ability to construct a more robust percept by integrating the information acquired by the different senses (Stein & Meredith, 1993). To further explore whether the multisensory gain obtained in bimodal condition reflects a true brain integration process, we tested whether redundant-target RTs are significantly faster than those predicted by a race between the two modalities independently (Miller, 1982; Ulrich et al., 2007); see Section 2.4 for details). Results for SC and LB in both posture conditions showed that the probability distribution of the response latency to the bimodal target was less than what could be expected from a simple probability summation of the two unimodal conditions. We therefore show for the first time, using race model violation, that SC as well as LB combine audiotactile stimuli in a truly integrative way across posture changes. In EB, however, race model violation with bimodal stimuli was obtained only in uncrossed-posture condition, suggesting audiotactile integration impairment when hands were crossed over the body midline. Because the auditory and tactile modalities initially code space in different reference systems (audition is external and touch is internal or body-centred), the brain has to align the spatial frames of reference used by our distal senses and the sensory information obtained from our bodies in order to merge audiotactile spatial information into a common percept. This is thought to be mediated by the automatic remapping process from somatotopic to external space, thereby providing a common spatial frame of reference for the coordination and integration of information obtained from touch and externally defined sensory cues acquired by audition or vision (Eimer, 2001; Gallace, Soto-Faraco, Dalton, Kreukniet, & Spence, 2008; Kennett, Eimer, Spence, & Driver, 2001; Lloyd et al., 2003; Soto-Faraco, Spence, & Kingstone, 2004). In the present study, the use of a common external spatial reference frame for action in SC and LB may have induced the alignment between audition and touch across posture changes, allowing multisensory integration in the uncrossed and crossed postures. However, if EB do not automatically remap touch into external spatial coordinates (Röder et al., 2004, 2008), the crossed posture may induce a conflict between the auditory and tactile frames of reference, which may prevent efficient multisensory integration. In other words, the absence of mandatory activation of an external reference frame for perception and action in EB may impair multisensory integration when there is a conflict between anatomical and external reference frames, for instance, when a sound has to be integrated with a touch in a hand-crossed posture.

These results could be related to developmental studies in humans and animals suggesting that multisensory functions develop gradually after birth and are greatly influenced by early sensory experiences (Gori, Del Viva, Sandini, & Burr, 2008; Lewkowicz, 2002; Nardini, Jones, Bedford, & Braddick, 2008; Neil et al., 2006; Wallace & Stein, 1997; Wallace & Stein, 2007; Wallace, Carriere, Perrault, Vaughan, & Stein, 2006). For example, Neil and collaborators recently investigated the development of audiovisual integration in spatial localization behavior in infants from 1 to 10 months of age. They found that infants less than 8 months of age did not exhibit a reliable violation of the race model inequality, whereas infants from 8 to 10 months old did. These findings are consistent with electrophysiological results in young cats and monkeys showing that multisensory integrative properties of neurons in the superior colliculus are not present at birth but emerge later in life (Wallace, Meredith, & Stein, 1998). These works show that multisensory processes in brain circuits mature slowly, suggesting that the multisensory circuitry is highly malleable and may be tied to sensory experiences acquired during postnatal life (Wallace, 2004). Recent research has demonstrated that neurons of the superior colliculus and the anterior ectosylvian sulcus (possibly the cat's homolog of posterior parietal cortex in primates) of cats raised in darkness showed highly altered multisensory integration properties for spatially corresponding audiovisual and audiotactile stimuli (Carriere et al., 2007; Champoux, Bacon, Lepore, & Guillemot, 2008; Wallace, Perrault, Hairston, & Stein, 2004). In a recent study, we also demonstrated a reduced engagement of the posterior parietal cortex for sound processing in early blind subjects (Collignon, Davare, Olivier, & De Volder, 2009). Note that these regions play a crucial role in the postural remapping processes that align spatial multisensory cues acquired from different coordinates (Avillac, Deneve, Olivier, Pouget, & Duhamel, 2005; Graziano, Cooke, & Taylor, 2000; Graziano, 1999; Knudsen & Brainard, 1991; Knudsen & Knudsen, 1985; Mullette-Gillman, Cohen, & Groh, 2005; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann, & Bremmer, 2005; Werner-Reiss, Kelly, Trause, Underhill, & Groh, 2003). These findings are also consistent with an event-related potential study demonstrating that the congenitally blind do not show cross-talk between tactile and auditory systems based on spatial features at the level of early sensory processing (Hotting, Rosler, & Röder, 2003). It is therefore possible that the absence of default external mapping coordinates combined with impaired multisensory interaction across posture changes in EB may be due to a dramatic change in the functional properties of neurons normally involved in these processes in SC as well as LB.

Acknowledgments

The authors thank S. Denis, J-P. Guillemot and P. Jolicoeur for their help with the experimental setup. This research was supported in part by the FRSQ Rehabilitation Network (REPAR; ML, FL, OC), an FRSQ Group grant (ML, FL), the Canada Research Chair Program (ML, FL), the Canadian Institutes of Health Research (ML, FL) and the Natural Sciences and Engineering Research Council of Canada (ML, FL, GC). OC is a postdoctoral researcher at the Belgian National Funds for Scientific Research (NFSR).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuropsychologia.2009.07.025.

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