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Research Report

Improved selective and divided spatial attention in early blind subjects

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ABSTRACT

Spatial attention paradigms using auditory or tactile stimulation were used to explore neural and behavioral reorganization in early blind subjects. Although it is commonly assumed that blind subjects outperform sighted subjects in such tasks, the empirical data to confirm this remain controversial. Moreover, previous studies have often confounded factors of sensory acuity with those of attention. In the present work, we compared the performance of individually matched early blind and sighted subjects during auditory and tactile tasks. These consisted of sensory acuity tests, simple reaction time task as well as selective and divided spatial attention tasks. Based on sensory measurements, we made sure that the reliability and salience of auditory and tactile information were identical between the two populations to estimate attentional performance independently of sensory influence. Results showed no difference between groups in either sensory sensitivity or simple reaction time task for both modalities. However, blind subjects displayed shorter reaction times than sighted subjects in both tactile and auditory selective spatial attention tasks and also in bimodal divided spatial attention tasks. The present study thus demonstrates an enhanced attentional performance in early blind subjects which is independent of sensory influence. These supra-normal abilities could be related to quantitative and qualitative changes in the way early visually deprived subjects process non-visual spatial information.

1. Introduction

Effect of visual loss on the remaining senses is an important issue in neuroscience today. It has long been debated whether blind individuals have perceptual advantages or disadvantages in processing information related to intact modalities (see for review Theoret et al., 2004). It was first thought that blindness might be detrimental to perception with the remaining senses since vision may be required to calibrate other sensory modalities (Locke, 1991; Rock, 1966). However, recent studies have re-examined this topic. It has been shown that blind people are at least as good (if not even better) than normal-sighted controls in non-visual processing, provided matching criteria with the control group are carefully selected (Neville and Bavelier, 2002). For example, several recent studies reported better performance (e.g., shorter reaction times) in blind versus sighted subjects when they were asked to attend various attributes of non visual stimulation (Hotting

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et al., 2004; Kujala et al., 1997b; Liotti et al., 1998; Röder et al., 1996, 1999a,b). Indeed, Kujala et al. compared selective (Kujala et al., 1995a) and divided (Kujala et al., 1997b) spatial attention capacity in early blind and sighted control subjects. They found faster reaction times in blind persons only during divided attention tasks. These authors thus suggested that enhanced performance of blind compared to sighted subjects in spatial attention tasks might be specific to conditions requiring the division of attention to simultaneously process auditory and tactile spatial information (Kujala et al., 1997b). However, other studies seem to indicate that blind subjects can also be more efficient than sighted subjects in selective attention tasks involving spatial discrimination (Hotting et al., 2004; Röder et al., 1996, 1999b).

A central problem for the interpretation the results of such experiments is possible confusion between the factors of sensory acuity and attentional processing. In a general evaluation of improved non-visual performance in blind persons, Hollins (1985) made a helpful distinction between basic sensitivity and sharpened attention to sensory cues which could be separated in terms of supra-normal abilities. Even though studies investigating basic acuity tasks have not demonstrated the same consistent superiority of the blind in tasks involving higher cognitive levels, sharpened sensitivity has been observed in this population. For example, a number of studies have demonstrated that early blind subjects have a better ability to discriminate basic features of auditory or tactile stimuli such as spectrum (Doucet et al., 2004), pitch (Gougoux et al., 2004; Hamilton et al., 2004; Witkin et al., 1968), timing (Muchnik et al., 1991; Röder et al., 2004; Stevens and Weaver, 2005), intensity (Benedetti and Loeb, 1972; Sterr et al., 1998), or fine spatial cues (Ashmead et al., 1998; Goldreich and Kanics, 2003; Grant et al., 2000; Lessard et al., 1998; Muchnik et al., 1991; Van Boven et al., 2000; Voss et al., 2004; Yabe and Kaga, 2005). Given the influence of stimulus saliency in reaction time task performance the superiority of early blind persons in attentional tasks may not involve attentional processes per se but rather supersensitivity, implying greater stimuli salience and reliability in this population. A greater sensitivity may thus lead to a better performance in attentional tasks that rely on this perceptual enhancement (Stevens and Weaver, 2005).

In order to further explore these unsolved questions about perceptual abilities of blind individuals, we designed an experiment to compare performance of matched blind and sighted individuals in sensory sensitivity tasks, simple reaction time task, and selective and divided attention tasks (see Fig. 1) with individually adjusted auditory and tactile stimuli. This stimuli adjustment would allow us to assess attentional performance independently of sensory influence. Our hypothesis was that blind persons would demonstrate an increased sensitivity to both auditory and tactile stimuli and would also be more efficient at both focusing and dividing their attention on these stimuli.

2. Results

Sensory thresholds and simple reaction time delays were compared between the two groups with Student's t test for independent samples. Data related to selective and divided attention tasks were then evaluated with repeated measures analysis of variance (ANOVA_{RM}) using the design of 2 groups (between-subjects factor: blind, sighted) × 3 attentional tasks (within-subjects factor: selective auditory, selective tactile, divided bimodal). Conditioned on significant F values, we used the Fisher LSD test for post hoc analyses. All significant results obtained with these parametric statistics were confirmed using non-parametric tests. Significance level for all statistics was fixed at $P < 0.05$.

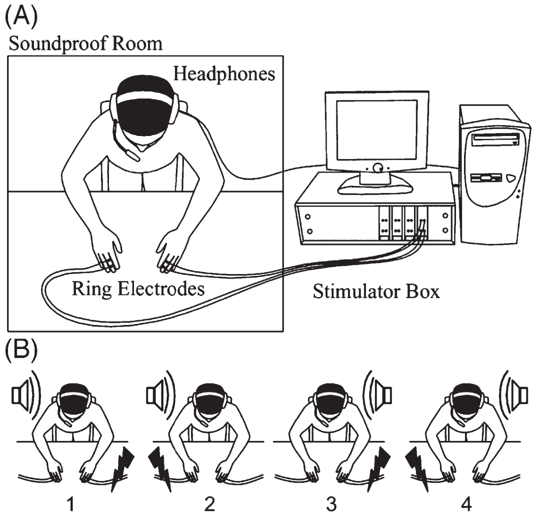

Fig. 1 – Experimental setup (A) and stimuli used in the experimental tasks (B). In the simple reaction time task, auditory and tactile selective attention tasks, and the bimodal divided attention task, participants were faced with four auditory–tactile stimulus combinations that depended on their spatial origin (left or right) as indicated in panel B. Subjects had to detect and respond vocally to specific stimuli depending on the task. In the simple reaction time task, subjects had to respond after every stimulus. In the attentional tasks, subjects had to detect either right-sided sounds [selective auditory condition as in panel B 1 or 2], or left-sided pulses [selective tactile condition as in panel B 1 or 3], or the combination of a right-sided sound and a left-sided pulse [divided bimodal condition as in panel B 1].

Based on "Hits" (hits rate, i.e., the proportion of targets correctly detected) and "FA" (false alarms rate, i.e., proportion of stimuli erroneously identified as target), accuracy scores in attentional tasks were computed in terms of discrimination measure "Pr" (Performance rating = Hits-FA) and the Response Bias "Br" (Bias rating = FA/(1 − Pr)) according to the Two-high Threshold Model (Snodgrass and Corwin, 1988).

2.1. Sensory discrimination and simple reaction time task

There was no significant difference between the two groups in terms of absolute auditory detection threshold expressed in dB SPL ($t(14) = -1.09$, $P = 0.29$; M ± SE: 1 ± 2.3 for the sighted; 2 ± 1.9 for the blind), absolute tactile detection threshold expressed in μA ($t(14) = -0.2$, $P = 0.84$; 2900 ± 1000 for the sighted; 3100 ± 2200 for the blind), and tactile pain threshold expressed in μA ($t(14) = -0.13$, $P = 0.9$; 5000 ± 1300 for the sighted; 4800 ± 2200 for the blind). Nor was there found significant difference between the two groups for just noticeable differences in interaural intensity expressed in percent of the reference tones ($t(14) = -1.17$, $P = 0.26$; 23 ± 5 for the sighted; 20 ± 7 for the blind), and no difference was found in just noticeable difference for intermanual intensity expressed in percent of the reference pulses ($t(14) = 0.35$, $P = 0.36$; 10 ± 6 for the sighted; 11 ± 4 for the blind). Moreover, there was no between-group difference in the simple reaction time task expressed in ms ($t(14) = 0.82$, $P = 0.43$; 327 ± 46 for the sighted; 300 ± 81 for the blind) (see Fig. 2).

2.2. *Selective and divided attention tasks*

ANOVAs on Pr score ($F(1/28) = 5.3$, $P = 0.01$) revealed a significant effect of the tasks. Post hoc analyses demonstrated that the divided attention task was significantly more difficult than the auditory selective attention task ($P = 0.003$) but not more so than the tactile selective attention task ($P = 0.1$). There was no between-group difference and no interaction effect between groups and tasks in terms of accuracy. However, as illustrated in Fig. 3, even if the overall ANOVA did not reach significance, blind subjects tended to be more accurate, at least in the selective auditory and the bimodal condition, than sighted subjects. The analysis of Br scores failed to reveal any significant results.

Consistent with the accuracy results, ANOVAs on reaction times revealed a significant effect of the tasks ($F(2/28) = 19.92$, $P = 0.000004$). Post hoc analyses demonstrated that reaction times in the divided attention task were significantly higher than in both auditory and tactile selective attention tasks ($P \leq 0.0001$). Moreover, analysis revealed that early blind subjects had significantly faster reaction times than sighted controls ($F(1/14) = 6.17$, $P = 0.026$). No interaction effect was found between groups and tasks ($F(2/28) = 2.18$, $P = 0.13$), suggesting an enhanced performance in the three tasks for the blind subjects (see Fig. 4).

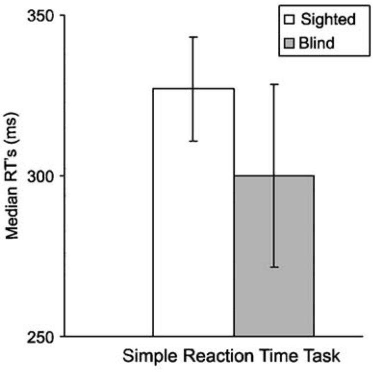

Fig. 2 – Processing speed in the simple reaction time task. Processing speed is illustrated with mean and standard errors of individual median reaction times (RTs) in both groups. The aim of this simple reaction time task was to estimate the time delay needed for a subject to produce a vocal reaction to our stimuli without any selection based on modality or spatial features. No significant difference between blind and sighted subjects was observed.

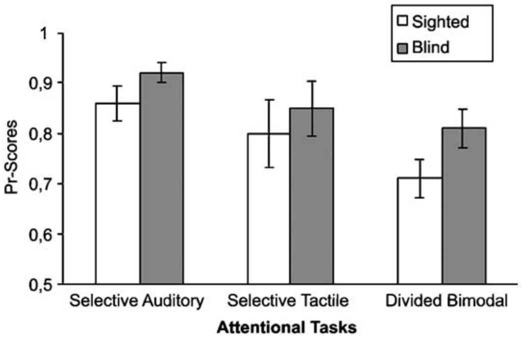

Fig. 3 – Accuracy performance in the attentional tasks. Accuracy performance is illustrated in both groups with mean and standard errors of individual Pr scores (Hits-FA) in the auditory and tactile selective attention tasks and in the bimodal divided attention task. No significant difference between blind and sighted subjects was observed.

Although there was no significant between-groups difference in simple reaction time task, we carried out an analysis of covariance in order to control the effect of simple reaction times on the results of selective and divided attention tasks. Results showed that the group main effect is still significant ($F(3/10) = 1.04$, $P = 0.04$). Thus, blind subjects' faster reaction times in these tasks were not due to simple reaction times.

It is known that task-irrelevant stimuli of a second modality can improve detection of stimuli when presented at the same location and impair detection when presented at a different spatial position (Stein and Meredith, 1990). In our selective attention tasks, there are two different target events (auditory stimuli on the right with tactile stimuli on the right or left, and tactile stimuli on the left with auditory stimuli on the right or left).

We separated performances for both the congruent and incongruent events to explore if the group differences changed when considering the two events separately. We thus carried out 2 (populations) × 3 (auditory, tactile and bimodal attentional tasks) ANOVAs on Pr scores (for accuracy) and reaction times, separately considering spatially congruent and incongruent events during the selective attention tasks.

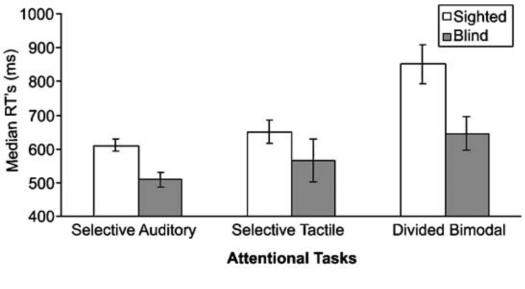

Fig. 4 – Processing speed in the attentional tasks. Processing speed is illustrated in both groups with mean and standard errors of individual median reaction times (RTs) in auditory and tactile selective attention tasks and in the divided attention task. Blind subjects had faster reaction times than sighted subjects in the spatial attention tasks.

ANOVAs on Pr scores with congruent events in selective auditory and tactile tasks revealed significant effect of the tasks ($F(2/28) = 18.06$, $P = 0.000009$). Post hoc analyses demonstrated that the divided attention task was significantly more difficult than the auditory ($P = 0.000002$) and tactile ($P = 0.0007$) selective attention tasks. ANOVAs on Pr scores with incongruent events in selective auditory and tactile tasks did not reveal any significant effects. Thus, it seems that differences between the selective and divided attention tasks in term of accuracy disappeared when considering only the spatially incongruent stimuli (physically identical stimuli in both attention conditions). The same ANOVAs on reaction times for congruent and incongruent events revealed significant effect of the tasks (Congruent: $F(2/28) = 19.55$, $P = 0.000005$; Incongruent: $F(2/28) = 20.93$, $P = 0.000003$) demonstrating longer RTs in the divided bimodal attention task as compared to both auditory (Congruent: $P = 0.000002$; Incongruent: $P = 0.000002$) and tactile (Congruent: $P = 0.00017$; Incongruent: $P = 0.000023$) selective attention tasks. Moreover, these ANOVAs revealed significant effects of the group (Congruent: $F(1/14) = 5.42$, $P = 0.04$; Incongruent: $F(1/14) = 7.42$, $P = 0.01$) demonstrating shorter reaction times in blind subjects with both congruent and incongruent events.

In order to further investigate differences between blind and sighted subjects regarding congruent and incongruent conditions, we carried out ANOVAs with the factors Group (blind/sighted) × Congruency (congruent/incongruent) × Modality (tactile/auditory) for Pr scores and reaction times in the selective attention tasks only. ANOVA on Pr scores showed a significant congruency effect ($F(1/14) = 7.17$, $P = 0.02$) demonstrating better accuracy performance in the congruent condition. Regarding ANOVA on reaction times, we found a significant effect of the group demonstrating shorter reaction times in blind subjects ($F(1/14) = 4.08$, $P = 0.05$). Absence of significant Group × Congruency interaction either for Pr scores ($F(1/14) = 0.34$, $P = 0.56$) or reaction times ($F(1/14) = 0.34$, $P = 0.57$) demonstrated that congruency did not influence between-group differences in our attentional tasks.

3. Discussion

The main finding of the present study was the demonstration of faster processing time in early blind compared to sighted subjects in selective auditory and tactile spatial attention tasks as well as in a bimodal divided attention task. Even if not statistically significant, accuracy scores also tended to indicate a better performance in blind subjects, demonstrating that differential reaction times did not result from a mere speed–accuracy trade-off. However, we observed no difference between the two groups, either in sensory sensitivity or in simple reaction time tasks. Our results thus demonstrate specific superior performance of early blind subjects when the task involved attending to some attributes of non-visual stimuli such as spatial location.

No difference was observed between blind and sighted people in basic sensory tasks. In agreement with previous studies (Benedetti and Loeb, 1972; Niemeyer and Starlinger, 1981), we did not find lower auditory detection thresholds in the blind. In the tactile domain, blind and sighted subjects were also equivalent in terms of detection threshold. Previously, Sterr et al. (1998) found lower detection thresholds in blind subjects when a light superficial pressure was applied by means of a pneumatic stimulator. However, in a second study by the same team using an identical method, this result was not confirmed (Sterr et al., 2003). Regarding tactile nociceptive sensibility, the present study demonstrated that early visual deprivation does not influence the perception of pain threshold. It seems thus that early visual deprivation does not lead to a significant decrease in either auditory, or tactile detection, or pain threshold.

Evaluation of just-noticeable differences for interaural and intermanual intensity also showed an absence of difference between the two groups. Several previous studies reported superiority of blind subjects in tactile acuity (Grant et al., 2000; Sterr et al., 1998; Sterr et al., 2003; Van Boven et al., 2000). However, methodological discrepancies between these studies and the present one make comparisons difficult. If recognition of fine spatial structures could be relevant for blind persons in their everyday life, as, e.g., for Braille reading, a high level of performance in the judgement of intermanual intensity difference would not be as crucial for them. Absence of blind superiority for the auditory just-noticeable difference in interaural intensity was more surprising. There exists an extensive literature demonstrating advantage of blindness in spatial hearing, suggesting that blind subjects made better use of acoustical indices in auditory spatial localization than sighted controls (Lessard et al., 1998; Röder et al., 1999b; Voss et al., 2004). Interaural intensity difference is one of the most important criteria for ecological sound localization, together with interaural time difference and spectral cues (Blauert, 1997). However, many experiments suggest that blind subjects are specifically better than sighted ones at using spectral localization cues. Investigation of spatial hearing in animals and humans has shown enhanced performance of blind compared to sighted subjects only when sounds were emitted from lateral positions (King and Parsons, 1999; Rauschecker and Kniepert, 1994; Röder et al., 1999b; Simon et al., 2002; Voss et al., 2004) or under monaural conditions (Doucet et al., 2004; Gougoux et al., 2005; Lessard et al., 1998), where binaural difference cues (time and sound level) are less reliable or absent (Lessard et al., 1998; Van Wanrooij and Van Opstal, 2004). Moreover, Doucet et al. (2004) showed that modifying spectral cues significantly decreased the supra-normal performance of early blind persons in monaural localization. This could explain the absence of blind person's superiority in the judgement of interaural intensity differences as investigated in the present study.

Given the results of the sensory adjustment phase and the absence of between-group differences in the simple reaction time task, the faster reaction times observed for blind subjects in selective and divided attention tasks could result neither from differences in stimuli relevance, nor from faster stimuli detection or voice production between the two groups. This suggests a more efficient modulatory role of attention in blind subjects when stimuli have to be selected according to modality and spatial features. On the basis of electrophysiological and behavioral findings, Kujala et al. (1995a, 1997b) suggested that one of the key differences between blind and sighted individuals in their use of non-visual modalities might result from the blind's improved ability to divide attention between two signal sources. However, like other investigations (Hotting et al., 2004; Röder et al., 1996, 1999b), we found enhanced performance in selective attention tasks. We believe that these discordant results could be explained by crucial differences in experimental paradigms. When looking closely at Kujala et al. (1995a, 1997b) results, reaction times were almost 150 ms faster in a bimodal divided attention task than in auditory or tactile selective attention tasks for all subjects, despite comparable accuracy scores. This unexpected result could perhaps be explained by attentional disengagement during selective attention due to the ease of the task. It is possible that the use of a monotonous oddball paradigm with easily discriminable stimuli in these studies could account for reduced attentiveness due to the reduced processing demand in this condition (see, e.g., Hazeltine et al., 2002). In contrast, when involved in a highly focusing attention paradigm, with individual calibration of stimuli like in the present study, blind subjects' superiority can also be observed in selective attention tasks.

As observed in the present study, the lack of visual experience would improve efficiency in non-visual selective and divided attention tasks. Abnormal development of the visual system is known to trigger cortical reorganization processes. For example, visual deprivation increases the amplitude of components of event-related potentials (ERPs) linked to attentional demand of the task in posterior regions of the brain during sound localization (Kujala et al., 1992; Leclerc et al., 2000, 2005; Röder et al., 1999b). In fact, studies that have reported cross-modal activations in the blind subjects used tasks requiring attentional processing of the stimuli (Gizewski et al., 2003; Kujala et al., 1995b, 2000, 2005; Liotti et al., 1998). Conversely, when blind subjects' attention was directed away from the stimulation, cross-modal activation could not be elicited by the stimulation. It was thus hypothesized that attention towards features of non-visual stimuli is a prerequisite for occipital–cortex activation in blind subjects (Kujala et al., 2005). Moreover, amplitudes of ERPs recorded in the occipital pole of blind subjects can also be affected by the difficulty of manipulation of the task (Rösler et al., 1993). Occipital activation in early blind subjects may appear as monotonically related to the amount of processing effort and always goes together with an equivalent amplitude covariation at other scalp sites (Röder et al., 1996). These results suggest that the better performance observed in our selective and divided attention tasks would represent an adaptative behavioral correlate of the cortical plasticity observed in early blind.

While recruitment of additional neural resources could induce quantitative differences in attentionally modulated non-visual perception in early blind persons, recent studies have also suggested that visual deprivation during early development results in important qualitative changes in non-visual spatial perception (Eimer, 2004). For example, Röder et al. (2004) asked participants to judge the temporal order in which two tactile stimuli were delivered to their left and right hands. As expected, these authors found that temporal order judgements of sighted participants were less accurate with crossed than with uncrossed hands, which would result from the conflict between external and somatotopic spatial codes. By contrast, a congenitally blind group was completely unaffected by crossing the hands. Thus, it seems that sighted persons always use a visually defined reference frame to localize tactile events in external space (Kitazawa, 2002) and are impaired by conflicting external and somatotopic spatial information. By contrast, congenitally blind subjects do not use external spatial coordinates and thus remain unaffected by this conflict. Authors (Röder et al., 2004) also reported a better temporal resolution in congenitally blind subjects, as compared to sighted ones for the crossed and uncrossed hand posture. The fact that there is no need, in the case of early blindness, to make a correspondence between a non-visual frame of reference and a visual one would contribute to a faster processing of non-visual spatial information. The same interpretation could fit with our results.

Another piece of evidence for qualitative changes in the early blind arises from recent studies on how such subjects perform multisensory processing using their remaining intact modalities. A recent ERP study demonstrated an altered auditory–tactile cross-modal link in congenitally blind subjects during a spatial attention task, suggesting that the blind subjects were less distracted by stimuli of a task of irrelevant modality (Hotting et al., 2004). Similarly, a task-irrelevant proprioceptive input influenced auditory localization in sighted but not in blind subjects (Warren, 1984). Such differences in cross-modal spatial interactions could also explain the shorter reaction times we observed in blind subjects because of a less distracting effect of our distractors.

However, even if we found classical multisensory effects such a decreased rate of target detection when task-irrelevant stimuli applied to a second modality are presented at a spatially incongruent position (Stein and Meredith, 1990), we did not find any between group differences for such effects. Indeed, this result does not support the idea of reduced multisensory interactions in early blind subjects. Alternatively, reduced multisensory interaction in blind subjects could be explained by enhanced perceptual skills of the blind within intact modalities (Hotting and Röder, 2004; Hotting et al., 2004). Since there is an inverse relationship between the reliability of a unimodal input and the amount of multisensory interaction (Ernst and Banks, 2002), it might be that the availability of more salient and reliable auditory and tactile information would attenuate multisensory interactions in the blind (Hotting et al., 2004). Absence of multisensory interaction differences between blind and sighted subjects in our attentional tasks might thus be explained by individual adjustment of our tactile and auditory stimuli allowing the selection of stimuli that had the same reliability for both groups. Further studies using tasks where auditory–tactile cross-modal links are extensively present should thus investigate more precisely the role of enhanced perceptual skills in multisensory interactions in blind subjects.

In studies exploring sharpened non-visual skills in blind people, spatial processing has been investigated in particular. This is probably due to the predominant role of vision in this cognitive ability and the related difficulty for blind individuals to efficiently extract crucial spatial information from touch and hearing to cope with their environment (Thinus-Blanc and Gaunet, 1997). Our observation that blind people outperform sighted subjects in non-visual spatial attention tasks should be relevant in their day-to-day cognitive interaction with the environment. Indeed, focusing their attention on an auditory or tactile space location to identify and quickly react to an event should be crucial for blind people to compensate for their lack of vision. However, compensatory mechanisms following visual deprivation could extend beyond the spatial domain. For example, faster processing and/or posterior distribution of ERP scalp topographies were also observed in non-spatial attention tasks involving pitch (Alho et al., 1993; Kujala et al., 1995b, 1997a; Röder et al., 1996, 1999a), intensity (Liotti et al., 1998), or verbal (Hugdahl et al., 2004) discrimination. It remains thus unanswered if enhanced performance in blind subjects during attentional tasks reflects a general modification of attentional process involved in any kind of cognitive processing or if reorganizations are specific to each separate cognitive process.

In conclusion, the present study shows enhanced attentional performance in early blind subjects compared to sighted controls, which is independent of sensory influence. Moreover, using a spatial attentional paradigm, we provide evidence that improvements could be present during selective and divided attention tasks. Therefore, these results further extend the view that blind individuals are able to compensate their lack of vision by developing capacities in their remaining senses that exceed those of sighted individuals.

4. Experimental procedure

4.1. Participants

This study included eight early blind and eight sighted control participants individually matched for age (range 19–67 years, mean ± SD: 35 ± 16 for blind subjects; respectively 23–61, 30 ± 13 for sighted subjects), gender (3 women in each group), handedness (6 right-handed, 1 left-handed and 1 ambidextrous in each group), and educational level. Blind subjects were totally blind (no light perception) due to congenital peripheral deficits except for one subject who lost sight completely at 18 months. Table 1 shows a summary of the blind subjects' characteristics. Sighted subjects were blindfolded during the experiment. No subjects reported a history of current or past neurological, psychiatric illness, or major auditory or somesthetic dysfunction. Subjects signed an informed consent form before testing and received monetary compensation for their participation. This experiment was approved by the Ethics committee of the School of medicine and University hospital of the Université Catholique de Louvain.

4.2. Stimuli

Auditory stimuli were prepared and generated using a computer. They consisted of pure sinusoidal tones of 2 kHz with a 170-ms duration delivered to the subject by headphones. The interaural level difference (a primary cue for sound localization in azimuth) was manipulated in order to induce intracranial left or right sound localization (Blauert, 1997). At the selected frequency of 2 kHz, the interaural level difference threshold is the lowest (Grantham, 1984) and is more efficient than interaural time delay for sound localization (Blauert, 1997). Tactile stimuli consisted of five short charge balanced biphasic square wave pulses (30 Hz, 105 μs). Their duration was 167 ms, close to the auditory stimuli duration. These electrical stimuli were applied to the skin using disposable ring electrodes (Nicolet Biomedical, Madison, USA) placed around the proximal and distal interphalangeal joints on the middle finger of each hand.

4.3. Stimuli adjustment

The advantage of not choosing stimuli intensities a priori was twofold. First, the perceptual salience of stimuli could be adjusted between the two groups. Moreover, given the age heterogeneity of the subjects and considering the age-related decline in acuity (Bonnet, 1986; Goldreich and Kanics, 2003), adjustment allowed the selection of stimuli that had the same reliability for all subjects.

Initially, the absolute detection threshold for right auditory stimulation was determined using the staircase method (Bonnet, 1986). Based on the Fechner law stating that intensity sensation varies as the logarithm of the physical stimulus intensity (Fechner, 1860), we transformed (multiplied by 2) the detection threshold logarithm in order to obtain a reference tone with individually adjusted intensity. Subjects were then requested to adjust the tone intensity in the left ear to reach the same intensity of sensation as that of the reference tone in the right ear, inducing midline sound localization. The absolute detection threshold was also measured for tactile stimulation. However, pretesting revealed that the Fechner law did not apply in this case. The multiplication by 2, when applied to tactile detection thresholds, induced stimuli that were either too weak or too painful, depending on the subject. The individual pain threshold was thus also determined for each hand using the staircase method (Bonnet, 1986). This pain threshold was decreased by 100 μA for each subject to get a prominent but nonetheless comfortable reference electrical stimulation for the experiment.

Just-noticeable stimulus intensity differences were then determined for both intermanual and interaural intensity levels and were expressed as a percent of either the reference tone or reference electrical stimulation, respectively. This was achieved using a two alternative forced choice task, where subjects had to determine if a delivered stimulation was stronger on the left or the right side. Localization was induced by decreasing the left or right intensity of the stereo channel for sounds and of the electrical

Table 1 – Characteristics of blind subjects

Subjects	Age	Educational level	Sex	Handedness	Onset of blindness	Cause of blindness
EB1	52	College degree	M	R	Congenital	Bilateral retinoblastoma
EB2	20	College degree	F	R	Congenital	Cytomégalovirus
EB3	30	High school degree	F	A	Congenital	Retrolental fibroplasia
EB4	19	College degree	M	L	Congenital	Premature birth
EB5	26	High school degree	M	R	Congenital	Genetic (*)
EB6	67	College degree	M	R	18 months	Accident (*)
EB7	30	Graduate school	F	R	Congenital	Bilateral retinoblastoma
EB8	37	College degree	M	R	Congenital	Premature birth

Note. EB: early blind; M: male; F: female; R: right handed; L: left handed; A: ambidextrous; (*) no additional details available.

stimulation for tactile stimuli. This allowed the determination of the individual intermanual and interaural intensity differences necessary to induce left or right localization sensations. However, because working at just-noticeable difference threshold levels resulted in selective and divided attention tasks that were too difficult for the subjects, the stimulus differences were emphasized by further decreasing the minimum auditory stimulus by a factor of 1.4 and the minimum tactile stimulus by a factor of 1.05. These constant transformations were selected using results from pretests performed on 10 additional subjects who did not participate in the main experiment (9 men; age range 23–60 years, mean age 29 ± 11 years).

4.4. *Selective and divided attention tasks*

Subjects were tested individually, comfortably seated on a chair in a completely dark and soundproof room (see Fig. 1A). They performed two selective attention tasks (one for each sensory modality) and one bimodal divided attention task. Task order was randomized across subjects and groups. In each attentional task, participants received four pairs of simultaneous auditory and tactile stimuli (see Fig. 1B). In the auditory selective attention task, subjects had to detect right-sided sounds (auditory target), in the tactile selective attention task, left-sided pulses (tactile target), and in the divided attention task, the combinations of a right-sided sound with a left-sided pulse (bimodal target). Opposite spatial location for auditory and tactile targets in the bimodal divided attention task was made to induce a real shift of attention. Indeed, Lloyd et al. (2003) demonstrated that it is possible to shift auditory attention without affecting the processing of tactile stimuli and vice versa when auditory and tactile attention are directed on the same side but not when directed on opposite sides.

We used a "Go–NoGo" procedure, in which subjects were instructed to say "oui" ("yes" in French) as quickly and accurately as possible when the target was perceived and to withhold their response if the stimulation was not a target. Each attentional task included 120 pairs of simultaneous auditory and tactile stimuli (50% targets and 50% distractors) presented in random order. A microphone was used in combination with the headphones to measure vocal reaction times within a range of 150–3000 ms post-stimulus. Mean interstimulus interval averaged 2250 ms within a range of 1500–3000 ms (rectangular distribution). Latencies of correct responses only were considered for analysis.

After these three attentional tasks, subjects performed one simple reaction time task. The sequence consisted of 120 pairs of the same auditory–tactile stimuli used in the attentional tasks. Compared to the previous tasks, the "oui" response was required after every stimulus. In addition, in order to decrease the attentional load, a warning signal (500-Hz sound, 50-ms duration, individually adjusted intensity) preceded each stimulus with a delay of 500 to 1500 ms. Interstimulus intervals varied to prevent anticipatory responses. Responses with a delay below 150 ms were not considered for analysis. The interstimulus interval between a subject's response and the following warning signal was set at 1000 ms. Whenever a subject did not respond, the warning signal appeared automatically 2000 ms after the previous stimulus.

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