## G Model NSY-3148; No. of Pages 6

## **ARTICLE IN PRESS**

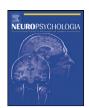
Neuropsychologia xxx (2009) xxx-xxx

FISEVIER

Contents lists available at ScienceDirect

## Neuropsychologia

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



## Interactions of cognitive and auditory abilities in congenitally blind individuals

Ariel Rokem<sup>a,1</sup>, Merav Ahissar<sup>a,b,\*</sup>

- <sup>a</sup> Department of Psychology, The Hebrew University of Jerusalem, Israel
- <sup>b</sup> Interdisciplinary Center for Neural Computation, The Hebrew University of Jerusalem, Israel

### ARTICLE INFO

Article history:
Received 16 July 2008
Received in revised form 11 December 2008
Accepted 12 December 2008
Available online xxx

Keywords: Blindness Cross-modal compensation Short-term memory Working memory Auditory perception Psychoacoustics

### ABSTRACT

Congenitally blind individuals have been found to show superior performance in perceptual and memory tasks. In the present study, we asked whether superior stimulus encoding could account for performance in memory tasks. We characterized the performance of a group of congenitally blind individuals on a series of auditory, memory and executive cognitive tasks and compared their performance to that of sighted controls matched for age, education and musical training.

As expected, we found superior verbal spans among congenitally blind individuals. Moreover, we found superior speech perception, measured by resilience to noise, and superior auditory frequency discrimination. However, when memory span was measured under conditions of equivalent speech perception, by adjusting the signal to noise ratio for each individual to the same level of perceptual difficulty (80% correct), the advantage in memory span was completely eliminated. Moreover, blind individuals did not possess any advantage in cognitive executive functions, such as manipulation of items in memory and math abilities. We propose that the short-term memory advantage of blind individuals results from better stimulus encoding, rather than from superiority at subsequent processing stages.

© 2008 Elsevier Ltd. All rights reserved.

## 1. Introduction

Folk traditions have long maintained that blind individuals manage to overcome some of the difficulties associated with their condition by developing extraordinary sensory and cognitive capacities (Wagner-Lampl & Oliver, 1994). In line with these traditions, recent studies found that early blind individuals perform better for a broad range of cognitive and perceptual skills, including short-term (Hull & Mason, 1995; Juurma, 1967; Smits & Mommers, 1976; Tillman & Bashaw, 1968) and long-term memory (Amedi, Raz, Pianka, Malach, & Zohary, 2003; Roder & Rosler, 2003), auditory frequency discrimination (Gougoux et al., 2004) and source localization (Gougoux, Zatorre, Lassonde, Voss, & Lepore, 2005; Lessard, Pare, Lepore, & Lassonde, 1998; Roder et al., 1999), and speech perception (Hugdahl et al., 2004; Muchnik, Efrati, Nemeth, Malin, & Hildesheimer, 1991; Starlinger & Niemeyer, 1981). In contrast, other studies found no advantage for blind individuals (Agrawal & Singh, 1988; Bliss, Kujala, & Hamalainen, 2004; Morrongiello, Timney, Humphrey, Anderson, & Skory, 1995; Sholl & Easton, 1986; Vecchi, 1998; Wyver & Markham, 1998).

0028-3932/\$ – see front matter © 2008 Elsevier Ltd. All rights reserved. doi:10.1016/j.neuropsychologia.2008.12.017

Bliss et al. (2004) found that blind individuals' performance in a tactile n-back task was equivalent to the performance of sighted individuals in the homologous visual task. Moreover, Vecchi (1998) found that blind individuals are more severely hampered by the requirement to actively manipulate the testing items in working memory when performing a tactile spatial memory task.

For sighted persons, the occipital cortex is activated by visual stimuli. For blind individuals, it is active during Braille reading (Burton et al., 2002; Sadato, Okada, Honda, & Yonekura, 2002; Sadato et al., 1996), verbal processing (Roder, Stock, Bien, Neville, & Rosler, 2002) and performance of memory tasks (Amedi et al., 2003; Burton, 2003). The spatial extent and level of the BOLD signal measured in these studies, was correlated with short-term memory performance (Amedi et al., 2003) and with episodic retrieval (Raz, Amedi, & Zohary, 2005). The functional relevance of this activity was also demonstrated by showing that reversibly inactivating occipital areas using transcranial magnetic stimulation (TMS) temporarily interferes with their Braille reading (Cohen et al., 1997) and with a verb generation task (Amedi, Agnes, Knecht, Zohary, & Cohen, 2004). These results suggest that the advantages found in the behavioural tests may rely on cross-modal plasticity that enables visual areas to encode stimuli and tasks of other modalities in early blind individuals. However, the actual role played by the occipital cortex of blind individuals performing these tasks is not yet resolved.

In this study, we asked whether the advantages that blind individuals possess in memory and perceptual tasks reflect sep-

<sup>\*</sup> Corresponding author at: The Department of Psychology, The Hebrew University of Jerusalem, Jerusalem 91905, Israel. Tel.: +972 2 5883409; fax: +972 2 5881159. E-mail address: msmerava@mscc.huji.ac.il (M. Ahissar).

<sup>&</sup>lt;sup>1</sup> Current address: Helen Wills Neuroscience Institute, University of California, Berkeley, USA.

# ARTICLE IN PRESS

A. Rokem, M. Ahissar / Neuropsychologia xxx (2009) xxx–xxx

**Table 1**Blind subjects and matched sighted controls.

Blind subject	Age	Sex	Education <sup>a</sup>	Cause of blindness	Control—age	Sex	Education	Comments
1	41	M	None; 12	Retinitis Pigmentosa	39	M	None; 12	Blind subject has some residual light vision
2	29	F	None; 12	Oxygen poisoning	29	F	None; 12	
3	30	F	BA; 15	Oxygen poisoning	32	F	BA; 15	
4	30	M	None; 12	Oxygen poisoning	33	M	MA; 17	
5	29	F	BA; 17	Microphthalmia	27	F	None; 14	
6	34	M	MA; 21	Oxygen poisoning	34	M	MA; 17	
7	23	F	None; 14	Oxygen poisoning	23	F	None; 14	
8	22	F	None; 13	Anophthalmia	22	M	None; 12	Both subjects are experienced musicians
9	27	F	None; 12	Glaucoma	25	F	None; 14	•
10	34	M	BA; 16	Oxygen poisoning	33	M	BA; 16	
11	30	M	None; 12		29	M	None; 12	
12	22	F	None; 14		21	F	None; 13	
13	22	F	None; 12	Retinopathy of prematurity	22	F	None; 12	Both subjects are experienced musicians
14	43	M	None; 11	Glaucoma	48	M	None; 12	•
15	55	M	None; 14	Glaucoma and trachoma	54	M	MA; 17	Both subjects are piano tuners. Control subject is not a native speaker of Hebrew
16	38	M	BA; 15		32	M	BA; 15	Blind subject has some residual light vision

<sup>&</sup>lt;sup>a</sup> Highest diploma earned; years of formal education.

arate compensation mechanisms (i.e. greater memory capacity in addition to their superior sensory processes), or alternatively, whether both stem from a common perceptual compensation mechanism.

In order to address this question, we measured both cognitive and sensory abilities in a group of congenitally blind individuals and compared their performance to that of a matched group of sighted individuals. In order to dissociate memory advantage resulting from improved retention and retrieval mechanisms from that resulting from better sensory encoding, we tested our participants' memory under matched perception: memory of pseudo-words was measured when the stimuli were played at the level of the participants' perceptual thresholds. This condition eliminated potential advantages in sensory representation of the remembered items. When we eliminated the improved stimulus encoding of blind individuals, their memory superiority was also eliminated, implying that their improved memory abilities result from improved stimulus encoding rather than superior abilities at subsequent memory-related processes.

## 2. Methods

## 2.1. Subjects

Sixteen congenitally blind and sixteen sighted individuals participated in this study (Table 1). Sighted individuals were recruited to match the blind participants in age (on average: Blind:  $31.8 \pm 2.2$  yrs.; Sighted:  $31.9 \pm 2.2$  yrs.), gender and education (on average: Blind:  $14.1 \pm 0.6$  yrs.; Sighted:  $14.1 \pm 0.5$  yrs.). Since musical experience may have an effect on the tasks we studied (Kishon-Rabin, Amir, Vexler, & Zaltz, 2001; Schon, Magne, & Besson, 2004), blind participants with special musical training (experienced musicians or piano tuners) were matched to control subjects with similar musical training. All participants, except one of the control subjects, chosen to match musical experience, were native Hebrew speakers. All participants reported normal hearing and gave informed consent for participation.

## 2.2. Apparatus, stimuli and procedure

## 2.2.1. Standard tasks

The standard measure we used for assessing short-term memory was Digit Span (Wechsler Adult Intelligence Scale, 3rd edition; Wechsler, 1997; Hebrew version: PsychTec, Jerusalem, Israel). This test is composed of two subtests, named Digit Forward (DF) and Digit Backward (DB). In both subtests, participants are presented with sequences of digits, which are gradually lengthened by one digit until the participant fails in two consecutive sequences. In DF, the participant is asked to repeat the sequence as presented, and in DB the participant is asked to repeat the sequence in reverse order. A standard score was derived for each participant, by normalizing performance to the age norms.

The Arithmetic subtest of the WAIS-III was also administered. This test requires rapid, simple calculations (e.g., "two apples cost 31 cents, how much would a dozen cost?").

#### 2.2.2. Auditory assessments

Auditory stimuli were played using in-house software designed for TDT system 3 (Tucker Davis Technologies, Alachua, FL, USA) and HD-280 headphones (Sennheiser Electronic GmbH, Wedemark, Germany). Assessments were administered in a sound-attenuated room. Sighted participants were blindfolded when performing the tasks in order to neutralize any visual cues. Proprioceptive feedback, in the form of a slight vibration whenever the participant made an error, was given through a Force-feedback Joystick (Microsoft, Redmond, WA, USA) held by the participant.

### 2.2.3. Speech perception

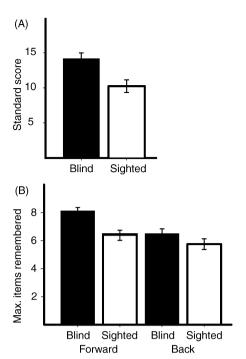
Verbal stimuli were a set of ten disyllabic pseudo-words designed to resemble Hebrew phonetics and phonology. Two instances of each pseudo-word were recorded in a sound-attenuated room. Thereafter the length of each word was set to 0.8 s, using Praat (Boersma & Weenik, 2002), and the RMS amplitude of all words was equated. Participants were familiarized with the stimuli by first hearing all the pseudo-words at 45 dB, a level at which participants were able to correctly repeat 100% of the words. Thereafter, thresholds for perception of the pseudo-words were determined using an assessment containing 100 trials. In each trial, the participant was asked to repeat the pseudo-word (randomly chosen in each trial from the set of ten pseudo-words). The level at which the stimulus was played in the following trial was adjusted, according to the participant's reply, using a three up-one down staircase procedure which converges to ~80% correct stimulus identification (Levitt, 1970).

This procedure was applied twice: first in a quiet background and then, after a short pause (1–2 min.), with a masking noise of 60 dB. The noise was a standard speech noise designed for use in audiological examinations of speech perception (Dreschler, Verschuure, Ludvigsen, & Westermann, 2001) composed of spectral and temporal components matched to those of human speech, with the phase spectrum scrambled. Thresholds were defined as the average intensity for the last five reversals of the staircase procedure.

## 2.2.4. Two-tone frequency discrimination

Thresholds were measured using two tasks, requiring same/different and high/low discriminations. These two tasks use the same stimuli but put different loads on working memory, with same-different requiring only change detection and high-low requiring a sign related comparison (Ahissar, Lubin, Putter-Katz, & Banai, 2006). In each task, two conditions were applied: in the first condition, one of the tones in each trial was 1 kHz (a reference tone). The other tone could either be 1 kHz or a higher frequency. In the other condition, there was no fixed reference tone: one tone was randomly chosen from a range of 1-2 kHz, and the other was either the same as or higher frequency than the first tone (the order of presentation of the two tones was randomized on each trial). This latter procedure put a greater demand on working memory, since the repeated reference could not be used as an anchoring stimulus, and a relative comparison had to be done in every trial (see discussion in Ahissar et al., 2006). In all four assessments, tone durations were 50 ms and intertone-intervals were 950 ms. Participants replied by pressing one of two buttons. The difference between the comparison tone and the standard tone in the following trial was adjusted according to the participant's reply, in the same staircase procedure which was used for speech perception, converging on  ${\sim}80\%$  correct responses. Each procedure (2 tasks × 2 conditions) was administered three times. The first assessment consisted of 30 trials, and the following two assessments consisted of 60 trials each. In each assessment, thresholds were defined as the average frequency difference for the last five reversals of the staircase procedure. Conditions and tasks were counterbalanced between participants. The thresholds reported here are the aver-

Please cite this article in press as: Rokem, A., & Ahissar, M. Interactions of cognitive and auditory abilities in congenitally blind individuals. *Neuropsychologia* (2009), doi:10.1016/j.neuropsychologia.2008.12.017



**Fig. 1.** Digit Span memory of blind individuals compared with that of sighted individuals. (A) Standard scores. Performance of the blind individuals (black) is compared with that of the sighted individuals (white). Task is standardized to an age-group norm so that population average is 10 with standard deviation of 1.5. (B) Maximal spans on each of the two tasks comprising the digit span subtest: 'Digits Forward' and 'Digits Backward'. Error bars denote S.E.M.

age of all 12 assessments. A three-way (repetition  $\times$  task  $\times$  condition) ANOVA was applied to the data.

## 2.2.5. Verbal memory under matched perception

Short-term memory was assessed by asking participants to repeat 1–5 item long sequences of pseudo-words. The set of items in this task was the same set of pseudo-words used in the speech perception tasks (see Section 2.2.3). Each sequence length was presented 5 times (with 5 different sequences). The different lengths were presented in a pseudo-random order. Sequences containing only one word were also included to ensure that the previously measured thresholds were reproduced. This procedure was repeated under three conditions:

- (i) Above threshold intensity: All stimuli were presented at 45 dB. This condition was applied first.
- (ii) At an intensity level yielding 80% identification: For each participant, stimuli were presented at the level previously determined as yielding 80% correct.
- (iii) At an intensity level yielding 80% correct identification in noise: Stimuli were embedded in 60 dB of speech noise. For each individual, speech stimuli were presented at the level determined as the 80% threshold in noise.

The order of administering assessments ii and iii was counter balanced across participants.

## 3. Results

Digit Spans of the blind participants were substantially better than their matched controls ( $F_{1,30}$  = 8.6, p<0.01). The average standard score of the blind individuals, 14.2 ± 0.8 (S.E.M.), was approximately three standard deviations higher than the standard score of the general population: 10 ± 1.5 (S.D.). The average of our control population, 10.2 ± 0.9 (S.E.M.), was not significantly different from the age-corrected norm.

However, when the standard scores from the two subtests were separated into forward and backward components, it became apparent that the significant advantage in Digit Span was mostly due to the large difference between the groups in the Digit Forward (DF) subtest, as shown in Fig. 1B (left bars). The forward span (defined as the maximal number of items which could be repeated without error) of the blind individuals was, on average,  $8.1 \pm 0.2$  (S.E.M.) digits compared to  $6.4 \pm 0.4$  (S.E.M.) of the controls ( $t_{30} = 4.1$ , p < 0.001).

In contrast to DF, the advantage of blind individuals in the Digit Backward (DB) subtest was quite small and failed to reach significance, as shown in Fig. 1B ( $t_{30}$  = 1.6, p>0.1). A statistically significant interaction between group and subtest ( $F_{1,30}$  = 6.8, p<0.05) indicates that the requirement to manipulate items (repeating the sequence in reverse order) hampered the performance of blind individuals more than it did so for the controls. Thus, while blind individuals could hold more items in their short-term memory, they had no such benefit when asked to manipulate these elements. Additionally, we found no advantage for blind participants in the arithmetic subtest of the WAIS (blind:  $10.8 \pm 0.9$  (S.E.M.), sighted:  $10.4 \pm 1.0$  (S.E.M.);  $t_{30}$  = 0.7, p>0.5), which also requires cognitive manipulation of remembered items. The scores in the arithmetic test were significantly correlated with scores in DB (r=0.53, p<0.01), suggesting that they tap similar mechanisms.

In order to measure verbal spans for untrained material with no semantic content, we assessed spans for pseudo-words. As shown in Fig. 2 (left graph), the blind participants performed significantly better in this task as well ( $F_{1,30}$  = 5.2, p < 0.05; mean maximal spans for the blind: 4.6  $\pm$  0.2 (S.E.M.) and sighted: 4.1  $\pm$  0.2;  $t_{30}$  = 1.9,  $p_{\text{one-tailed}}$  < 0.05). Note that even though both tasks are formally rather similar, the magnitude of superior performance on this task did not match the magnitude of superior performance in DF. A 2  $\times$  2 ANOVA (with group and task as factors) comparing the maximal span achieved in DF with the maximal span achieved in the pseudowords shows not only a main effect of group ( $F_{1,30}$  = 12.8, P < 0.001)

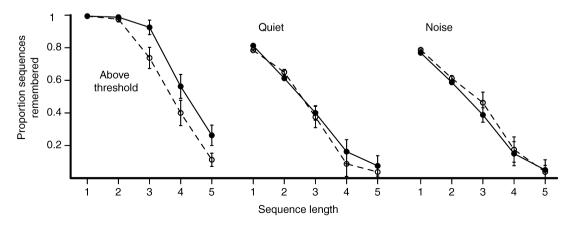


Fig. 2. Pseudo-word memory. Performance of blind (filled circles, solid line) and sighted (empty circles, dashed line) individuals on a test of pseudo-word spans. The task was repeated under three conditions: supra-threshold presentation (left graphs), at threshold in quiet background (middle graph), and at threshold with background noise (right graph). The proportion of correctly repeated sequences is plotted as a function of the length of the sequence. Error bars denote S.E.M.

## ARTICLE IN PRESS

A. Rokem, M. Ahissar / Neuropsychologia xxx (2009) xxx-xxx

**Fig. 3.** Speech perception thresholds. Threshold values of signal intensity for correctly repeating pseudo-words in a quiet background (A) and embedded in a background of speech noise (B). Population means (black cross) and single participant data points (grey). Blind individuals (triangles) have lower thresholds than sighted matched controls (circles). Error bars denote S.E.M.

but also an interaction between the group and the task ( $F_{1,30}$  = 13.9, p < 0.001), suggesting that the superior performance in the pseudoword span did not fully account for the superior performance in DF.

To assess whether the blind participants encoded speech stimuli (i.e. these pseudo-words) better than the sighted controls, we measured their perceptual thresholds for identifying these word and the robustness of their speech perception to noise. Signal levels required by the blind participants under both conditions were significantly lower, as shown in Fig. 3 ( $F_{1.30} = 4.5$ , p < 0.05).

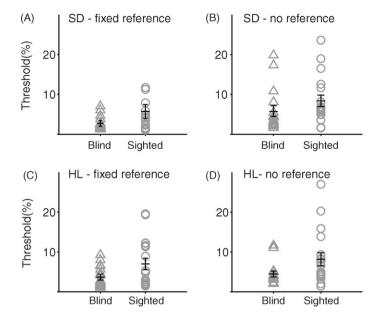
Participants also performed frequency discrimination tasks. Overall performance in all frequency discrimination tasks was better in the blind population (main effect of group:  $F_{1,30} = 4.2$ , p < 0.05; no significant interactions were found).

To evaluate whether there was an interaction between the superior performance in the sensory domain and the superior performance in the cognitive domain, we equated perceptual performance in blind and sighted individuals and assessed memory spans under matched speech perception. Rather than measuring pseudo-word span under equal physical conditions (e.g. suprathreshold conditions, as shown in Fig. 2, left graph), we assessed the span of each individual at his/her threshold for 80% correct identification of the pseudo-words. Under these conditions, the difference between the blind and the sighted individuals' memory span was completely eliminated. Rates of successful repetitions of 2-5 pseudo-word lists were similar in the two populations, both when the assessment was conducted in quiet (Fig. 2, middle plot) and when conducted in noise (Fig. 2, right plot). Note that in both groups identification of one pseudo-word was not significantly different from 80% (verified by t-tests, p > 0.05 for all four cases). This means that the previously measured threshold levels were replicated in the context of the span assessment.

## 4. Discussion

In this study we found that blind individuals possess a substantial advantage in memory tasks, when they are tested on familiar items in what are probably highly trained tasks, such as Digit Span forward. When tested with unfamiliar items (pseudo-words) this advantage decreased, though it remained significant. This memory advantage was fully accounted for by improved perception. Thus, when perception of the blind and sighted controls was matched by adding more noise to the speech sounds presented to blind individuals, memory span of these groups overlapped. In a complementary manner, blind individuals did not perform better when manipulating items in memory, an ability that is presumably not limited by perceptual encoding.

One concern with this kind of research is the matching of appropriate controls. For example, several of our experimental par-



**Fig. 4.** Thresholds in psychoacoustic frequency discrimination tasks. Population means (black cross) and single participant data points (grey). Four tasks were performed: (A) Same–Different discrimination, with a fixed standard. (B) Same–Different discrimination, with a random standard. (C) High–Low discrimination, with a fixed standard. (D) High–Low discrimination, with a random standard. Blind individuals (triangles) have overall lower thresholds than sighted matched controls (circles). Error bars denote S.E.M.

ticipants are proficient musicians (including a piano tuner, see Table 1). Since musicians are known to possess better abilities in psychoacoustic tasks (Tervaniemi, Just, Koelsch, Widmann, & Schröger, 2005), if we had matched these individuals with non-musician sighted control participants, we would not have been able to determine the relative contributions of blindness and expertise to the differences between the groups. Therefore, we formed a control group matched on a *participant-by-participant* basis for potentially relevant factors, including age, education and musical experience.

Even after matching for these factors, we have replicated previous findings of inter-group differences. Blind individuals were superior in tests of auditory abilities: thresholds in pitch discriminations were lower in the blind than in the matched controls, replicating previous studies (Gougoux et al., 2004), and speech perception thresholds, in a quiet background and when embedded in noise, were also lower in the blind individuals, also replicating previous results (Hugdahl et al., 2004; Muchnik et al., 1991; Starlinger & Niemeyer, 1981). However, these differences, though significant, were not large (in terms of difference in standard deviations). Thus the signal threshold difference in speech perception was approximately 2 dB SPL, and groups differed by approximately 0.3 S.D. Similarly, the differences found in the frequency discrimination tasks were approximately 5%, which was approximately 0.5 S.D. This should be compared with the 3 S.D.s difference found in Digit Span. Moreover, the range of abilities spanned by the entire population was similar for both groups (Figs. 3 and 4). We found no blind individuals with extremely superior perceptual skills in our tasks. However, there were more participants with slightly better performance in this group. Previous studies have found qualitatively different performance among blind individuals in some tasks. For example, some blind individuals could perform precise monaural sound source localization, a task that could not be performed by sighted individuals (Lessard et al., 1998).

The most substantial inter-group superiority of the blind individuals was found for Digit Forward, replicating previous findings.

Please cite this article in press as: Rokem, A., & Ahissar, M. Interactions of cognitive and auditory abilities in congenitally blind individuals. Neuropsychologia (2009), doi:10.1016/j.neuropsychologia.2008.12.017

5

Performance in the blind group was 3 S.D.s better than the average controls. Note that the controls' average span (6.4 digits) was slightly lower than the "magical" 7 usually mentioned as the average digit span in the normal population (Miller, 1956). The slightly lower average probably results from two factors. First, our population was somewhat older than average student age. Performance in this test is expected to decline by 0–1 digits between age 20 and 31 (Hester, Kinsella, & Ong, 2004; Wechsler, 1997). Second, most digit names (9 of 10) in Hebrew (the native language spoken by most of our participants and the language of testing) are disyllabic and therefore take more time to pronounce and require more phonological memory than their English counter-parts (an effect known as the word-length effect; Naveh-Benjamin & Ayres, 1986).

When tested on the memory of a set of previously unfamiliar pseudo-words, blind individuals still did better than the sighted individuals, yet the difference was much smaller and could not fully account for the difference observed in DF. Since memorizing series of digits is probably a highly trained task (for example, at least until recently, it was useful for memorizing telephone numbers), the superiority demonstrated by the blind individuals in this task may also reflect better strategies that were specifically developed for this task, rather than a generally improved verbal span.

Having found that both perception and short-term memory are superior in the group of early blind individuals, we asked whether these two advantages reflect separate compensation mechanisms at different processing levels, e.g. encoding versus retention and retrieval. Alternatively, there may be no separate short-term memory superiority, but rather the perceptual benefit leads to a memory benefit, since better encoding of speech signals yields larger spans. Indeed, we found that the superiority in pseudo-word span could be explained by the superiority in speech perception: when memory for sequences of pseudo-words was assessed under matched speech perception conditions, the memory advantage of the blind individuals was completely eliminated. A possible interpretation of this result is that improved sensory encoding may allow sequencing and chunking, which in turns supports better memory performance (see for example Pelli, Farell, & Moore, 2003 for a demonstration of hampered chunking under noisy conditions, in the visual domain). The ability to chunk remembered items could also be a part of the specifically trained skills that blind individuals acquire in development. A recent study showed that memory advantages in the blind may stem from their ability to chunk together consecutively presented items (Raz, Striem, Pundak, Orlov, & Zohary, 2007).

Finally, when a memory repetition task (Digit Forward) was modified into a memory manipulation task (Digit Backward), blind individuals lost most of their advantage. The latter finding suggests that the superior short-term memory could not be attributed to improved executive functions (Baddeley, 2003). The lack of arithmetic performance differences between blind and sighted individuals and the finding that scores in the arithmetic test were correlated with scores in DB is consistent with this interpretation. This interpretation is also consistent with previous findings, showing that blind individuals performed no better than sighted individuals when a memory task required manipulation or elaboration of the remembered items (Bliss et al., 2004; Vecchi, 1998).

Our overall findings that blind individuals possess superior auditory and verbal encoding indicate a significant degree of behavioural compensation. It would be of interest to further study whether this superiority results from recruitment of typically-visual areas (e.g. occipital cortex; Amedi et al., 2003; Burton, 2003; Burton et al., 2002; Raz et al., 2005; Roder et al., 2002; Sadato et al., 1996, 2002) or can be fully accounted for by enhanced perceptual learning processes, whose nature is similar to those of the general sighted population.

## Acknowledgements

We thank Ehud Zohary and Noa Raz for help in locating participants for this study and for helpful discussions and comments on an earlier version of the manuscript. We thank Michael Silver and Thomas Naselaris for many helpful comments on the manuscript. We thank Yedida Lubin, Mor Nahum and Mark Shovman for technical assistance in conducting this study. We thank Galit Hasan-Rokem for help in locating references on the folklore of blindness.

This study was supported by a Center of Excellence grant from the Israeli Science Foundation, and by the Volkswagen foundation. Ariel Rokem was partially supported through a scholarship from the Vera and David Finkel Student Aid Endowment Fund.

### References

- Agrawal, R., & Singh, M. P. (1988). Primacy and recency effects among the blind. Journal of Psychological Researches, 32, 26–30.
- Ahissar, M., Lubin, Y., Putter-Katz, H., & Banai, K. (2006). Dyslexia and the failure to form a perceptual anchor. *Nature Neuroscience*, 9(12), 1558–1564.
- Amedi, A., Agnes, F., Knecht, S., Zohary, E., & Cohen, L. G. (2004). Transcranial magnetic stimulation of the occipital pole interferes with verbal processing in blind subjects. *Nature Neuroscience*, 7(11), 1266–1270.
- 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*(7), 758–766.
- Baddeley, A. (2003). Working memory: Looking back and looking forward. Nature Reviews Neuroscience, 4, 829–839.
- Bliss, I., Kujala, T., & Hamalainen, H. (2004). Comparison of blind and sighted participants' performance in a letter recognition working memory task. *Cognitive Brain Research*, 18, 273–277.
- Boersma, P., & Weenik, D. (2002). Praat: Doing phonetics by computer. Retrieved from: http://www.praat.org
- Burton, H. (2003). Visual cortex activity in early and late blind people. *Journal of Neuroscience*, 23(10), 4005–4011.
- Burton, H., Snyder, A. Z., Conturo, T. E., Akbudak, E., Ollinger, J. M., & Raichle, M. E. (2002). Adaptive changes in early and late blind: A fMRI study of Braille reading. *Journal of Neurophysiology*, 87, 589–607.
- 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.
- Dreschler, W. A., Verschuure, H., Ludvigsen, C., & Westermann, S. (2001). ICRA noises: Artificial noise signals with speech-like spectral and temporal properties for hearing instrument assessment. International Collegium for Rehabilitative Audiology. *Audiology*, *40*(3), 148–157.
- Gougoux, F., Lepore, F., Lassonde, M., Voss, P., Zatorre, R. J., & Belin, P. (2004). Neuropsychology: Pitch discrimination in the early blind. *Nature*, *430*(6997), 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*(2), e27.
- Hester, R. L., Kinsella, G. J., & Ong, B. (2004). Effect of age on forward and backward span tasks. *Journal of the International Neuropsychological Society*, 10(4), 475– 481
- Hugdahl, K., Ek, M., Takio, F., Rintee, T., Tuomainen, J., Haarala, C., et al. (2004). Blind individuals show enhanced perceptual and attentional sensitivity for identification of speech sounds. *Cognitive Brain Research*, 19(1), 28–32.
- Hull, T., & Mason, H. (1995). Performance of blind children on digit span tests. *Journal of Visual Impairment and Blindness*, 89(2), 166–169.
- Juurma, J. (1967). Ability structure and loss of vision. New York: American Foundation for the blind.
- Kishon-Rabin, L., Amir, O., Vexler, Y., & Zaltz, Y. (2001). Pitch discrimination: Are professional musicians better than non-musicians? *Journal of Basic and Clinical Physiology and Pharmacology*, 12, 125–143.
- Lessard, N., Pare, M., Lepore, F., & Lassonde, M. (1998). Early-blind human subjects localize sound sources better than sighted subjects. *Nature*, *395*(6699), 278–280.
- Levitt, H. (1970). Transformed up-down methods in psychoacoustics. *Journal of Acoustic Society of America*, 49, 467–477.
- Miller, G. A. (1956). The magical number seven, plus or minus two: Some limits on our capacity for processing information. *The Psychological Review*, *63*, 81–97.
- Morrongiello, B. A., Timney, B., Humphrey, G. K., Anderson, S., & Skory, C. (1995). Spatial knowledge in blind and sighted children. *Journal of Experimental Child Psychology*, 59, 211–233.
- Muchnik, C., Efrati, M., Nemeth, E., Malin, M., & Hildesheimer, M. (1991). Central auditory skills in blind and sighted subjects. Scandinavian Audiology, 20(1), 19–23.
- Naveh-Benjamin, M., & Ayres, T. J. (1986). Digit span, reading rate and lingustic relativity. *Quarterly Journal of Experimental Psychology*, 38A, 739–751.
- Pelli, D. G., Farell, B., & Moore, D. C. (2003). The remarkable inefficiency of word recognition. *Nature*, 423(6941), 752–756.

# ARTICLE IN PRESS

A. Rokem, M. Ahissar / Neuropsychologia xxx (2009) xxx-xxx

- Raz, N., Amedi, A., & Zohary, E. (2005). V1 activation in congenitally blind humans is associated with episodic retrieval. *Cerebral Cortex*, *15*(9), 1459–1468.
- Raz, N., Striem, E., Pundak, G., Orlov, T., & Zohary, E. (2007). Superior serial memory in the blind: A case of cognitive compensatory adjustment. *Current Biology*, 17(13), 1129–1133.
- Roder, B., & Rosler, F. (2003). Memory for environmental sounds in sighted, congenitally blind and late blind adults: Evidence for cross-modal compensation. International Journal of Psychophysiology, 50, 27–39.
- Roder, B., Stock, O., Bien, S., Neville, H. J., & Rosler, F. (2002). Speech processing activates visual cortex in congenitally blind humans. *European Journal of Neu*roscience, 16, 930–936.
- Roder, B., Teder-Salejarvi, W., Sterr, A., Rosler, F., Hillyard, S. A., & Neville, H. J. (1999). Improved auditory spatial tuning in blind humans. *Nature*, 400(6740), 162–166
- Sadato, N., Okada, T., Honda, M., & Yonekura, Y. (2002). Critical period for cross-modal plasticity in blind humans: A functional MRI study. NeuroImage, 16, 389-400.
- Sadato, N., Pascual-Leone, A., Grafman, J., Ibanez, V., Deiber, M., Dold, G., et al. (1996). Activation of primary visual cortex by Braille reading in blind subjects. *Nature*, 380, 526–528.
- Schon, D., Magne, C., & Besson, M. (2004). The music of speech: Music training facilitates pitch processing in both music and language. *Psychophysiology*, 41(3), 341–349

- Sholl, M. J., & Easton, R. D. (1986). Effect of referent object familiarity on verbal learning in the sighted and the blind. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 12(2), 190–200.
- Smits, B. W. G. M., & Mommers, M. J. C. (1976). Differences between blind and sighted children on WISC verbal subtests. *The New Outlook*, 240–246.
- Starlinger, I., & Niemeyer, W. (1981). Do the blind hear better? Investigations on auditory processing in congenital or early acquired blindness. II. Central functions. Audiology, 20, 510–515.
- Tervaniemi, M., Just, V., Koelsch, S., Widmann, A., & Schröger, E. (2005). Pitch discrimination accuracy in musicians vs nonmusicians: An event-related potential and behavioral study. *Experimental Brain Research*, 161(1), 1.
- Tillman, H. M., & Bashaw, W. L. (1968). Multivariate analysis of the WISC scales for blind and sighted children. *Psychological Reports*, 23(2), 523–526.
- Vecchi, T. (1998). Visuo-spatial imagery in congenitally totally blind people. *Memory and Cognition*, 6(1), 91–102.
- Wagner-Lampl, A., & Oliver, G. W. (1994). Folklore of blindness. *Journal of Visual Impairment and Blindness*, 88, 267–276.
- Wechsler, D. (1997). Wechsler adult intelligence scale. San Antonio, TX: The Psychological Corporation.
- Wyver, S. R., & Markham, R. (1998). Do children with visual impairment demonstrate superior short-term memory, memory strategies and metamemory? *Journal of Visual Impairment and Blindness*, 92, 799–811.

6