



Superior verbal but not nonverbal memory in congenital blindness

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Abstract

Previous studies suggest that people who are congenitally blind outperform sighted people on some memory tasks. Whether blindness-associated memory advantages are specific to verbal materials or are also observed with nonverbal sounds has not been determined. Congenitally blind individuals ($n=20$) and age and education matched blindfolded sighted controls ($n=22$) performed a series of auditory memory tasks. These included: verbal forward and backward letter spans, a complex letter span with intervening equations, as well as two matched recognition tasks: one with verbal stimuli (i.e., letters) and one with nonverbal complex meaningless sounds. Replicating previously observed findings, blind participants outperformed sighted people on forward and backward letter span tasks. Blind participants also recalled more letters on the complex letter span task despite the interference of intervening equations. Critically, the same blind participants showed larger advantages on the verbal as compared to the nonverbal recognition task. These results suggest that blindness selectively enhances memory for verbal material. Possible explanations for blindness-related verbal memory advantages include blindness-induced memory practice and ‘visual’ cortex recruitment for verbal processing.

Keywords Congenitally blind · Verbal · Nonverbal · Memory · Recognition memory

Introduction

A distinguishing feature of humans is their ability to adapt to variation in experience. A key illustration comes from studies of sensory loss. People born blind gather information through nonvisual means, including not only audition and touch, but also linguistic communication and social learning. Language in particular serves as an efficient source of information about phenomena that sighted people observe through vision, such as person identity, spatial layouts, color, fashion, appearance of animals and distal objects, and visual events (Bedny et al. 2019; Bigham et al. 2010; Burton et al. 2012b; Kim et al. 2019). Some evidence suggests that blindness enhances aspects of linguistic abilities, perhaps as a result of relying heavily on language as an information

source. For example, people born blind show speeded lexical access and outperform the sighted when answering comprehension questions about grammatically complex sentences (Loiotile et al. 2019; Röder et al. 2003, 2000).

Blind individuals outperform sighted controls on verbal memory tasks

A particularly pronounced blindness-related advantage is observed in verbal memory. People who are blind recall longer lists of letters, words, and numbers, both with long (e.g., one week) and short delays (e.g., four seconds Occelli et al. 2017; Pasqualotto et al. 2013; Raz et al. 2007; Rokem and Ahissar 2009; Smits and Mommers 1976; Stankov and Spilsbury 1978; Tillman and Bashaw 1968; Withagen et al. 2013). Blind individuals remember more items and are also more likely to recall them in the correct order (Pasqualotto et al. 2013; Raz et al. 2007). One study found that people born blind could remember twice as many words as sighted people (Raz et al. 2007).

People who are blind also show superior memory on tasks involving manipulating or updating verbal information, although evidence is more mixed (e.g. Castronovo and Delvenne 2013; Pigeon and Marin-Lamellet 2015).

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Blind adults outperform sighted people on backward span tasks that require recalling digits in reverse order (Ocelli et al. 2017). One study found superior performance on an n-back task with raised tactile letters but only at intermediate load levels (Bliss et al. 2004). Blind individuals also recall lists of consonants in serial order better than sighted participants, even when required to complete an intervening pitch discrimination task prior to recall (Dormal et al. 2016). Although pitch discrimination may not provide sufficient interference for a verbal memory task. In another study, blind adults were better able to remember sentence-final words in an incidental encoding paradigm (Röder et al. 2001). Some evidence suggests that such blindness-related memory advantages emerge in childhood. One study found that 10-year-old blind children outperform sighted children on listening word span and on backward digit span tasks (Withagen et al. 2013). Blindness-related memory advantages have been documented as early as six years of age (Hull and Mason 1995). In sum, blind adults and children outperform sighted participants on a range of verbal memory tasks.

One outstanding question is whether blindness specifically enhances verbal memory or memory more generally. Blindness arguably enhances demand for remembering many types of information, including spatial routes in the absence of visual landmarks, voices in the absence of access to visual facial features, and distal object sounds' in the absence of constant visual access to the objects (Föcker et al. 2012; Fortin et al. 2008; Voss et al. 2004). One possibility is that people who are blind demonstrate improved memory for all these varied types of information, including nonverbal sounds, spatial layouts, and smells. On the other hand, blindness could selectively improve verbal memory. As noted above, language may serve as a particularly efficient source of information about varied contents and be an effective tool for encoding and maintaining information. Studies with other expert populations suggest that memory for different information types often improves independently. For example, simultaneous translators show superior working memory for linguistic material but not spatial layouts, and musicians show improved verbal memory as compared to non-musicians (Chan et al. 1998; Christoffels et al. 2006; Cohen et al. 2011; for review, see Ericsson and Lehmann 1996; Franklin et al. 2008; Ho et al. 2003). Therefore, verbal memory in people who are blind might selectively improve.

Whether blind individuals outperform sighted people on nonverbal tasks remains unclear

Several studies find superior memory among blind individuals for meaningful, verbalizable sounds, such as the sound of a clock ticking, turning a book's pages, and linoleum floor squeaks (Cornell Kärnekull et al. 2016). These advantages

persist, even when participants complete intervening tasks involving generating words beginning with a certain letter and discriminating nonverbal pitches (Cornell Kärnekull et al. 2016). Interestingly, the advantage among people born blind was more pronounced with a semantic (naming the sound) as compared to a physical encoding strategy (stating the noises' volume Röder and Rösler 2003). Verbalizing the sounds may therefore mediate the blindness-related advantages when the sounds are easily verbalizable.

Consistent with the idea that blindness-related advantages are restricted to verbal or verbalizable material, a number of studies with non-verbalizable materials have failed to find blindness-related advantages. For example, one study found no blindness advantage when participants listened to verbal stimuli but remembered nonverbal information. In this study, blind and sighted individuals performed with equal accuracy when listening to a pseudoword and making n-back judgments on the speaker's identity (as specified by the voice, Gudi-Mindermann et al. 2018). While some studies do find superior memory for voices and tones among people born blind, the findings are inconsistent (Bull et al. 1983; but see Stankov and Spilsbury 1978). Several studies with spatial tactile tasks similarly find no advantage among people who are blind. In one recent study, sighted and blind participants were not different in their ability to recall haptically encoded target cubes' locations on a 2D matrix (Ocelli et al. 2017). Crucially, the same group of blind participants outperformed sighted people on two verbal memory tasks, including a backwards digit span task and a word list recall task (Ocelli et al. 2017). This study demonstrates that blind participants who show verbal memory advantages do not also show spatial memory advantages. Converging evidence comes from spatial memory navigation tasks and an adaptive tactile n-back task (Cornoldi et al. 1991; Gudi-Mindermann et al. 2018; for a review, see Struiksma et al. 2009).

In summary, prior evidence suggests blind individuals outperform sighted controls on verbal memory but not spatial memory tasks (Gudi-Mindermann et al. 2018; Ocelli et al. 2017; Raz et al. 2007; Sinclair et al. 2011). Evidence from memory studies using nonverbal sounds is mixed (Gudi-Mindermann et al. 2018; Röder and Rösler 2003; Sinclair et al. 2011).

Motivating the current study

One possible interpretation of the available evidence is that blind individuals exhibit a specific verbal memory advantage. An alternative possibility is that blindness improves memory for verbal and nonverbal material alike. The available evidence falls short of distinguishing between the verbal memory and general memory advantage hypotheses. As noted above, previous studies show

some blindness-related memory advantages for nonverbal meaningful sounds (Cornell Kärnekull et al. 2016). These advantages may be related to verbalizability, yet whether this is the case is unknown. Evidence from spatial tasks is complicated to interpret with respect to the verbal memory hypothesis since prior evidence suggests blind and sighted individuals' performance differs on some spatial tasks. For example, one study found that sighted individuals outperformed blind participants when navigating through a previously explored 3D matrix of cubes (for a review, see Cattaneo et al. 2008; Cornoldi et al. 1991). An additional study found that when following imaginary pathways in two and 3D matrices, sighted participants recalled final locations better (Vecchi 1998). Spatial and imagery performance differences between blind and sighted people could mask a nonverbal memory advantage among people born blind.

Critically, no prior study has compared the same blind and sighted participants' performance on matched verbal and nonverbal tasks. One reason for this is that most verbal memory tasks require generating responses (e.g., reporting a remembered list of words), which is impractical for nonverbal material. To address this question, we used matched verbal and nonverbal recognition memory tasks. Participants heard either a target sequence of letters (5–15 letters long) or a sequence of target nonmeaningful complex sounds (3–15 sounds long). They then heard a probe sequence and decided whether it was identical to the target sequence. To respond correctly, participants had to remember both the identity and the order of the letters and sounds. Non-match lists were created by either interchanging two items' positions, replacing one item with another, or moving an item two or more positions. To ensure that any differences between verbal and nonverbal tasks were not related to difficulty alone, we manipulated load to match the verbal (with letters) and nonverbal (with sounds) recognition memory tasks on difficulty.

To compare the current results to prior literature, we also tested the same blind and sighted participants on forward and backward letter span tasks. Finally, we used a complex span task to determine whether blindness-related advantages would persist even with difficult interfering verbal material. One possibility is that blindness-related verbal memory advantages are only observed in tasks allowing rehearsal of verbal material, perhaps because of more efficient rehearsal strategies in blind participants. In the current study, we used a complex span task in which participants remember letter sequences while judging interfering math equations' validity. If blind individuals continue to outperform the sighted on this task, this would suggest that blindness-related advantages persist even when an intervening task precludes rehearsal.

Methods

Participants

Twenty participants who are congenitally blind (13 female) and 22 age and education matched sighted controls (14 female) took part in the study (see Table 1 for demographic details). One sighted participant only took part in recognition tasks. Three participants who are blind did not perform the Woodcock–Johnson III (WJIII) standardized test.

All participants were native English speakers, except one sighted participant who learned English at age five. We collected data from participants who are blind at three separate national conventions of the National Federation of the Blind (2014, 2016, and 2018). Sighted participants were tested at Johns Hopkins University. Participants who are blind had minimal-to-no light perception from birth due to pathologies in or anterior to the optic chiasm (see Table 1 for list of etiologies). All participants reported no cognitive or neurological disabilities and scored within two standard deviations of their own group on every WJIII task (max z-score within each group: sighted = 1.4, max blind = 2.02).

The Johns Hopkins University Homewood Institutional Review Board approved the study (HIRB00001291). All participants provided written informed consent and were compensated for their time at \$30 per hour.

Procedures

Participants completed the experimental tasks in the following order: simple verbal forward and backward letter spans (together Experiment 1); complex span (Experiment 2); and nonverbal recognition and verbal recognition (together Experiment 3). WJIII scores were obtained either after all of the experimental tasks or in a separate session. Data were collected as part of a larger testing session.

A female native English speaker recorded all verbal materials. Auditory stimuli were delivered over Audio-Technica headphones. All tasks were administered using a PC laptop running MATLAB (Mathworks, Inc.) and Psychtoolbox (Brainard 1997; Pelli 1997). Participant responses were recorded using a button box (Cedrus, RB-730).

Experiment 1: recall in simple verbal forward and backward letter spans

The forward and backward span tasks were adapted from the Wechsler Adult Intelligence Scale (WAIS) digit span tasks. Digits 1–9 were mapped to letters A–I. On each trial, participants heard a list of letters at a rate of one letter per second. After hearing the final letter, participants were asked to repeat the list back to the experimenter in the exact order

Table 1 Participants' demographic information

Participant	Gender	Age	Cause of blindness	Light perception	Years of education
CB_01	F	34	Leber's congenital amaurosis	None	17
CB_02	M	38	Leber's congenital amaurosis	None	19
CB_04	F	34	Leber's congenital amaurosis	Minimal	17
CB_05	F	19	Leber's congenital amaurosis	Minimal	15
CB_07	F	35	Anophthalmia	None	19
CB_08	M	40	Bilateral amnethalpia	None	17
CB_09	F	38	Micro-ophthalmia	None	16
CB_10	F	22	Leber's congenital amaurosis	Minimal	19
CB_13	F	19	Optic nerve displacia	None	13
CB_14	F	28	Leber's congenital amaurosis	None	16
CB_15	F	18	Leber's congenital amaurosis	Minimal	13
CB_16	M	19	Glaucoma	None	12
CB_18	M	24	Retinopathy of prematurity	Minimal	13
CB_19	M	61	Congenital glaucoma	Minimal	17
CB_20	F	21	Fraser's syndrome	None	16
CB_21	F	25	Bilateral amnethalpia	None	17
CB_22	M	38	Leber's congenital amaurosis	None	17
CB_23	F	24	Leber's congenital amaurosis	Minimal	16
CB_24	F	48	Septo-optic dysphasia	None	17
CB_25	M	18	Leber's congenital amaurosis	Minimal	13
Average					
Blind (<i>N</i> =20)	13F	30.26	–	–	15.95
Sighted (<i>N</i> =22)	14F	32.86	–	–	16.64

Individual participant information is provided for congenitally blind (CB) participants

(forward) or the reverse order (backward). All participants in both groups heard the same lists of letters presented in the same order. Participants heard two trials per load (i.e. number of items to recall) with load increasing from two to nine for the forward span task and two to eight for the backward span. Trial accuracy was scored as the proportion of letters recalled in the correct position. The task self-terminated if participants were unable to recall any of the letters in the correct position across the two trials.

Experiment 2: recall in complex verbal letter span task

The complex verbal span task was similar to the letter span task described above. However, an interfering math equation was inserted after each letter within the lists. Participants were thus required to do two tasks at once: remember the letter sequence and judge math equations' validity. The intervening math equations were intended to preclude participants from rehearsing the letters.

Equations and letter sequences consisted of the following. Math equations were comprised of multiplying or dividing two digits followed by either adding or subtracting a third

digit. All incorrect answers were selected to be within 3 digits of the correct answer to discourage reliance on estimation techniques. Letter lists were constructed from 13 letters (A–M). For each list, letters were chosen pseudo-randomly, allowing only for non-consecutive repetitions of one letter at most twice per trial. All participants in both groups heard the same lists of letters and equations presented in the same order.

The event order within each trial was as follows: Participants first heard an equation and a proposed solution (“ $5 \times 3 + 8 = 23$,” 5000 ms). Participants decided whether the solution was correct or incorrect. They pressed one of two buttons (first or second from left to right, respectively) to respond. Following the equation and a 300 ms pause, participants heard a to-be-remembered letter (500 ms). The pattern of equations and letters continued until the final letter was reached. Participants then heard a tone indicating the end of the trial (75 ms). Following the tone, participants repeated the full list of letters back to the experimenter in the presented order.

Because math abilities can differ substantially within and across groups, participants had an individualized amount of time to respond to the interfering math equations

(Blind—Mean = 2.02 s, SD = 2.28; Sighted—Mean = 1.37 s, SD = 0.93). To calculate a participant’s individualized equation time, participants performed 15 practice equations prior to the task. On experimental trials, they were given the mean practice equation response time + 2.5 times the standard deviation of the practice equation response time.

Participants completed three trials per span, with load increasing from two to 10. Trial accuracy was scored as the proportion of letters recalled in the correct position. As with the simple letter spans, the complex verbal letter span self-terminated if participants were unable to recall any letters in the correct position across trials for a load. Because the highest load any participant reached was nine, only loads two through nine were analyzed for each participant.

Experiment 3: nonverbal and verbal recognition tasks

Nonverbal recognition Participants identified whether two lists of nonverbal sounds were matching or non-matching. The lists were comprised of a combination of 13 nonverbal sounds (500 ms), followed by a 400 ms delay. Sounds are posted on Open Science Framework (<https://osf.io/etgyh>). The nonverbal sounds were created using Audacity (<https://www.audacityteam.org/>). Across the 13 sounds, dominant frequencies ranged from 172 to 20,155 Hz. Sounds were played at a comfortable volume for each participant based on self-report. The sounds were chosen to minimize similarity to real sound categories (e.g., barking, sneezing, rain) and thus to minimize verbalizability.

The event order within each trial was as follows. Participants heard a target list of sounds (500 ms per sound with a 400 ms delay between sounds), followed by a 1500 ms delay and a probe list of sounds. Participants then indicated whether the target and probe lists were identical by pressing the first (match) or the second (non-match) buttons. Participants could respond at any time while listening to the probe list, and they could also pause the task after completing a trial. (Trials timed out after 1000 s). After the current trial’s list finished playing and a response was received, a verbal cue of “Next Trial” indicated the beginning of the following trial.

Each load contained four match and four non-match trials. On non-match trials, the probe lists could differ from the target lists in three possible ways: one item was replaced with a new one (“identity change”), two items interchanged positions (“swap two”), or one item shifted two or more positions (“slide one over”), causing subsequent items between the new and old positions to shift as well.

Loads ranged from three to 15, with eight trials per load. Accuracy on each trial was scored as correct (1) or incorrect (0). Following the eight trials within a load, the participant’s overall score for the load was calculated. If the participant performed at or below chance (0.50), the task terminated.

Performance on the last completed load and at subsequent loads was set to chance.

Verbal recognition The verbal forward recognition task was structured and scored similarly to the nonverbal forward recognition task, except lists of letters were presented as opposed to lists of nonverbal sounds. Similar to the complex span, lists of letters were comprised of 13 possible letters (A–M). For each list, letters were chosen randomly, allowing for non-consecutive repetitions of a single letter at most twice per trial. The lists were screened to ensure they did not coincidentally spell out a word. Loads ranged from 5 to 15.

Woodcock–Johnson III (control)

To measure general vocabulary and verbal ability, five subtests of the WJIII were administered: (Word Identification, Word Attack, Synonyms, Antonyms, and Analogies). These tasks were used as controls to determine whether any potential differences among sighted and blind participants were specific to verbal memory or general to all measures of verbal ability, including vocabulary. Blind participants used a Braille version of the WJIII. On Word Identification, participants read and correctly pronounced 60 English words (e.g. “bouquet”). On Word Attack, participants read and pronounced 32 non-words (e.g., “paraphonity”). On Oral-Vocabulary Synonyms, participants read 12 words and provided a synonym for each (e.g. “wild” → “untamed”). On Oral-Vocabulary Antonyms, participants read 12 words and provided an antonym for each (e.g., “authentic” → “fake”). On Oral-Vocabulary Analogies, participants generated words to complete 12 unfinished analogies (e.g., “Wrist is to shoulder, as ankle is to...” → “hip”). Items on each section were increasingly more difficult. Participants had no time limit and were given no feedback. Participants were allowed to skip any questions but could not return to them. Section accuracy was scored as the percent correct on all possible items in that section. Skipped trials were scored as incorrect (Table 2; Fig. 1).

Data analysis

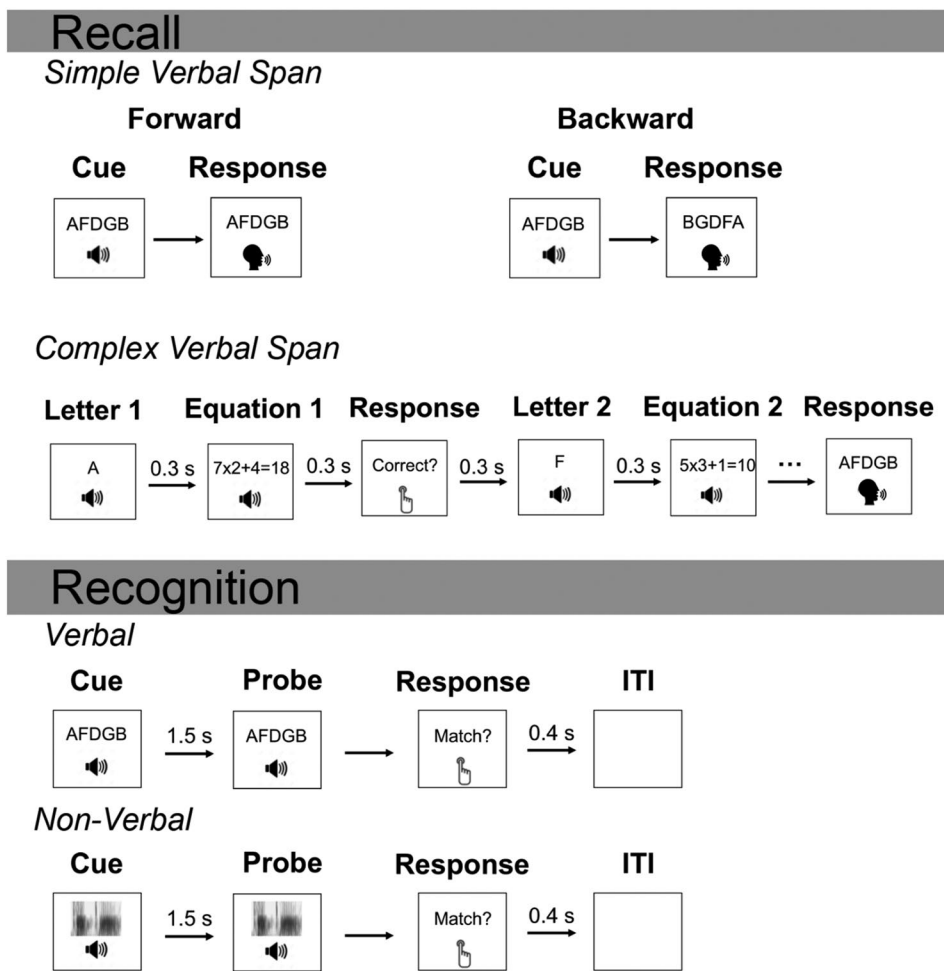
Analysis was conducted in R 4.1.1 (R Core Team 2021) and used the rstatix Package (Kassambra 2020). Analyses of variance (ANOVAs) were conducted with group (blind

Table 2 Average Woodcock–Johnson III Scores per group

Group	Word ID	Word attack	Synonyms	Antonyms	Analogies
Blind	96% (4)	92% (6)	89% (12)	79% (15)	68% (16)
Sighted	95% (4)	92% (6)	82% (14)	78% (16)	71% (15)

Group means and standard deviations for task performance

Fig. 1 Tasks. Recall: participants repeated sequences of letters presented to them in an audio format. For forward recall, participants repeated the list in the same order as presented but for backward recall, in the opposite order as presented. During complex recall, participants determined the validity of a math equation followed by hearing each letter to be remembered. Recognition: participants were given two lists and determined if they matched. For the verbal task, the lists consisted of letters. For the nonverbal task, the list consisted of non-verbalizable sounds



vs. sighted) as the between subjects factor and direction (forward vs. backward), load (2–9 spans), and task (letter recall, equation judgment, and verbal and nonverbal recognition) as the within-subjects factors. The Huynh–Feldt Correction was applied to all ANOVAs to account for violations of sphericity. *P*-values for post-hoc *t*-tests were corrected for multiple comparisons using the Holm–Bonferroni method.

Recall: forward, backward, and complex

Accuracy per trial was calculated as the proportion of letters recalled in their correct position in the cue list. Measuring load accuracy as the proportion of correctly recalled letters is more sensitive than traditional span length because individuals who reach the same span may recall different proportions of letters correctly. Accuracy per load was calculated by averaging accuracy across each load’s two trials. If a participant was not tested on a load (e.g. load 8) because of poor performance on prior loads (e.g. 6 and 7) and the task self-terminated, performance on the untested load (i.e. load 8) was set to chance, 0. A subset of participants who were blind (*n* = 8) completed

all trials regardless of performance, i.e., the task continued after two incorrect responses. To combine data consistently across participants, their data were scored in the same way as those who’s task self-terminated i.e., all trials occurring after two consecutive errors were set to 0.

Recognition: verbal and nonverbal

Prior to the nonverbal recognition task, participants performed a short sound discrimination task to ensure sighted and blind participants could discriminate the sounds to be used during the recognition task. Blind and sighted participants were both at near perfect performance (Blind—Mean = 0.998, SD = 0.0041; Sighted—Mean = 0.992, SD = 0.02; *t*-test between groups—*t*(39) = - 1.93, *p* = 0.06, *d* = 0.55).

On the nonverbal and verbal recognition tasks, accuracy per load was averaged across the load’s eight trials. *d*’, a measure of memory discrimination, was calculated using the equation below:

$$d' = z(H) - z(F)$$

where z is a Z-transformation, H is the hit rate, and F is the false alarm rate.

If a participant was not tested on a load due to poor performance on prior loads, then performance was set at chance and d' was set to 0 for that load. If a participant completed a load but performance was below chance, then performance was also set at chance and d' set at 0 in order to equate with those participants that were not tested on that particular load due to poor performance on prior loads. For the nonverbal task, only loads 3–6 were analyzed. During piloting, these loads were found to produce similar performance as loads 5–8 in the verbal task.

Results

Experiment 1: recall in simple verbal span task, forward and backward

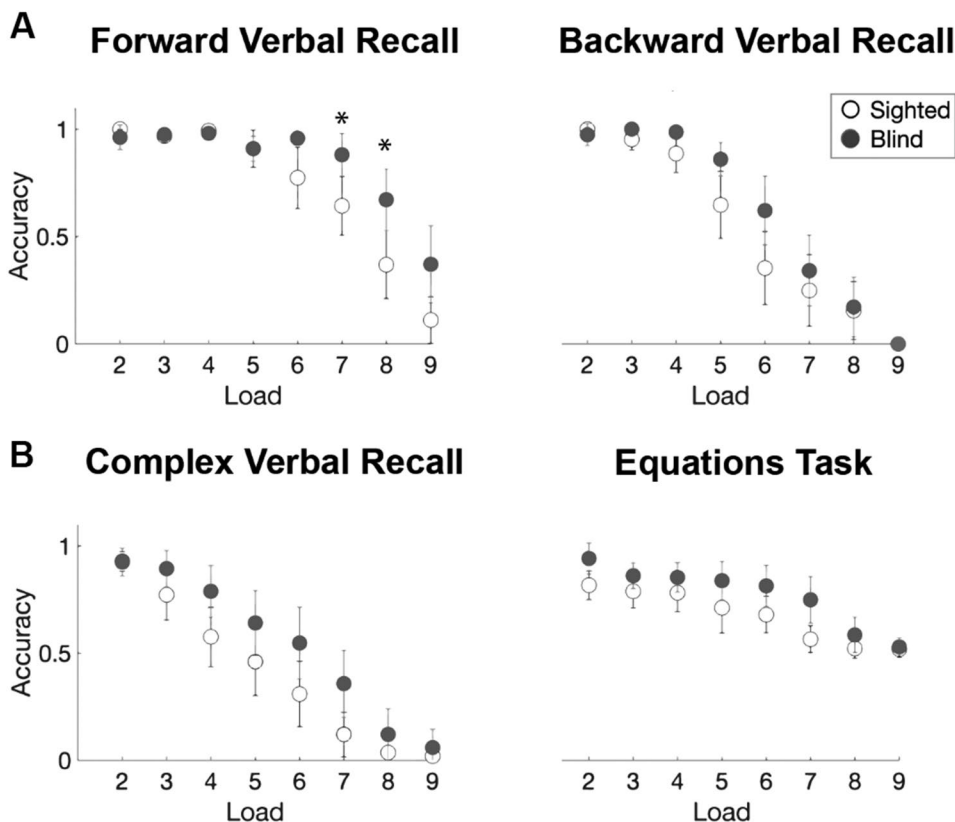
Consistent with prior studies, individuals who are blind showed enhanced short-term memory recall on a simple verbal span task (e.g. Ocelli et al. 2017; Pasqualotto et al. 2013; Rokem and Ahissar 2009). In a group (blind vs. sighted) by direction (forward vs. backward) by load (2

through 9 spans) $2 \times 2 \times 8$ ANOVA (Fig. 2a), participants who are blind performed overall better than the sighted across loads for both forward and backward recall (main effect of group, $F(1,39) = 8.25, p = 0.01, \eta_p^2 = 0.18$). Both groups performed worse with increasing load (main effect of load, $F(3.13, 121.9) = 210.86, p < 0.001, \eta_p^2 = 0.84$), with load effects more pronounced in the backward than forward recall task (direction \times load interaction, $F(4.48, 174.53) = 20.73, p < 0.001, \eta_p^2 = 0.35$). Notably, increasing load affected individuals who are blind less (group \times load interaction, $F(3.13, 121.9) = 3.62, p = 0.01, \eta_p^2 = 0.085$), consistent with prior work (Ocelli et al. 2017; Pasqualotto et al. 2013; Rokem and Ahissar 2009). By contrast, direction of recall (forward vs. backward) affected both participant groups equally (directionality \times group interaction, $F(1,39) = 0.37, p = 0.55, \eta_p^2 = 0.01$), both groups performing more poorly on the backwards than forwards span task (directionality effect, $F(1, 39) = 76.09, p < 0.001, \eta_p^2 = 0.66$).

Experiment 2: recall in complex verbal span task

Individuals who are blind continued to show enhanced short-term memory recall in the face of interference (with math equations) on a complex span task. In a 2×8 group by load ANOVA, main effects of group (blind > sighted), increasing load, and task (letter recall and equation judgment)

Fig. 2 Performance on verbal recall tasks. **A** Average recall accuracy per load for simple verbal forward and backward span tasks. **B** Average recall accuracy per load for the complex verbal span task and the equations task. Error bars indicate 95% confidence intervals. The black stars indicate significance after correcting p -values for multiple comparisons with the Holm-Bonferroni method: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$



on accuracy were found (Fig. 2b; group, $F(1,39)=6.55$, $p=0.01$, $\eta_p^2=0.14$; load, $F(3.31, 129.16)=104.86$, $p<0.001$, $\eta_p^2=0.73$; task, $F(1,39)=26.70$, $p<0.001$, $\eta_p^2=0.41$), but not a group by load interaction effect ($F(3.31, 129.16)=1.93$, $p=0.12$, $\eta_p^2=0.05$, Fig. 2).

Blind participants' superior letter recall was not a result of trade-off with the equation task: participants who are blind performed better than the sighted on the equations task across loads (Fig. 2b; 2×8 group-by-load ANOVA group, $F(1, 39)=6.61$, $p=0.01$, $\eta_p^2=0.15$). Though participants received individualized amounts of time to solve interfering equations, duration did not differ across groups (Blind—Mean = 2.02 s, SD = 2.28; Sighted—Mean = 1.36 s, SD = 0.93; $t(39)=1.21$, $p=0.23$, $d=0.38$). Increasing load in the concurrent letter-working memory task negatively impacted both groups' performance on the equations task (load, $F(3.83, 149.33)=67.13$, $p<0.001$, $\eta_p^2=0.63$).

Experiment 3: verbal and nonverbal recognition task

When using raw accuracy as the outcome measure, individuals who are blind only showed enhanced recognition memory with verbal material. A group (blind vs. sighted) by load (4 loads) by task (verbal vs. nonverbal) $2 \times 4 \times 2$ ANOVA revealed main effects of group and load (Fig. 3a; main effect of group (blind > sighted), $F(1,40)=16.20$, $p<0.001$, $\eta_p^2=0.29$, main effect of load ($F(3, 119.86)=106.76$, $p<0.001$, $\eta_p^2=0.73$; main effect of task $F(1,40)=3.92$, $p=0.06$, $\eta_p^2=0.09$). The main effect of group was qualified by a group by task interaction, such that the difference between blind and sighted groups was more pronounced in the verbal than nonverbal task, ($F(1,40)=4.61$, $p=0.04$, $\eta_p^2=0.10$). We also found a task by load interaction, such that the effect of load was more pronounced

in the nonverbal task (task \times load, $F(3.11, 124.50)=7.16$, $p<0.001$, $\eta_p^2=0.15$).

D' was also used as an outcome measure to account for any potential differences in decision criterion across groups and yielded qualitatively similar results. Main effects of group and load were found (Fig. 3, group, $F(1,40)=13.90$, $p<0.001$, $\eta_p^2=0.26$; load, $F(3, 123.76)=93.13$, $p<0.001$, $\eta_p^2=0.70$). The effect of task was marginal, $F(1,40)=3.038$, $p=0.07$, $\eta_p^2=0.08$). The group \times task (verbal/nonverbal) interaction was marginal ($F(1,40)=3.82$, $p=0.06$, $\eta_p^2=0.09$) while the task by load interaction was significant (task \times load, $F(3.05, 121.83)=8.56$, $p<0.001$, $\eta_p^2=0.18$). On the nonverbal recognition task, a single load drove the effect of group, whereas all loads showed an effect of group in the verbal task. These results are consistent with the hypothesis that blindness preferentially enhances verbal memory as stated in the introduction (Occelli et al. 2017; Raz et al. 2007).

Woodcock–Johnson III (control)

Blind and sighted participants were matched on their general vocabulary and verbal ability. The two groups performed equally well on each of the administered Woodcock–Johnson III subtests (Word identification— $t(37)=-0.37$, $p=0.72$, $d=-0.12$; Word attack— $t(37)=-0.16$, $p=0.87$, $d=-0.05$; Synonyms— $t(37)=0.40$, $p=0.69$, $d=0.13$; Antonyms— $t(37)=0.30$, $p=0.76$, $d=0.10$; Analogies— $t(36)=-1.01$, $p=0.32$, $d=-0.33$).

Discussion

Verbal memory selectively improved in blindness

We report that congenital blindness is associated with a selective advantage for verbal memory.

Replicating and extending prior results, we show that adults who are blind from birth outperform sighted people on verbal recall tasks, recalling more letters and digits in the correct order on forward, backward, and complex span tasks (Cohen et al. 2010; Hull and Mason 1995; Occelli et al. 2017; Raz et al. 2007; Rokem and Ahissar 2009; Swanson and Luxenberg 2009; Withagen et al. 2013). The same blind and sighted participants performed equally well on vocabulary and reading tasks, as measured by the WJIII standardized test, and on a nonverbal memory task discussed in detail below.

We also found that blind participants' verbal memory advantage persisted on the complex span task in the face of interference. Blind participants continued recalling more letters in the correct order while solving a math equation

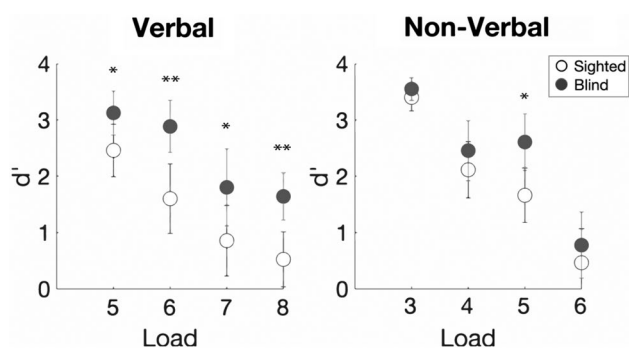


Fig. 3 Performance on recognition tasks. Average d' per load for each group is shown for verbal and nonverbal tasks. Error bars indicate 95% confidence intervals. The black stars indicate significance after correcting p -values for multiple comparisons with the Holm-Bonferroni method: * $p<0.05$, ** $p<0.01$, *** $p<0.001$

between each letter presentation. The secondary task of solving equations arguably interferes with explicit articulatory rehearsal. Blind participants were also more accurate at solving the equations themselves, suggesting no tradeoff between equation and memory tasks. This finding suggests that verbal memory advantages in blindness are resilient to interference.

Consistent with the current complex span task results, prior studies also find blindness-related verbal memory advantages persist amidst interference. As compared to sighted individuals, blind participants recall more letters and verbalizable sounds after completing an intervening pitch discrimination task (Dormal et al. 2016; Röder et al. 2003). On a long-term memory task, blind participants recognized more verbalizable sounds than sighted participants after generating words beginning with a certain letter during the 8–9 min delay period (Cornell Kärnekull et al. 2016). Similarly, blind children recalled more sentence-final words than sighted children while judging the same sentences as true or false during a listening span task (Withagen et al. 2013). One study found better memory on an incidental memory paradigm, where blind participants recognized more previously heard sentence-final words as compared to sighted participants after judging the same sentences as meaningful in an intervening task (Röder et al. 2001). To the extent that these intervening tasks prevent articulatory rehearsal, these findings suggest that more efficient articulatory rehearsal strategies do not fully explain blindness-related advantages.

We also find that blindness-related advantages extend to verbal recognition memory. Blind participants distinguished between previously heard lists of letters and lists of foil letters better than sighted participants. Although both blind and sighted participants made more errors with increasing list lengths, on average people born blind recognized approximately 10% more letters correctly.

Crucially, the goal of the current study was to compare verbal and nonverbal memory performance using a recognition memory paradigm. We observed a group-by-verbal material interaction on the recognition memory task, such that blindness-related advantages were more pronounced for verbal as compared to nonverbal recognition memory. Blind participants significantly outperformed sighted participants on all loads of the verbal recognition task. No group difference emerged on the nonverbal recognition task except at one load level, and this effect was nonsignificant when collapsing across loads. These results support the hypothesis that blindness promotes enhanced memory specifically for verbal material. Notably, since the recognition task had no concurrent dual task to prevent rehearsal, we cannot rule out the possibility that articulatory rehearsal contributes to blindness-related advantages in letter recognition.

Larger verbal as opposed to nonverbal memory advantages observed among people born blind are consistent with

a number of prior studies. One study reported that blind participants outperformed sighted ones on verbal but not spatial memory tasks (Occelli et al. 2017). Specifically, blind participants outperformed sighted ones on a backward digit span task and on short and long-term word list recall tasks, while the same blind and sighted participants showed no differences on a haptic spatial corsi-block task. The present findings show that blind individuals exhibit a verbal versus nonverbal memory dissociation even when using a nonverbal, nonspatial task for comparison, thus extending previous results. The current results are also consistent with evidence that congenitally blind individuals' higher performance using nonverbal sounds or tactile stimuli is related to verbalizability. Prior studies find blind individuals recall more verbalizable sounds (e.g., musical instruments or turning book pages) than sighted participants (Cornell Kärnekull et al. 2016; Röder and Rösler 2003). In contrast, with nonverbalizable stimuli, such as voices or vibrotactile rhythms, blindness-related advantages are absent (e.g. n-back tasks matching vibrations and voices Burton et al. 2010; Gudi-Mindermann et al. 2018; and a recognition memory task using vibrotactile rhythms Sinclair et al. 2011). Therefore, the existing evidence supports the hypothesis that verbal memory is improved in blindness, not memory in general.

Why and how does blindness improve verbal memory?

One hypothesis is that blindness provides a form of memory practice, thus improving memory. People who are blind rely on memory to access some information accessible to sighted people through vision, including not only environmental information (e.g., visual landmarks) but also culturally transmitted information. Many cultural tools that reduce memory load are designed for people who are sighted (e.g., visual slides during a talk, signs for navigation, printed object labels). Since language provides an efficient means of encoding and maintaining a wide variety of content in memory, verbal memory may get abundant practice and thus improve selectively. In this regard, language might serve as a mental tool for retaining information (for related argument, see Frank et al. 2008).

Under a practice-based account, sighted people given similar practice, could, in principle achieve similar memory improvements. As noted in the introduction, superior verbal memory has also been observed among subgroups of sighted people with particular expertise, such as simultaneous translators and musicians (Chan et al. 1998; Christoffels et al. 2006; Cohen et al. 2011; Franklin et al. 2008; Ho et al. 2003). Under this practice-based view, the cognitive and neural mechanisms of blindness-related memory improvements might be similar to what is observed in sighted expert populations.

An alternative possibility is that blindness-related memory improvements are cognitively and neurally unique and unachievable for sighted people. One potential reason is the availability of unique neural resources. People who are blind recruit ‘visual’ cortices during a range of non-visual tasks (Bedny et al. 2011; Collignon et al. 2011; Röder et al. 2002; Thaler et al. 2011; Vercillo et al. 2015). Verbal memory is among the functions that engages ‘visual’ cortices in blindness. People who are blind activate ‘visual’ cortices when retrieving words from long-term memory. This activation is observed in the anatomical location of the primary visual cortex (V1), along the calcarine sulcus, as well as in secondary visual areas, including in ventral occipito-temporal cortex (vOTC), lateral occipital cortex (LOC), and dorsal occipital areas (Raz et al. 2005). People who are blind also show larger ‘visual’ cortex activity for new over previously heard words, and these effects are observed both in primary and secondary visual cortices (vOTC, LOC, and anatomical locations of V2–V8).

Verbal memory is not the only task that recruits ‘visual’ networks in blindness. ‘Visual’ cortices have also been implicated in tasks such as spatial localization, language comprehension, echolocation, braille reading, and solving math equations (Bedny et al. 2011; Burton et al. 2012b, a; Collignon et al. 2011; Kanjlia et al. 2016; Röder et al. 2002; Voss et al. 2004). In some of these cognitive domains, such as spatial localization and sentence processing, performance across blind individuals is also related to the degree of cross-modal occipital activity (Gougoux et al. 2005; Lane et al. 2015). How these responses are anatomically situated with respect to each other remains to be fully described. Two prior studies suggest that within ‘visual’ cortex of blind people, different cognitive operations are anatomically segregated. One study showed that responses to language and math are segregated within general anatomical locations, including within V1 itself, with different portions of V1 responding preferentially to math and language (Kanjlia et al. 2016). Likewise, another study reported that responses during a long-term memory retrieval task with sentences are anatomically separable from activity observed during verb-generation (Abboud and Cohen 2019). At the same time, subspecialization of ‘visual’ cortices in blindness for different cognitive functions does not appear to follow subdivisions of the visual hierarchy. Many tasks, including language processing and memory tasks, activate both low level and high level visual areas: including V1, ventral, dorsal, and lateral occipital cortices. The anatomical location of verbal memory responses within ‘visual’ cortices remains to be fully characterized. The other critical outstanding question concerns the behavioral relevance of these cross-modal responses. Blind individuals with larger V1 responses during verbal tasks also show better verbal memory performance (Amedi et al. 2003; Raz et al. 2005).

‘Visual’ cortices are also recruited when blind individuals process verbal material, such as sentences and words and activity correlates across individuals with comprehension performance (e.g. Bedny et al. 2011; Burton et al. 2012b, a; Lane et al. 2015; Röder et al. 2002). Transcranial magnetic stimulation to the occipital pole impairs verb generation and Braille reading (Amedi et al. 2004; Cohen et al. 1999; Kupers et al. 2007). Recruiting additional cortical resources in ‘visual’ cortex could enhance verbal memory in people born blind. Recruiting ‘visual’ cortex does not always confer a behavioral advantage to people who are blind, however (e.g., Gudi-Mindermann et al. 2018; Rimmele et al. 2019). Further studies are needed to clearly establish a causal link between visual cortex plasticity and enhanced memory in blindness.

Finally, practice-related and ‘visual’ cortex plasticity accounts of verbal memory advantages in blindness are not mutually exclusive. Blindness may confer verbal memory practice while ‘visual’ cortex plasticity enables pronounced behavioral gains. Furthermore, behavioral pressure to rely on remembered verbal information may enhance recruiting visual cortex for verbal processing.

Conclusion

In sum, we find that people who are born blind show memory advantages but only for verbal material. These advantages persist even in the context of interference and are observed during recall and recognition. Such advantages could stem either from enhanced memory practice conferred by blindness, recruiting ‘visual’ cortices for verbal memory, or both.

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Declarations

Conflict of interests The authors declare that they have no conflicts of interest or competing interests.

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Code availability Data analysis code is available in an OSF project (<https://osf.io/etgyh>).

References

- Abboud S, Cohen L (2019) Distinctive interaction between cognitive networks and the visual cortex in early blind individuals. *Cereb Cortex* 29(11):4725–4742. <https://doi.org/10.1093/cercor/bhz006>
- Amedi A, Raz N, Pianka P, Malach R, Zohary E (2003) Early “visual” cortex activation correlates with superior verbal memory performance in the blind. *Nat Neurosci* 6(7):758–766. <https://doi.org/10.1038/nm1072>
- Amedi A, Floel A, Knecht S, Zohary E, Cohen LG (2004) Transcranial magnetic stimulation of the occipital pole interferes with verbal processing in blind subjects. *Nat Neurosci* 7(11):1266–1270. <https://doi.org/10.1038/nm1328>
- Bedny M, Koster-Hale J, Elli G, Yazzolino L, Saxe R (2019) There’s more to “sparkle” than meets the eye: Knowledge of vision and light verbs among congenitally blind and sighted individuals. *Cognition* 189:105–115. <https://doi.org/10.1016/j.cognition.2019.03.017>
- Bedny M, Pascual-Leone A, Dodell-Feder D, Fedorenko E, Saxe R (2011) Language processing in the occipital cortex of congenitally blind adults. *Proc Natl Acad Sci* 108(11):4429–4434. <https://doi.org/10.1073/pnas.1014818108>
- Bigham JP, Jayant C, Ji H, Little G, Miller A, Miller RC, Yeh T (2010) VizWiz: nearly real-time answers to visual questions. Paper presented at the Proceedings of the 23rd annual ACM symposium on User interface software and technology. https://dl.acm.org/doi/abs/https://doi.org/10.1145/1866029.1866080?casa_token=eqdciLsaAKsAAAA:v_iSvCJKVqaa-xY5ls_4fwveOme0IVWxs0hy40kPYpp_vBoRYqOVaGI-i6tDdYMTqiBvusMwGw1eZg
- Bliss I, Kujala T, Hämäläinen H (2004) Comparison of blind and sighted participants’ performance in a letter recognition working memory task. *Cogn Brain Res* 18(3):273–277. <https://doi.org/10.1016/j.cogbrainres.2003.10.012>
- Brainard DH (1997) The psychophysics toolbox. *Spat vis* 10(4):433–436. <https://doi.org/10.1163/156856897X00357>
- Bull R, Rathborn H, Clifford BR (1983) The voice-recognition accuracy of blind listeners. *Perception* 12(2):223–226. <https://doi.org/10.1068/p120223>
- Burton H, Sinclair RJ, Dixit S (2010) Working memory for vibrotactile frequencies: comparison of cortical activity in blind and sighted individuals. *Hum Brain Mapp* 31(11):1686–1701. <https://doi.org/10.1002/hbm.20966>
- Burton H, Sinclair RJ, Agato A (2012a) Recognition memory for Braille or spoken words: an fMRI study in early blind. *Brain Res* 1438:22–34. <https://doi.org/10.1016/j.brainres.2011.12.032>
- Burton MA, Brady E, Brewer R, Neylan C, Bigham JP, Hurst A (2012b) Crowdsourcing subjective fashion advice using VizWiz: challenges and opportunities. In: Paper presented at the Proceedings of the 14th international ACM SIGACCESS conference on Computers and accessibility. https://dl.acm.org/doi/abs/https://doi.org/10.1145/2384916.2384941?casa_token=6ooogNdG0QAAAA:wKavzQwyNOERUaGzbCjEktqKh_Y6qS1mQty8otfhCsLdPazrBzTehrAK1Ftlhc7Tbj0PA5tm7HbZA
- Castronovo J, Delvenne JF (2013) Superior numerical abilities following early visual deprivation. *Cortex* 49(5):1435–1440. <https://doi.org/10.1016/j.cortex.2012.12.018>
- Cattaneo Z, Vecchi T, Cornoldi C, Mammarella I, Bonino D, Ricciardi E, Pietrini P (2008) Imagery and spatial processes in blindness and visual impairment. *Neurosci Biobehav Rev* 32(8):1346–1360. <https://doi.org/10.1016/j.neubiorev.2008.05.002>
- Chan AS, Ho Y-C, Cheung M-C (1998) Music training improves verbal memory. *Nature* 396(6707):128–128. <https://doi.org/10.1038/24075>
- Christoffels IK, De Groot AM, Kroll JF (2006) Memory and language skills in simultaneous interpreters: the role of expertise and language proficiency. *J Mem Lang* 54(3):324–345. <https://doi.org/10.1016/j.jml.2005.12.004>
- Cohen LG, Weeks R.A, Sadato N, Celnik P, Ishii K, Hallett M (1999). Period of susceptibility for cross-modal plasticity in the blind. *Annals of Neurology: Official Journal of the American Neurological Association and the Child Neurology Society*, 45(4):451–460. [https://doi.org/10.1002/1531-8249\(199904\)45:4<451::AID-ANA6>3.0.CO;2-B](https://doi.org/10.1002/1531-8249(199904)45:4<451::AID-ANA6>3.0.CO;2-B)
- Cohen H, Voss P, Lepore F, Scherzer P (2010) The nature of working memory for Braille. *PLoS ONE* 5(5):e10833. <https://doi.org/10.1371/journal.pone.0010833>
- Cohen MA, Evans KK, Horowitz TS, Wolfe JM (2011) Auditory and visual memory in musicians and nonmusicians. *Psychon Bull Rev* 18(3):586–591. <https://doi.org/10.3758/s13423-011-0074-0>
- Collignon O, Vandewalle G, Voss P, Albouy G, Charbonneau G, Lassonde M, Lepore F (2011) Functional specialization for auditory-spatial processing in the occipital cortex of congenitally blind humans. *Proc Natl Acad Sci* 108(11):4435–4440. <https://doi.org/10.1073/pnas.1013928108>
- Cornell Kärnekull S, Arshamian A, Nilsson ME, Larsson M (2016) From perception to metacognition: auditory and olfactory functions in early blind, late blind, and sighted individuals. *Front Psychol* 7:1450. <https://doi.org/10.3389/fpsyg.2016.01450>
- Cornoldi C, Cortesi A, Preti D (1991) Individual differences in the capacity limitations of visuospatial short-term memory: research on sighted and totally congenitally blind people. *Mem Cognit* 19(5):459–468. <https://doi.org/10.3758/BF03199569>
- Dormal V, Crollen V, Baumans C, Lepore F, Collignon O (2016) Early but not late blindness leads to enhanced arithmetic and working memory abilities. *Cortex* 83:212–221. <https://doi.org/10.1016/j.cortex.2016.07.016>
- Ericsson KA, Lehmann AC (1996) Expert and exceptional performance: evidence of maximal adaptation to task constraints. *Annu Rev Psychol* 47(1):273–305. <https://doi.org/10.1146/annurev.psych.47.1.273>
- Föcker J, Best A, Hölig C, Röder B (2012) The superiority in voice processing of the blind arises from neural plasticity at sensory processing stages. *Neuropsychologia* 50(8):2056–2067. <https://doi.org/10.1016/j.neuropsychologia.2012.05.006>
- Fortin M, Voss P, Lord C, Lassonde M, Pruessner J, Saint-Amour D, Lepore F (2008) Wayfinding in the blind: larger hippocampal volume and supranormal spatial navigation. *Brain* 131(11):2995–3005. <https://doi.org/10.1093/brain/awn250>
- Frank MC, Everett DL, Fedorenko E, Gibson E (2008) Number as a cognitive technology: evidence from Pirahã language and cognition. *Cognition* 108(3):819–824. <https://doi.org/10.1016/j.cognition.2008.04.007>
- Franklin MS, Sledge Moore K, Yip C-Y, Jonides J, Rattray K, Moher J (2008) The effects of musical training on verbal memory. *Psychol Music* 36(3):353–365. <https://doi.org/10.1177/0305735607086044>

- Gougoux F, Zatorre RJ, Lassonde M, Voss P, Lepore F (2005) A functional neuroimaging study of sound localization: visual cortex activity predicts performance in early-blind individuals. *PLoS Biol* 3(2):e27. <https://doi.org/10.1371/journal.pbio.0030027>
- Gudi-Mindermann H, Rimmele JM, Nolte G, Bruns P, Engel AK, Röder B (2018) Working memory training in congenitally blind individuals results in an integration of occipital cortex in functional networks. *Behav Brain Res* 348:31–41. <https://doi.org/10.1016/j.bbr.2018.04.002>
- Ho Y-C, Cheung M-C, Chan AS (2003) Music training improves verbal but not visual memory: cross-sectional and longitudinal explorations in children. *Neuropsychology* 17(3):439. <https://doi.org/10.1037/0894-4105.17.3.439>
- Hull T, Mason H (1995) Performance of blind children on digit-span tests. *J vis Impairment Blind* 89(2):166–169. <https://doi.org/10.1177/0145482X9508900213>
- Kanjlia S, Lane C, Feigenson L, Bedny M (2016) Absence of visual experience modifies the neural basis of numerical thinking. *Proc Natl Acad Sci* 113(40):11172–11177. <https://doi.org/10.1073/pnas.1524982113>
- Kim JS, Elli GV, Bedny M (2019) Knowledge of animal appearance among sighted and blind adults. *Proc Natl Acad Sci* 116(23):11213–11222. <https://doi.org/10.1073/pnas.1900952116>
- Kupers R, Pappens M, de Noordhout A.M, Schoenen J, Ptito, M, Fumal A (2007). rTMS of the occipital cortex abolishes Braille reading and repetition priming in blind subjects. *Neurology*, 68(9): 691–693. <https://doi.org/10.1212/01.wnl.0000255958.60530.11>
- Lane C, Kanjlia S, Omaki A, Bedny M (2015) “Visual” cortex of congenitally blind adults responds to syntactic movement. *J Neurosci* 35(37):12859–12868. <https://doi.org/10.1523/JNEUROSCI.1256-15.2015>
- Loiotile R, Omaki A, Bedny M (2019) Enhanced sentence processing abilities among congenitally blind adults. *PsyArXiv*. <https://doi.org/10.17605/OSF.IO/M87SV>
- Ocelli V, Lacey S, Stephens C, Merabet LB, Sathian K (2017) Enhanced verbal abilities in the congenitally blind. *Exp Brain Res* 235(6):1709–1718. <https://doi.org/10.1007/s00221-017-4931-6>
- Pasqualotto A, Lam JS, Proulx MJ (2013) Congenital blindness improves semantic and episodic memory. *Behav Brain Res* 244:162–165. <https://doi.org/10.1016/j.bbr.2013.02.005>
- Pelli DG (1997) The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spat vis* 10(4):437–442. <https://doi.org/10.1163/156856897X00366>
- Pigeon C, Marin-Lamellet C (2015) Evaluation of the attentional capacities and working memory of early and late blind persons. *Acta Physiol (oxf)* 155:1–7. <https://doi.org/10.1016/j.actpsy.2014.11.010>
- Raz N, Amedi A, Zohary E (2005) V1 activation in congenitally blind humans is associated with episodic retrieval. *Cereb Cortex* 15(9):1459–1468. <https://doi.org/10.1093/cercor/bhi026>
- Raz N, Striem E, Pundak G, Orlov T, Zohary E (2007) Superior serial memory in the blind: a case of cognitive compensatory adjustment. *Curr Biol* 17(13):1129–1133. <https://doi.org/10.1016/j.cub.2007.05.060>
- Rimmele JM, Gudi-Mindermann H, Nolte G, Röder B, Engel AK (2019) Working memory training integrates visual cortex into beta-band networks in congenitally blind individuals. *Neuroimage* 194:259–271. <https://doi.org/10.1016/j.neuroimage.2019.03.003>
- Röder B, Demuth L, Streb J, Rösler F (2003) Semantic and morpho-syntactic priming in auditory word recognition in congenitally blind adults. *Lang Cognit Process* 18(1):1–20. <https://doi.org/10.1080/01690960143000407>
- Röder B, Rösler F (2003) Memory for environmental sounds in sighted, congenitally blind and late blind adults: evidence for cross-modal compensation. *Int J Psychophysiol* 50(1–2):27–39. [https://doi.org/10.1016/s0167-8760\(03\)00122-3](https://doi.org/10.1016/s0167-8760(03)00122-3)
- Röder B, Rösler F, Neville HJ (2000) Event-related potentials during auditory language processing in congenitally blind and sighted people. *Neuropsychologia* 38(11):1482–1502. [https://doi.org/10.1016/s0028-3932\(00\)00057-9](https://doi.org/10.1016/s0028-3932(00)00057-9)
- Röder B, Rösler F, Neville HJ (2001) Auditory memory in congenitally blind adults: a behavioral-electrophysiological investigation. *Cogn Brain Res* 11(2):289–303. [https://doi.org/10.1016/S0926-6410\(01\)00002-7](https://doi.org/10.1016/S0926-6410(01)00002-7)
- Röder B, Stock O, Bien S, Neville H, Rösler F (2002) Speech processing activates visual cortex in congenitally blind humans. *Eur J Neurosci* 16(5):930–936. <https://doi.org/10.1046/j.1460-9568.2002.02147.x>
- Rokem A, Ahissar M (2009) Interactions of cognitive and auditory abilities in congenitally blind individuals. *Neuropsychologia* 47(3):843–848. <https://doi.org/10.1016/j.neuropsychologia.2008.12.017>
- Sinclair RJ, Dixit S, Burton H (2011) Recognition memory for vibrotactile rhythms: An fMRI study in blind and sighted individuals. *Somatosens Mot Res* 28(3–4):48–62. <https://doi.org/10.3109/08990220.2011.602765>
- Smits B, Mommers M (1976) Differences between blind and sighted children on WISC verbal subtests. *J vis Impairment Blind* 70(6):240–246. <https://doi.org/10.1177/0145482X7607000604>
- Stankov L, Spilsbury G (1978) The measurement of auditory abilities of blind, partially sighted, and sighted children. *Appl Psychol Meas* 2(4):491–503. <https://doi.org/10.1177/014662167800200403>
- Struiksma ME, Noordzij ML, Postma A (2009) What is the link between language and spatial images? Behavioral and neural findings in blind and sighted individuals. *Acta Physiol (oxf)* 132(2):145–156. <https://doi.org/10.1016/j.actpsy.2009.04.002>
- Swanson HL, Luxenberg D (2009) Short-term memory and working memory in children with blindness: support for a domain general or domain specific system? *Child Neuropsychol* 15(3):280–294. <https://doi.org/10.1080/09297040802524206>
- Thaler L, Arnott S, Goodale M (2011) Neural correlates of natural human echolocation in early and late blind echolocation experts. *PLoS ONE* 6(5):e20162. <https://doi.org/10.1371/journal.pone.0020162>
- Tillman MH, Bashaw WL (1968) Multivariate analysis of the WISC scales for blind and sighted children. *Psychol Rep* 23(2):523–526. <https://doi.org/10.2466/pr0.1968.23.2.523>
- Vecchi T (1998) Visuo-spatial imagery in congenitally totally blind people. *Memory* 6(1):91–102. <https://doi.org/10.1080/741941601>
- Vercillo T, Milne JL, Gori M, Goodale MA (2015) Enhanced auditory spatial localization in blind echolocators. *Neuropsychologia* 67:35–40. <https://doi.org/10.1016/j.neuropsychologia.2014.12.001>
- Voss P, Lassonde M, Gougoux F, Fortin M, Guillemot JP, Lepore F (2004) Early- and late-onset blind individuals show supra-normal auditory abilities in far-space. *Curr Biol* 14(19):1734–1738. <https://doi.org/10.1016/j.cub.2004.09.051>
- Withagen A, Kappers AM, Vervloed MP, Knoors H, Verhoeven L (2013) Short term memory and working memory in blind versus sighted children. *Res Dev Disabil* 34(7):2161–2172. <https://doi.org/10.1016/j.ridd.2013.03.028>

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