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Enhanced performance on a sentence comprehension task in congenitally blind adults

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Abstract

People born blind habitually experience linguistic utterances in the absence of visual cues and activate "visual" cortices during sentence comprehension. Do blind individuals show superior performance on sentence processing tasks? Congenitally blind (n=25) and age and education matched sighted (n=52) participants answered yes/no who-did-what-to-whom questions for auditorily-presented sentences, some of which contained a grammatical complexity manipulation (long-distance movement dependency or garden path). Short-term memory was measured with a forward and backward letter-spans. A battery of control tasks included two speeded math tasks and vocabulary and reading tasks from Woodcock Johnson III. The blind group outperformed the sighted on the sentence comprehension task, particularly for garden-path sentences, and on short-term memory span tasks, but performed similar to the sighted on control tasks. Sentence comprehension performance was not correlated with span performance, suggesting independent enhancements.

Keywords

Sentence processing; blindness; garden path; plasticity; practice

Introduction

Humans adapt flexibly to changes in experience. A key example of this adaptability comes from studies of sensory loss, such as in blindness and deafness. The loss of one modality is associated with selective improvements in other senses. Individuals who are blind from birth are better than sighted controls at judging whether an auditory pitch is falling or rising, localizing sounds in the horizontal plane and detecting orientations of tactually-presented gratings (Lessard, Pare, Lepore, & Lassonde, 1998; Goldreich & Kanics, 2003). Improvements are thought to result, in part, from practice in relying on and extracting information from non-visual senses.

Behavioral improvements associated with blindness may further be enabled by availability of extra cortical real-estate. Neuroimaging studies with blind and deaf individuals find that deprived sensory cortices—i.e., visual and auditory cortices, respectively—participate in

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new cognitive functions (e.g. Sadato, et al., 1996; Bavelier & Neville, 2002; Kupers & Ptito, 2014; Merabet & Pascual-Leone, 2009; Noppeney, 2007). In blindness, "visual" cortices are active during auditory and tactile tasks. Although not all "visual" cortex plasticity is associated with behavioral benefits (e.g. Kanjlia et al., 2016), some of the tasks associated with "visual" cortex activity are the very ones on which blind individuals outperform the sighted e.g. auditory localization and fine-grained tactile discrimination (Collignon, Vandewalle, & Voss, 2011; Collignon, Voss, Lassonde, & Lepore, 2008; Gougoux, Zatorre, Lassonde, Voss, & Lepore, 2005; Kujala, Alho, Paavilainen, Summala, & Näätänen, 1992; Roder, Teder-Sälejärvi, Sterr, & Rösler, 1999; Voss, Gougoux, Zatorre, Lassonde, & Lepore, 2008; Weeks et al., 2000).

Blindness-related repurposing of "visual" cortex is not restricted to sensory processes. In congenitally blind individuals, a large subset of "visual" cortices is recruited during language tasks. Visual cortices are active during spoken sentence comprehension and the amount of activity varies as a function of meaning and syntactic structure: "visual" cortices respond more to sentences than lists of unconnected words, more to sentences than grammatical but meaningless "Jabberwocky", and more to Jabberwocky than to lists of non-words (e.g., glorf, blig, marp, ...) (Abboud & Cohen, 2019; Bedny, Pascual-Leone, Dodell-Feder, Fedorenko, & Saxe, 2011; Burton, Diamond, & McDermott, 2003; Röder, Stock, Bien, Neville, & Rösler, 2002). Larger "visual" cortex responses are observed for grammatically complex sentences with a syntactic long-distance dependency (e.g., "The girl, that the boy admires, is vacationing in Spain") (Lane, Kanjlia, Omaki, & Bedny, 2015; Röder et al., 2002).

Language-responsive parts of visual cortex augment, rather than replace the classic frontotemporal language regions, which show similar functional profiles across blind and sighted groups. Language-responsive "visual" cortex areas are co-lateralized with inferior frontal language regions across blind individuals and correlated with fronto-temporal language networks, even at rest (Bedny et al., 2011; Lane et al., 2015; Watkins et al., 2012). These results suggest that parts of "visual" cortex are incorporated into the language network in blindness (see Tomasello et al., 2019 for modeling on the neurobiological mechanisms mediating plasticity). The behavioral relevance of this language-related plasticity remains unclear. Studies using transcranial magnetic stimulation (TMS), show that interfering with "visual" cortex function impairs performance on verb generation and Braille reading tasks (Amedi, Floel, Knecht, Zohary, & Cohen, 2004; Cohen, Celnik, Pascual-Leone, & Corwell, 1997). However, behavioral relevance to core language functions, such as sentence processing, remains uncertain. In one fMRI study blind participants who showed larger "visual" cortex responses to grammatically complex sentences also show superior performance at answering comprehension questions (Lane et al., 2015). In this experiment blind participants as a group were marginally better than the sighted at answering comprehension questions for all sentence types. However, behavior was measured in a noisy fMRI environment and the sample was relatively small and heterogenous (e.g. including individuals who are blind due to premature birth and a wide age range), potentially obscuring benefits associated with blindness.

Apart from "visual" cortex responses to language, another reason blindness could benefit sentence comprehension performance is by increased practice in relying on language internal cues to extract meaning. Vision and language often provide analogous information about the identity of objects and agents and about who did what to whom. Sighted listeners rapidly integrate linguistic and visual information during online comprehension to build situation models. According to constraint-based models of sentence processing, comprehension occurs by integrating various sources of information, including not only syntactic and lexical information, but also extra-linguistic cues such as what objects are present in the environment (Bader, 1998; Bailey & Ferreira, 2003; Chambers, Tanenhaus, Eberhard, Filip, & Carlson, 2002; MacDonald, Pearlmutter, & Seidenberg, 1994; McRae, Spivey-Knowlton, & Tanenhaus, 1998; Nagel, Shapiro, & Nawy, 1994; Tanenhaus, Magnuson, Dahan, & Chambers, 2000; Tanenhaus, Spivey-Knowlton, Eberhard, & Sedivy, 1995; Trueswell & Gleitman, 2004; Trueswell, Tanenhaus, & Garnsey, 1994; Tyler & Marslen-Wilson, 1977). Sighted listeners rapidly use visual cues to disambiguate temporarily ambiguous garden-path sentences, for example, using the number and location of objects present to determine whether a propositional phrase indicates a destination or a modifier of the preceding noun "put the frog on the napkin, into the box" (Chambers, Tanenhaus, & Magnuson, 2004; Farmer, Anderson, & Spivey, 2007; Huettig, Rommers, & Meyer, 2011; Spivey, Tanenhaus, Eberhard, & Sedivy, 2002; Tanenhaus et al., 1995). Although audition and touch also contain relevant contextual information, vision may be a particularly efficient source of information about the types of things that language refers to: object and agent identity, their location and the events in which they participate. While sighted individuals habitually make use of extralinguistic information during comprehension, blind individuals may conversely develop better abilities to use languageinternal information during sentence comprehension. Such practice-based enhancements could be thought of as analogous to better attention to, and extraction of, information from audition and touch (Fieger, Röder, Teder-Sälejärvi, Goldreich & Kanics, 2003; Hillyard, & Neville, 2006; Lessard, Pare, Lepore, & Lassonde, 1998; Van Boven, Hamilton, Kauffman, Keenan, & Leone, 2000; Voss et al., 2004; Wan, Wood, Reutens, & Wilson, 2010; Wong, Gnanakumaran, & Goldreich, 2011). Such practice could lead blind listeners to outperform the sighted on sentence comprehension tasks, when extralinguistic cues are absent. The goal of the current study was to test this hypothesis.

Previous studies of language in blindness have focused on whether blind individuals have superior speech perception and word recognition abilities but have not examined higherorder aspects of language (i.e. syntax and semantics). Blind adults are, indeed, better than the sighted at identifying syllables in a task of dichotic listening (Hugdahl et al., 2004) and at identifying words under high-noise conditions (Muchnik, Efrati, Nemeth, Malin, & Hildesheimer, 1991). Two studies also suggest faster lexical access among individuals who are blind. One study found faster lexical decision times for spoken words and non-words among blind individuals (Röder, Demuth, Streb, & Rösler, 2003). Blind individuals also show a faster onset of the N400 component upon encountering an incongruent word at the end of a sentence—e.g. "Tomorrow Bobby will be ten years hill" (Roder, Rösler, & Neville, 2000). Traditionally these results have been interpreted as evidence for more efficient

perceptual speech processing. However, an open question is whether blind individuals also show superior high-level linguistic abilities, such as enhancements in sentence processing.

One higher-cognitive domain in which blind individuals are known to show an advantage is memory. Blind children and adults recall larger numbers of words, letters and digits over both short and long delays and more accurately reproduce the serial order of encoded words (Amedi, Raz, Pianka, Malach, & Zohary, 2003; Dormal, Crollen, Baumans, Lepore, & Collignon, 2016; Hull & Mason, 1995; Pasqualotto, Lam, & Proulx, 2013; Raz, Striem, Pundak, Orlov, & Zohary, 2007; Roder, Rösler, & Neville, 2001; Rokem & Ahissar, 2009; Swanson & Luxenberg, 2009; Tillman & Bashaw, 1968; Withagen, Kappers, Vervloed, Knoors, & Verhoeven, 2013). Analogous to improvements observed in audition and touch, improvement in memory may result from compensatory reliance on memory in the absence of visual cues together with availability of extra "visual" cortex wetware (Raz, Striem, Pundak, Orlov, & Zohary, 2007). There is evidence that verbal memory tasks activate visual cortex and amount of activity predicts memory performance among blind individuals (Amedi et al., 2003; Raz, Amedi, & Zohary, 2005).

The goal of the current study was to ask whether blind individuals develop superior spoken sentence processing abilities and, if so, whether these improvements are related to previously reported advantages in verbal short-term memory among blind individuals. We measured accuracy and reaction time while blind individuals answered yes/no comprehension questions based on spoken sentences that varied in syntactic complexity. Syntactic complexity was manipulated in two independent ways, by introducing syntactic movement and using garden paths (See Table 1 for example stimuli). Sentences with syntactic movement displace referents with respect to their modifying phrase. For example, in "The actress that the creator of the gritty HBO crime series admires often improvises her lines," the object "actress" is displaced from the verb "admires." Garden path sentences are a form of temporary syntactic ambiguity in which the listener is lead to a syntactic parse that later turns out to be incorrect. For example, in "While the little girl dressed the doll that she was playing with sat on the floor of her bedroom," the initial interpretation that the girl dressed the doll turns out to be incorrect, rather the girl dressed herself. The verb "dressed" is most often followed by its object, but in this particular case is being used reflexively. Performance of blind and sighted participants on syntactically complex sentences was compared to matched control sentences. We hypothesized that blind individuals would show superior sentence-comprehension ability relative to the sighted and that this advantage would be most pronounced for syntactically complex sentences.

We measured short term memory for spoken letters, in blind and sighted participants. The goal was to replicate the previous finding that blind participants show enhancements in verbal working memory and to determine whether these enhancements are related to improvements in sentence comprehension performance (Amedi et al., 2003; Hull & Mason, 1995).

Blind and sighted participants were also tested on a series of control tasks, including two symbolic math tasks and verbal portions of the Woodcock-Johnson III, which test vocabulary and reading ability. These tasks enabled us to test the specificity of sentence

comprehension performance. We predicted that sentence-comprehension advantages and working memory advantages in blind individuals would persist, even when blind and sighted groups are matched on other cognitive abilities.

Methods

Participants.

25 congenitally blind individuals (15 female) and 52 sighted age and educated matched controls (36 female) took part in the study (age: blind mean=32.64, SD=9.86; sighted mean=33.31, SD=11.51; blind vs. sighted t(75)=-0.25, p=0.80; years of education: blind mean=16.68, SD=2.61, sighted mean=16.59, SD=2.20; blind vs. sighted t(75)=0.15, p=0.88). All but one blind and one sighted participant completed all of the experimental tasks. One blind participant was not tested on the Analogies and Division portions of WJIII and one sighted participant did not perform the working memory task. An addition 2 blind and 2 sighted participants were tested but excluded for poor performance on the Woodcock-Johnson III (outliers on any individual measure, defined according to Rosner's extreme studentized deviate test for multiple outliers, two-sided, p < 0.05, maximal 10 (Rosner, 1975)). Reported numbers of blind and sighted participants do not include these excluded participants.

All participants were native English speakers, majority having spoken only English since birth. 1 (of 25) blind and 3 (of 52) sighted learned English through immersion between 3 and 4 years of age. We collected data from blind participants at two separate conventions of the National Federation for the Blind (2014 and 2016). Sighted participants were tested at Johns Hopkins University. Blind participants had minimal-to-no light perception since birth, due to pathologies in or anterior to the optic chiasm (see Table 2 for cause of blindness). Since premature birth can be associated with cognitive disabilities, participants who were blind due to retinopathy of prematurity (ROP) were not recruited for this study (Dann, Levine, & New, 1964). All participants reported no cognitive or neurological disabilities.

To match visual conditions across groups, sighted participants were blindfolded for all tasks except for the participant-read portions of the Woodcock Johnson-III (WJ-III). Participants listened to all auditory tasks via headphones. Volume was adjusted for each participant, according to their own comfortable listening volume. All experiments were run using either PsychoPy or Matlab's Psychoolbox (Brainard, 1997; Peirce, 2007).

Sentence Processing Task: Materials and Procedure

Each participant listened to 180 sentences and answered a yes/no comprehension question for each sentence (see Appendix 1). Participants had 6 seconds from the onset of the question to make a button press.

The syntactic complexity of sentences was manipulated in two ways: by introducing a longdistance movement dependency or a garden path syntactic ambiguity (described in detail below). Each of these two conditions was paired to a matched, control condition that lacked the critical syntactic manipulation—i.e. no-move and non-garden path sentences (see Table 1). In addition to the critical sentences, we included filler sentences to reduce syntactic

priming. Fillers varied in their grammatical constructions and did not contain either longdistance dependencies or garden paths. Overall there were 120 move/no-move sentence pairs (every participant heard 60 of each version), 10 garden path, 10 non-garden path, and 40 filler sentences. A subset of initial participants (5 blind and 13 sighted; proportion of total approximately matched across groups) received a longer version of the paradigm with 248 total questions, consisting of 84 move, 84 no-move, 10 garden path, 10 non-garden path, and 60 filler trials. The experiment was subsequently shortened to reduce testing time. To control for item effects, only the items that appeared in the short-form were analyzed— i.e., 60 of 84 move and 60 of 84 non-move— even for those participants who received the longer version of the paradigm.

Sentences with syntactic movement contain words or phrases that are displaced, or "moved," with respect to their modifying phrases (See Table 1 for example sentences). Syntactic movement was achieved via object-extracted relative clauses. For example, in "The actress that the creator of the gritty HBO crime series admires often improvises her lines," "actress," as the object of the verb "admires," is extracted from its normal position after the transitive verb and moved to the head of the relative clause. The non-movement counterpart used a sentential complement clause structure, which was similar in meaning to the relative clause version and contained nearly identical words but did not include a long-distance movement dependency. Matched movement and non-movement sentences were counterbalanced across two lists, such that each participant heard only one version of the sentence. Comprehension questions required participants to attend to thematic relations of words in the sentence (i.e., who did what to whom), and could not be answered based on recognition of individual words. Half of the move and half of the non-move stimuli had comprehension questions in which "yes" was the correct response. The stimuli were a subset of those used in a previously published study (Lane et al., 2015).

The second type of syntactic complexity manipulation was garden path, i.e. temporary syntactic ambiguities, where the listener is led down a "garden-path" in which an initially favored sentence parse turns out to be irreconcilable with subsequent words in the sentence. (Garden path and non-garden-path control sentences were adapted from a published set of stimuli (Christianson et al., 2001)). For example, in "While the little girl dressed the doll that she was playing with sat on the floor of her bedroom.," "dressed" could either be used transitively with "the doll" as the direct object (i.e. the little girl dressed the doll) or reflexively (i.e. the little girl dressed *herself*). The former interpretation is favored because the verb "dressed" is more frequently used transitively (i.e. this use has a higher subcategorization frequency), but the subsequent verb "sat" requires "the doll" to be its subject, and hence disambiguates the two alternatives in favor of the reflexive form. A relative clause modifier was added to the critical, ambiguous noun phrase in order to amplify the garden-path effect (Christianson, Hollingworth, Halliwell, & Ferreira, 2001; Ferreira & Henderson, 1991). Thus, all garden path sentences were of the following form: While [Noun Phrase 1] [Reflexive Verb] [Noun Phrase 2] [Verb Phrase]. Non-garden path control sentences were formatted as follows: While [Noun Phrase 1] [Transitive Verb] [Noun Phrase 2] [Noun Phrase 3] [Verb Phrase]. In the control sentences, the additional [Noun Phrase 3] requires the ambiguous verb to be transitive, consistent with the listener's initial parse. The non-garden-path control sentences were not voked to their garden path counterparts (i.e. had

different words), but followed the same structure templates, with the exception of the additional Noun Phrase in non-garden path sentences. All questions tested correct comprehension of the verb, in the format: Did [Noun Phrase 1] [Reflexive/Transitive Verb] [Noun Phrase 2]? For example, "Did the little girl/nanny dress the doll/baby?" Therefore, the correct response for garden path and non-garden path control questions was always "no" and "yes," respectively. All subjects heard all garden-paths and non-garden-path control sentences.

Condition ordering, across trials, was pseudo-randomized such that each condition could not appear in more than 2 contiguous trials, and the conditions were evenly dispersed across each 1/8th block of the experiment. Altogether, for half of the trials the correct response was "yes." Before starting, all participants performed a set of 10 practice trials with feedback. Sentences were pre-recorded and spoken by a male voice in a flat intonation, in order to minimize cues to correct syntactic parsing.

We removed all trials in which a participant either failed to respond or false started (i.e. responded in < 150 MS). On average, blind and sighted participants missed fewer than 1 question per each condition (overall misses: mean blind 1.48 items; mean sighted 1.92 items; n.s. difference between groups t(75)=0.92, p =0.36). Sighted participants had more missed responses than blind participants, but this difference was not significant (move: t(75)=0.66, p>0.5; non-move: t(75)=1.25, p=0.21; garden-path: t(75)=1.75, p=0.08; non-garden path: t(75)=0.61, p>0.5). The dependent measure was accuracy (binary success or failure on each trial) and speed (reaction-time, from question onset, for correct trials only).

Working Memory Tasks

Forward and Backward Letter Span tasks were adapted from the Forward and Backward Digit Span components of the Wechsler Adult Intelligence Scale (WAIS) by mapping the digits 1–9 to the letters A-I. For both letter span tasks, participants listened to a recording of a female speaking a series of letters. After the last presented letter, participants were asked to repeat all letters back to the experimenter in either the exact order (Forward) or the exact opposite order (Backward). Trials were presented according to span-length, starting with a length of 2 and going up to 9 (for Forward) and 8 (for Backward), with 2 trials for each span length. Failure to get two trials of a given span length correct terminated the task. Accuracy was calculated as a percentage correct out of all possible trials, with incorrect recall assumed for un-tested spans. All participants did the Forward Letter Span followed immediately by the Backward Letter Span.

Woodcock-Johnson III (Control)

We collected control measures to ensure that blind and sighted groups did not differ on general cognitive abilities. Participants were tested on 5 sections of the Woodcock-Johnson III (WJ-III). Blind participants completed the WJIII in printed Braille. The following sections were tested: Letter-Word Identification in which the participant are asked to read and correctly pronounce 60 English words (e.g. "bouquet"); Word Attack in which the participant read and correctly pronounce 33 nonsense words (e.g. "paraphonity"); Oral Vocabulary-Synonyms in which the participant read each of 12 words and generate a

synonym (e.g. "wild" \rightarrow "untamed"); Oral Vocabulary-Antonym in which the participant read each of 13 words and generated an antonym (e.g. "authentic" \rightarrow "fake"); and Oral Vocabulary-Analogies in which participants read each of 12 incomplete analogies and generate a word analogous to the unpaired word according to the relationship established by the first word pair (e.g. "Wrist is to shoulder, as ankle is to ..." \rightarrow "hip"). Participants were allowed to skip any items they could not complete but were not allowed to go back. Responses were considered correct if they matched one of the words designated by the WJ-III. Accuracy for each section was scored as percentage correct of all trials. All participants performed the WJ-III sections in the order listed above.

Arithmetic (Control)

Participants were tested on speeded arithmetic calculations in 2 separate tasks: subtraction and division. All problems contained 2 operands, with the following digit lengths: minuends and subtrahends (2), divisors (1), and dividends (2–3). For each task, participants were given 4 minutes to accurately complete as many problems as possible. (Participants were allowed to complete any problems begun before the 4 minutes had expired.) Problems were pre-recorded to minimize differences in presentation between participants. Participants pressed a button to initiate auditory presentation of each problem and had to state their answer to the researcher. Participants could choose to skip problems and to repeat auditory presentation of the current problem but were not allowed to go back to skipped problems. Participants were not allowed to use writing devices to solve the problems. The subtraction and division sections contained 30 and 33 problems, respectively. Accuracy was scored as percentage correct of all trials, regardless of whether they were attempted. All participants performed the subtraction task immediately before the division task. Problems were taken from the Kit of Factor-Referenced Cognitive Tests (Ekstrom, French, Harman, & Dermen, 1976).

Results

Sentence Comprehension

We compared performance across groups for the movement and garden path manipulations. For all accuracy analyses, we used a mixed-effect generalized-linear (logit) model with participant and item included as random effects (Baayen, Davidson, & Bates, 2008; Clark, 1973; Jaeger, 2008). For all reaction time analyses, we used a mixed-effect general linear model with participant and item included as random effects. Due to differing numbers of trials across movement and garden-path sentences, we analyzed them separately and compared each to their respective control sentences. Filler data were modeled separately.

Blind participants were overall more accurate for both move and non-move control sentences (sighted non-move mean=86.61%, SD=8.74%; sighted move mean=74.53%, SD=11.63%; blind non-move mean=90.16%, SD=6.69%; blind move mean=80.91%, SD=8.91%; group X complexity ANOVA, main effect of group, log-odds coefficient B=0.39 (SE=0.16), p=0.014; corresponding odds coefficient e^B =1.48). For both blind and sighted participants, accuracy was worse for move sentences than for non-move sentences (main effect of complexity, log-odds coefficient B=0.90 (SE=0.12), p<0.001; corresponding odds

coefficient e^B =2.46, n.s. group X complexity interaction, log-odds coefficient B=-0.06 (SE=0.13), p>0.5; corresponding odds coefficient e^B =0.94) (Figure 1, left panel).

Better accuracy of the blind group for move and non-move sentences was not driven by a speed-accuracy tradeoff (Figure 1, right panel) (sighted non-move mean=3.37 s, SD=0.27 s; sighted move mean=3.48 s, SD=0.26 s; blind non-move mean=3.29 s, SD=0.26 s; blind move mean=3.42 s, SD=0.30 s; group X complexity ANOVA: n.s. main effect of group, B=-0.07 (SE=0.06), p=0.28, n.s. group X complexity interaction, B=0.1 (SE=0.03), p>0.5). Both groups responded to move sentences more slowly than to non-move sentences (main effect of sentence-type, B=-0.12 (SE=0.03), p=0.001).

Blind participants were overall more accurate across garden-path (blind mean=76.00%, SD=27.08%; sighted mean=56.99%, SD=30.18%) and control sentences (blind mean=96.00%, SD=7.07%; sighted mean=91.80%, SD=8.43%; group X complexity ANOVA: main effect of group, log-odds coefficient B=1.03 (SE=0.39), p=0.008, corresponding odds coefficient e^B =2.79). Although the group difference was numerically more pronounced for the garden-path sentences, the group-by-sentence type interaction did not reach significance (group X complexity interaction, log-odds coefficient B=-0.28 (SE=0.43), p>0.5; corresponding odds coefficient e^B =0.75). Accuracy was worse for garden path than non-garden path control sentences for both groups (main effect of complexity, log-odds coefficient B=2.74 (SE=0.47), p<0.001; corresponding odds coefficient e^B =15.49).

Blind participants were overall faster than the sighted at answering questions about gardenpath and non-garden path control sentences and in this case the main effect of group was qualified by a group-by-condition interaction: While sighted participants were slower to respond to garden-path than non-garden path sentences, blind participants responded with equal speed to both sentence types (sighted non-garden path mean=2.87 s, SD=0.22 s; sighted garden path mean=3.09 s, SD=0.42 s; blind non-garden path mean=2.84 s, SD=0.20s; blind garden path mean=2.84 s, SD=0.44 s; group X complexity ANOVA, main effect of group, B=-0.14 (SE=0.06), p=0.03, group X complexity interaction, B=0.22 (SE=0.06), p=0.001; n.s. main effect of sentence-type, B=-0.07 (SE=0.14), p>0.5).

Since all garden-path sentences required a "no" response, we checked if group differences in response-bias might have driven the observed difference in performance. We measured bias to respond "no" for difficult questions as the percentage of "no" responses on incorrect move, non-move, and filler items. Blind participants were not more biased to respond "no" (n.s. difference between groups: t(75)=1.01, p=0.31).

Above movement and garden path sentences are analyzed separately due to large differences in the number of items in each of the conditions. Since we observed a more pronounced group difference in the garden-path sentence model, we additionally ran a joint model to test for three-way sentence type (movement/garden path) by grammatical complexity by group interactions in accuracy and reaction time, neither of which were significant (Accuracy vision group X grammatical complexity X grammatical manipulation interaction, B=-0.15(SE=0.43), p>0.5; Reaction Time vision group X grammatical complexity X grammatical

manipulation interaction, B=0.09 (SE=0.07), p=0.18). Differences between movement and garden path sentences should thus be interpreted with caution.

Blind and sighted participants did not differ in their accuracy or reaction on filler trials (Accuracy: blind mean=88.38%, SD=7.01%; sighted mean=85.70%, SD=8.42%, effect of group log-odds coefficient B=-0.31 (SE=0.21), p=0.14; Reaction time: blind mean=3.27 S, SD=0.24 S; sighted mean=3.36 S, SD=0.21 S; effect of group B=0.08 (SE=0.05), t=1.47, p=0.15.)

WJ-III & Arithmetic (Control)

Blind and sighted participants performed equivalently on the WJ-III subsections (group X WJ-III measure ANOVA, main effect of group not significant, F(1,74)=0.05, p>0.5; group X measure interaction not significant, F(4,296)=0.49, p>0.5) (Figure 2). For the math tasks, a group by operation (division vs. subtraction) ANOVA revealed a main effect of math operation with division more difficult than subtraction, F(1,74)=185.81, p < 0.001). Overall, blind and sighted participants did not differ in their math performance (main effect of group not significant, F(1,74)=1.29, p=0.26). However, there was a significant interaction between group and math-operation with blind participants showing a bigger difference between subtraction and division tasks, and performing worse than the sighted only on the division task (F(1,74)=7.05, p=0.01) (Figure 2).

Working Memory Span

A group X direction (forward vs. backward) ANOVA, revealed a main effect of span direction, with forward span significantly easier than backward span (F(1,74)=13.70, p<0.001) (Figure 2, right-most columns). Across spans, blind participants had better working memory than sighted participants (main effect of group, F(1,74)=33.21, p<0.001; n.s. group X direction (forward vs. backward) interaction, F(1,74)=0.94, p=0.34).

Relationship between Short-term Memory Span and Sentence Comprehension

Short-term memory span did not significantly predict sentence comprehension performance in either the blind or the sighted groups for any sentence types (correlation with average forward & backward span: blind accuracy: move: r=0.31, p=0.13, non-move: r=0.31, p=0.12, garden path: r=0.28, p=0.17, non-garden path: r=0.33, p=0.10; sighted accuracy: move: r=0.17, p=0.23, non-move: r=0.17, p=0.23, garden path: r=0.17, p=0.24, non-garden path: r=0.16, p=0.28) (Figure 3).

Short-term memory span also did not significantly predict sentence comprehension response times in either the blind or the sighted group for any sentence types (correlation with average forward & backward span: blind RT: move: r=-0.23, p=0.27, non-move: r=-0.20, p=0.35, garden path: r=-0.18, p=0.38, non-garden path: r=-0.04, p>0.5; sighted RT: move: r=-0.09, p>0.5, non-move: r=-0.26, p=0.07, garden path: r=0.11, p=0.45, non-garden path: r=0.02, p>0.5).

However, performance on garden path and movement sentences was correlated across participants, both in the sighted r=.61, p<.0001 and in the blind r=.73, p<.0001 groups.

Performance was also significantly correlated across forward and backward spans in the sighted r=.32, p<.05 and blind group r=.58, p<.005 (Figure 4).

Discussion

Blindness confers an advantage on a sentence comprehension task, how and why?

We find that when presented with spoken sentences, congenitally blind individuals are more accurate than matched, sighted controls at answering who-did-what-to-whom questions. An accuracy advantage was observed for movement and garden path sentences and even for their control sentences (see also Lane et al., 2015). Blind participants are faster, particularly for garden-path sentences: Unlike sighted adults, blind individuals responded as quickly to questions about garden-path sentences as they do to matched, non-garden-path control sentences, showing no garden path cost in reaction time. Advantages on the sentence comprehension task cannot be explained by differences in general cognitive abilities across groups: blind participants performed no better than sighted participants on standardized tasks assessing reading, vocabulary, analogies, and arithmetic. Though blind participants outperformed the sighted on forward and backward letter span tasks, letter-span and sentence comprehension performance were not correlated. By contrast, performance on the sentence comprehension task was correlated across sentence types: those participants who performed well at answering who-did-what to whom questions for garden path sentences also performed better on movement sentences. Furthermore, forward and backward span performance was correlated.

As noted in the introduction, unlike the sighted, congenitally blind individuals recruit "visual" cortices during sentence processing tasks and more so for syntactically complex sentences (Bedny et al., 2011; Lane et al., 2015; Röder et al., 2002). Larger "visual" cortex responses are associated with better sentence comprehension performance and better verbal memory across blind individuals (Lane et al., 2015, Amedi et al., 2003). TMS to "visual" cortex impairs verb-generation and Braille reading among blind individuals (Amedi et al., 2004, Cohen et al., 1997). Together with the present results, these findings are consistent with the hypothesis that in blindness "visual" cortex plasticity confers a behavioral advantage in language processing. However, further work using techniques such as TMS is needed to directly test the hypothesis that "visual" cortex is functionally relevant to sentence-processing per se. One interesting question that remains to be tested in future work is whether sentence comprehension improvements are specific to people born blind or also observed among individuals who lose their sight as adults. Some evidence suggests that "visual" cortex plasticity for language is either absent or substantially reduced in people who are adult-onset as opposed to congenitally blind (e.g. Bedny et al., 2012), leading to the prediction that any sentence comprehension benefits will be restricted to people born blind.

It is important to point out that the relationship between increased cortical territory devoted to a particular function and performance is complex. While blind individuals show improved behavior on some tasks that activate "visual" cortices this is not uniformly the case. For example, blind individuals activate "visual" cortices when solving math equations and outperform the sighted on some memory intensive arithmetic tasks (Dormal et al., 2016). However, for many math tasks, including those that activate "visual" cortex in blindness,

there are no blindness-related advantages (e.g. Crollen et al., 2019, Kanjlia et al., 2016, Kanjlia et al., 2018). In the current study, the blind group performed no different from the sighted on a timed subtraction task and less well than the sighted on a timed division task. Blindness could influence performance on a given task in multiple different and even opposing ways. For example, barriers to accessing mathematical education could produce disadvantages on some math tasks and "wash out" subtle benefits conferred by "visual" cortex plasticity. Further research is needed to determine how additional "visual" cortical territory influences performance on sentence-processing and other tasks.

The availability of "visual" cortex territory is only one of several non-mutually exclusive explanations for why blindness enhanced performance on the current sentence comprehension task. Another possibility noted in the introduction is habitual practice interpreting spoken language in the absence of visual cues. Such a practice-based argument is not inconsistent with the hypothesis that "visual" cortex plasticity enables behavioral improvements. The availability of extra language wetware in the "visual" cortex could make behavioral improvements possible in the presence of environmental pressure to perform better. Conversely, reliance on language as a source of information may increase pressure for language (as opposed to other cognitive functions) to colonize available territory in the "visual" cortex.

What cognitive mechanisms are responsible for the observed behavioral improvements in sentence comprehension? One logical possibility is that improvements are related to previously documented enhancements in short-term memory associated with blindness (Amedi, et al., 2003; Hull & Mason, 1995; Raz et al., 2007; Rokem & Ahissar, 2009; Tillman & Bashaw, 1968; Withagen et al., 2013). Consistent with prior work, in the current study blind participants performed significantly better than the sighted on forward and backward short-term memory span tasks. Working memory mechanisms are relevant to sentence processing. During sentence comprehension, as a sentence unfolds in time, listeners maintain previously heard linguistic information in working memory and blind listeners may maintain more of this information, with higher fidelity and perhaps for a longer amount of time. However, we found no evidence for a relationship between performance on sentence comprehension and span-based short-term memory tasks: those blind individuals that showed the best performance on the auditory sentence comprehension were not the same as those who showed maximal performance on the span tasks. This suggests that the sentence comprehension and span tasks in the current study may be measuring independent blindness-related improvements.

Blindness-related improvements in short-term memory and sentence processing could, nevertheless, occur for analogous reasons. It has previously been suggested that the sentence-relevant short-term memory system is distinct from the one used during span tasks (e.g. Caplan & Waters, 1999). Blindness may therefore independently improve the capacity to maintain information online before it can be integrated into the sentence structure. For example, maintaining the matrix subject in memory across the intervening clause until the associated relative clause verb is encountered. In the case of garden path sentences, blind individuals may maintain the initially dis-preferred sentence parse active to greater extent than sighted participants (Gibson, 1998; Hickok, 1993; Just & Carpenter, 1992; MacDonald

et al., 1994; McRae et al., 1998; Stevenson, 1998). If so, when this dis-preferred parse turns out to be the correct one, blind individuals would show a reduced performance cost.

An alternative to the memory based account is the possibility that blindness improves executive function mechanisms that are involved in selection of the preferred sentence interpretation in the context of syntactic ambiguity (January, Trueswell, & Thompson-Schill, 2009; Novick et al., 2012; Novick, Trueswell, & Thompson-Schill, 2005; 2010; Thompson-Schill, Bedny, & Goldberg, 2005; Woodard, Pozzan, & Trueswell, 2016). This particular interpretation is consistent with the more pronounced advantage of blind participants on the garden-path as opposed the movement sentences. Although, future work is needed to determine whether blindness selectively enhances garden-path interpretation relative to other sentence types, since we did not find a significant three-way interaction (sentence type (movement vs. garden path) by complexity (complex vs. simple) by group (blind vs. sighted)). Future studies should also test whether blindness enhances performance on other tasks that involve ambiguity resolution. Although here we focused on sentence comprehension performance, advantages may or may not be specific to sentence-level syntax. Do blind individuals outperform the sighted on lexical ambiguity resolution (e.g. selecting context-appropriate meanings of homonymous words)? If sentence comprehension enhancements are mediated by sentence-specific memory mechanisms we would not expect advantages in lexical tasks, whether they involve ambiguity or not. By contrast, if ambiguity resolution mechanisms are involved then both lexical and grammatical ambiguity may be affected. In future studies it will also be important to replicate the current results using synthesized rather than recorded sentences to rule out the possibility that differences among blind and sighted groups are related to differential use of subtle prosodic cues. It is also possible that blindness independently enhances multiple different aspects of linguistic processing (e.g. sentence-relevant working memory and ambiguity resolution mechanisms). Testing blind and sighted participants on a comprehensive battery of linguistic tasks could uncover multiple distinct benefits.

A further outstanding question is whether enhancements are mediated by domain-specific language mechanisms or domain general executive or memory mechanisms. Both domain specific and domain general mechanisms are involved in processing for complex sentences (January, Trueswell & Thompson-Schill, 2009; Just & Carpenter, 1992, Fedorenko, 2014). Previous work has shown that domain general executive processes, such as those involved in ambiguity resolution outside of language (e.g. in auditory STROOP tasks), play a role in ambiguous sentence comprehension. It will be important to test whether blind individuals show enhancements on non-linguistic ambiguity resolution tasks and if so whether such enhancements predict sentence comprehension performance. Similarly, although we did not find a relationship between span memory performance and sentence comprehension performance in the current study, future studies could examine other memory tasks (e.g. tasks with lists of words, complex span tasks) to see whether these predict sentence advantages among blind participants.

The present results raise questions about whether other types of variation in experience, apart from blindness, could improve human capacity to make better use of language internal information and if so whether behavioral improvements would occur even in the absence of

extra available "wetware" in visual cortex. Efforts to train sighted speaker to become better at parsing complex sentences in the laboratory have met with mixed success. One study reported that training on a demanding N-back task improved performance on syntactically ambiguous sentences (Novick, Hussey, Teubner-Rhodes, Harbison, & Bunting, 2012). Some studies suggest that experience with particular types of grammatical constructions enhances performance with those constructions (Fine, Jaeger, Farmer, & Qian, 2013; Long & Prat, 2008; Roth, 1984; Wells, Christiansen, Race, Acheson, & MacDonald, 2009). However, the improvements are specific to the trained constructions (Long & Prat, 2008; Roth, 1984; Wells et al., 2009). Blindness-related improvements may be more general because blindness causes more extensive and varied "training" or because of extra "wetware" availability. In future work it would be interesting to test whether other naturalistic experiences, such as extensive reading or extensive listening to audiobooks, also improves aspects of sentence processing.

Conclusions

We observed independent advantages in sentence comprehension and short-term memory tasks in blind participants. These improvements may be analogous to previously reported blindness-related advantages in audition and touch (Fieger et al., 2006; Lessard et al., 1998; Rice, 2017; Roder et al., 1999; Voss et al., 2004). According to this hypothesis, lack of visual experience enhances not only perception through other senses, but also higher cognitive abilities that can be used to achieve similar behavioral goals, including language. These results suggest that individual variation in non-linguistic experience can enhance the capacity of the language system to function in the absence of extrinsic cues.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.

Mean accuracy (left) and response times (right) for sighted and blind participants in syntactic movement (Move), matched non-movement (No-Move), garden path (GP) and matched non-garden path (No-GP) sentences. Error bars reflect SEM.

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Figure 2.

Mean accuracy of sighted and blind participants in Woodcock-Johnson III measures—Word Letter Identification (WD-ID), Word Attack (WD-ATTCK), Synonyms (SYN), Antonyms (ANT), and Analogies (ANT), arithmetic—subtraction (SUB) and division (DIV), and shortterm memory span—forward (FWD) and backward (BWD). Error bars reflect SEM.

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Figure 3.

Correlation plots showing relationship between each participants' mean performance on forward and backward letter span (% correct) and accuracy at answering comprehension questions for each of the sentence conditions (% correct, move, no move, garden path, no garden path). Sighted (top) and blind (bottom). No significant relationship between letter span and sentence processing performance was observed.



Figure 4.

Correlation plots showing significant relationship between each participants' performance on garden-path sentences and movement sentences (left) and a significant relationship between each participants' performance on forward and backward span tasks (right). Sighted (top) and blind (bottom).

Table 1.

Sample stimuli

Move	The actress that the creator of the gritty HBO crime series admires often improvises her lines.	
No-Move	The creator of the gritty HBO crime series admires that the actress often improvises her lines.	
Garden-Path	While the little girl dressed the doll that she was playing with sat on the floor of her bedroom.	
No Garden-Path	While the nanny dressed the baby that was small and cute the baby's mother was in the kitchen preparing dinner.	
Filler	The precocious child thought that the rude waitress's purple cotton dress and orange shoes clashed horribly.	

Table 2.

Number of participants per cause of blindness

Blindness Etiology		N LP
Leber Congenital Amaurosis		5
Glaucoma		1
Optic Nerve Hypoplasia		1
Anopthalmia		0
Micropthalmia		0
Retinal Blastoma		1
Septo-optic dysplasia		0

Number of participants per cause of blindness (N) and with light perception (N LP).