Blind people are more sensitive than sighted people to binaural sound-location cues, particularly inter-aural level differences

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1. Introduction

Many blind people develop impressive hearing skills that help them navigate in their environment (Thaler et al., 2011). Studies have found that some blind listeners outperform sighted listeners on sound localization tasks, such as determining the horizontal or vertical position of sound sources (Ashmead et al., 1998; Collignon et al., 2009; Muchnik et al., 2004), and tasks involving the detection or localization of sound reflections from nearby objects (Kolarik et al., 2014), i.e., echolocation (Stoffregen and Pittenger, 1995). Sound-source localization benefits from the hearing system’s ability to suppress potentially misleading sound reflections (the precedence effect), whereas echolocation would benefit from “unsuppressing” the same reflections (Dufour et al., 2005; Wallmeier et al., 2013). We tested basic discrimination abilities relevant to both source localization and echolocation to clarify how these potentially conflicting aspects of spatial hearing interact in sighted and blind listeners.

Two main cues for sound source localization in the horizontal plane are inter-aural time differences (ITDs) and inter-aural level differences (ILDs). In most environments, the direct sound from the source is accompanied by reflections from nearby objects and surfaces. Such reflections have their own ITDs and ILDs, which may indicate another direction than the ITDs and ILDs of the direct sound. The auditory system’s solution to this problem is to suppress reflected (or lagging) sounds in favor of the direct (or leading) sound. This results in a set of perceptual phenomena known as the “precedence effect,” including perceptual fusion of leading and lagging sounds, localization dominance of the leading sound, and discrimination suppression of inter-aural differences in lagging sounds (Brown et al., 2015; Litovsky et al., 1999).

Blind listeners have displayed impressive acuity in...
discriminating between closely spaced reflecting objects (Dufour et al., 2005; Teng et al., 2012), as have sighted listeners after extensive training (Rowan et al., 2013; Schörnich et al., 2012; Wallmeier et al., 2013). However, it is unclear to what extent the ability of blind and trained sighted listeners to localize sound-reflecting objects involves increased sensitivity to binaural differences in general, or increased ability to unsuppress lagging sounds, or both. Perceptual training studies suggest that both ILD and ITD discriminations improve with training (Sand and Nilsson, 2014), whereas it is less clear whether training leads to increased ability to unsuppress lagging sounds (Litovsky et al., 2000; Saberi and Perrott, 1990; Saberi and Antonio, 2003). Studies suggest that the ILDs of lagging sounds are particularly useful for echolocation (Rowan et al., 2013) and that echolocators tend to use high-frequency sounds (Schörnich et al., 2012), for which ILDs provide more efficient location cues than do fine-structure ITDs (e.g., Hartmann and Macaulay, 2014). However, the envelope ITDs of time-varying sounds may be useful for localizing high-frequency sounds (e.g., Bernstein and Trahiotis, 2002).

In most real-life situations, ITDs and ILDs are correlated. However, they can be manipulated independently using headphone presentation. In this setup, the sounds are usually localized inside the head of the listener, and the effect of changing the ILD or ITD is the lateralization from one ear to the other. To our knowledge, blind and sighted listeners’ ITD and ILD sensitivities have not previously been compared in the same lateralization experiment. However, Simon et al. (2002) asked listeners to match an ILD to a given ITD, and found that blind listeners used larger ILDs to match ITDs, suggesting between-group differences in how one or both of the binaural cues affect perceived lateralization. Two studies measured detection of ITD changes and found support (Yabe and Kaga, 2005) as well as lack of support (Starling and Niemeyer, 1981) for higher ITD sensitivity in blind compared to sighted listeners, and one study reported no difference in ILD sensitivity between blind and sighted listeners (Collignon et al., 2006).

The precedence effect can also be demonstrated in lateralization experiments. A sound pair consisting of a short leading and a short lagging sound will be perceived as a single sound provided that the time separation between the component sounds is less than approximately 4 ms (Litovsky et al., 1999). Inter-aural discrimination thresholds are substantially higher if the ITD or ILD is present in the lagging components of the sound pair rather than the leading component (Tollin and Henning, 1998) or in a single click (Saberi and Antonio, 2003; Saberi et al., 2004).

We tested blind and sighted listeners’ ability to discriminate inter-aural differences present in (a) single clicks, (b) in the leading component of click pairs, or (c) in the lagging component of click pairs (Fig. 1). Performance on the single-click task relates solely to the ability to discriminate ILDs or ITDs, whereas performance on the tasks involving lead- or lag-click discrimination also relates to the ability to suppress and unsuppress lagging clicks. We tested both ILD and ITD discrimination, because the two inter-aural cues are effective for different frequency ranges and are processed differently by the auditory system. Blind people may therefore have acquired a heightened sensitivity to one or both cues, which would lead to better performance on the single-click condition for one or both cues. If blind people have acquired an increased ability to overcome the precedence effect, we would expect them to outperform the sighted on the lag-discrimination task but not on the lead-discrimination task. In the latter task, they might instead be distracted by the unsuppressed click and perform worse, as suggested by one previous study (Dufour et al., 2005).

The temporal resolving capacity of the auditory system degrades with age (Frisina, 2010), reducing ITD sensitivity, whereas ILD sensitivity seems to be less affected by age (Babkoff et al., 2002; Strouse et al., 1998). To assess and control for potential age effects, we included two groups of sighted listeners: one group matched in age to the sample of blind listeners (mean age = 54 y) and one group of young listeners (mean age = 26 y).

2. Method

We used procedures and experimental sounds similar to those used by Saberi et al. (Saberi and Antonio, 2003; Saberi et al., 2004). Novel in our study was that we added a lead-click condition (cf., Tollin and Henning, 1998), tested both ILD and ITD discrimination in the same experiment, and included both sighted and blind listeners. The experimental protocol was approved by the regional ethics committee and informed consent was obtained from all listeners.

2.1. Stimuli

Experimental sounds were composed of 125-μs rectangular pulses (clicks) with an inter-aural time or an inter-aural level difference (Fig. 1). The inter-aural difference click (the signal) was presented alone (“single-click” condition), as the leading component of a click pair (“lead-click” condition), or as the lagging component of a click pair (“lag-click” condition). In the lead-click condition, the signal was always presented 2 ms before a lagging click with no inter-aural differences (the distracter). In the lag-click condition, the signal was always presented 2 ms after the leading distracter. To keep the overall loudness of the clicks approximately equal in the ILD conditions, ILDs were created by attenuating the stronger and amplifying the weaker signal by half the ILD. The peak sound pressure level of the distractor click was 94 dB.

2.2. Staircase procedure

We used a two-interval, two-alternative forced-choice task with an adaptive two-down, one-up rule that tracks the listener’s 71° discrimination threshold (Levitt, 1971). On the first interval of each trial, the signal’s ILD or ITD favored one randomly selected ear, whereas in the second interval, it favored the other ear by the same ILD or ITD. The listener’s task was to decide whether the two intervals in each trial were heard in left-then-right or right-then-left sequence. Auditory feedback was provided after each trial.

The ITD runs started with an ITD of 650 μs and the ILD runs with an ILD of 20 dB. Two successive correct responses led to a reduction of the ITD or ILD by 37% (a step size of 0.2 log units) until the fourth reversal and by 11% (0.05 log units) thereafter. An incorrect response led to an ITD or ILD increase by the step size, or to the starting value if the rule implied an exceedance of this value. ITDs were rounded to the nearest 5.2 μs, the resolution determined by the sampling rate of 192 kHz.

The experiment was conducted in a sound-proof listening room with an ambient sound pressure level below 25 dB(A). Sounds were presented through earphones (Sennheiser HD 580 Precision) using an earphone amplifier (Lake People Phone-Amp G109) connected to a computer equipped with an external sound card (RME Fireface 400) that allowed a sampling frequency of 192 kHz (24-bit depth). A script written in MATLAB generated the sounds and collected the listener’s responses, which were entered via a keyboard on which the relevant keys were indicated with small plastic tags to allow touch identification. Both sighted and blind listeners were tested blindfolded.

2.3. Threshold estimates

Two runs were conducted for each of the six stimulus conditions...
in a random order unique to each listener. For each run, we calculated the geometric mean stimulus value at reversal points, after the fourth reversal. The geometric mean of the two runs for each condition was used as the estimate of the listener’s threshold for that condition. The experiment took about 2 h to complete, and it was not practically feasible to include more than two repetitions of each condition. Many psychophysical studies include considerably more repetitions of each stimulus condition, typically tested on a few perseverant listeners. Though the large sample size is a strength of the present study, the small number of repetitions reduces the reliability of individual threshold estimates, so therefore we concentrate on group level analyses.

2.4. Listeners

The blind listeners were recruited through advertising in two audio newspapers for the blind and among participants of previous studies (Schenkman and Nilsson, 2010, 2011). We tested 23 blind listeners (11 women) aged 25–73 y (mean age = 54 y), of whom 12 were blind from birth, one became blind at age three, and 10 became blind after age 10. Sixteen of the blind listeners reported that they used echolocation “often” or “almost always” when navigating the environment, whereas six reported that they did so “sometimes” and one “never.” Self-reported diagnoses of the blind listeners are given in Table 1.

We tested two groups of sighted listeners. The first group (“sighted-young”) consisted of 42 listeners (22 women) aged 20–35 y (mean age = 26 y). The second group (“sighted-age-matched”) consisted of 23 listeners (13 women) aged 25–72 y (mean age = 54 y), each of whom was age-matched to one of the blind listeners (±0–2 years).

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1 Our threshold estimates refer to the binaural differences in a single interval of the 2AFC task. Saberi et al. (Saberi and Antonio, 2003; Saberi et al., 2004) defined a threshold as the sum of binaural differences across the two intervals, that is, two times the value implied by our definition.
We tested the hearing of all listeners using an audiometer (Interacoustic Diagnostic Audiometer, model AD226). Pure-tone average thresholds (PTAs) were calculated across the left and right ears for the frequencies 0.5, 1, 2, 3, 4, and 6 kHz. PTA ranges were 0–35 dB for the blind (mean = 12 dB), 0–9 dB for the sighted-young (mean = 4 dB), and 1–38 dB for the sighted-age-matched listeners (mean = 10 dB).

3. Results

For most conditions, distributions of individual threshold estimates were positively skewed and contained a few outlying high threshold estimates (see Fig. 2). The median is more robust to extreme values than is the arithmetic mean, so we compared groups in terms of between-group differences in medians (Table 2). To facilitate group-level comparison across the ITD and ILD conditions, we also calculated the probability of superiority (PS) of one group over another. The PS is the probability of a randomly drawn member of one group performing better (i.e., having a lower threshold) than a randomly drawn member of the other group (Ruscio, 2008). Finally, we used robust linear regression (MM-estimator method, Andersen, 2008) and locally weighted scatter-plot smoothing (LOWESS) to explore associations between thresholds and age.

The general pattern of results was in agreement with previous research, i.e., lead-click thresholds were slightly higher and lag-

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### Table 1

| #  | Age (y) | Sex | Self-reported onset age and cause of blindness | Self-reported echolocation use |
|----|---------|-----|-----------------------------------------------|-------------------------------|
| 1  | 52      | F   | Birth Retinoblastoma                          | "almost always"               |
| 2  | 48      | M   | 38 Retinitis pigmentosa                       | "almost always"               |
| 3  | 63      | M   | Birth Retrolental fibroplasi                  | "almost always"               |
| 4  | 65      | M   | Birth Lack functional rods and cones          | "almost always"               |
| 5  | 39      | M   | 20 Retinitis pigmentosa                       | "almost always"               |
| 6  | 64      | M   | Birth Retrolental fibroplasi                  | "almost always"               |
| 7  | 52      | F   | 35 Retinitis pigmentosa                       | "sometimes"                  |
| 8  | 57      | M   | Birth Sclerocornea                            | "often"                       |
| 9  | 56      | F   | 20 Glaukom                                    | "sometimes"                  |
| 10 | 53      | F   | 3 Retinoblastoma                              | "almost always"               |
| 11 | 40      | M   | Birth Optic nerve atrophy                     | "often"                       |
| 12 | 42      | M   | Birth Retinal degeneration                    | "sometimes"                  |
| 13 | 66      | M   | 63 Retinitis pigmentosa                       | "sometimes"                  |
| 14 | 62      | F   | Birth Heredo retinopathia congenitalis        | "almost always"               |
| 15 | 62      | F   | Birth Retrolental fibroplasi                  | "often"                       |
| 16 | 25      | M   | Birth Retrolental fibroplasi                  | "almost always"               |
| 17 | 55      | M   | 15 Amotio retinae                             | "almost always"               |
| 18 | 44      | F   | 29 Optic glioma                               | "sometimes"                  |
| 19 | 32      | F   | Birth Aniridi                                  | "never"                       |
| 20 | 73      | M   | 40 Retinitis pigmentosa                       | "almost always"               |
| 21 | 56      | F   | 46 Retinitis pigmentosa                       | "often"                       |
| 22 | 70      | F   | 60 Optic glioma                               | "sometimes"                  |
| 23 | 62      | F   | Birth Undeveloped retinas                     | "almost always"               |

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**Fig. 2.** Boxplots of inter-aural time-difference thresholds (left) and inter-aural level-difference thresholds (right), separately for sighted-young (white boxes), sighted-age-matched (light gray boxes), and blind (dark gray boxes) listeners. The boxes indicate the 25th, 50th (median), and 75th percentiles of the threshold distribution (lower, middle, and upper horizontal lines of the box). The upper hinges indicate the maximum value of thresholds located within a distance of 1.5 times the inter-quartile range above the 75th percentile. The lower hinges indicate the corresponding distance to the 25th percentile value. Circles indicate values outside these hinges (outliers).
click thresholds were much higher than single-click thresholds (Saberi et al., 2004; Tollin and Henning, 1998), and the variability of individual thresholds was considerably higher in the lag-click condition than the single- and lead-click conditions (Saberi and Antonio, 2003; Saberi et al., 2004). In absolute terms, the single-click and lag-click thresholds for the sighted-young listeners were slightly lower than those obtained by Saberi et al. for young listeners using similar stimuli and methodology (Saberi and Antonio, 2003; Saberi et al., 2004).

The blind and sighted-young listeners performed about equally well in ITD discrimination and both these groups performed better (i.e., had lower thresholds) than did the sighted-age-matched group (Fig. 2, left). The blind and the sighted-young groups’ median thresholds ranged between 16 and 29 μs for the single-click and lead-click conditions (between group differences < 7 μs). Also for the lag-click condition, the sighted-young group (median = 208 μs) and the blind group (median = 221 μs) performed about equally well. In comparison, the sighted-age-matched group performed worse on all three ITD conditions (medians for single-, lead-, and lag-click condition: 36, 66, and 320 μs), although the 95% confidence interval for the lag-click-condition difference between blind and sighted-age-matched listeners also included values favoring the sighted group (Table 2).

The pattern of ILD discrimination results differed from that for the ITD results: The distributions of the blind group’s ILD thresholds were lower than the corresponding distributions for both sighted groups (Fig. 2, right). Median thresholds for the blind group were 0.7, 0.8 and 2.6 dB for the single-, lead-, and lag-click condition, compared to 1.2, 1.5 and 5.6 dB for the sighted young and 1.5, 1.9 and 5.9 dB for the sighted age-matched group. Differences in median thresholds between blind and sighted listeners ranged between 0.4 and 1.1 dB for the single-click and lead-click conditions, and between 3.0 and 3.3 dB for the lag-click condition. In contrast, the two sighted groups’ median thresholds differed little (<0.4 dB, Table 2).

Between-group comparisons in terms of probability of superiority (PS) confirmed the general pattern of results reported above, that is, the blind performed better than the sighted-age-matched in both ITD and ILD discrimination (Fig. 3, left) and better than the sighted-young in ILD but not in ITD discrimination (Fig. 3, right). Comparisons of the two sighted groups confirmed that the sighted-young performed clearly better than did the sighted-age-matched in ITD discrimination, but not in ILD discrimination (Fig. 4).

The additional information provided by the PS analyses includes (1) a meaningful comparison across binaural cues, as the PS measure expresses between-group comparisons of ILD and ITD thresholds on a common scale, and (2) a comparison across click conditions that takes into account the much larger variability in the lag-click condition than in the single- or lead-click condition (see Fig. 2). These two aspects of the results are discussed below.

The better ITD performance of the blind than of the sighted-age-matched but not of the sighted-young group is consistent with a less rapid decline in temporal auditory processing with age among blind individuals. This agrees with the more pronounced trend toward higher single-click ITD thresholds with age for the sighted-age-matched group (Fig. 5, upper left panel) than for the blind group (Fig. 5, upper right: symbols denote subgroups of blind listeners discussed further below). For the age-matched sighted group, the slope of the fitted linear regression line corresponds to a threshold increase of 5.7 μs per decade and the smoother line was fairly consistent with a linear increase starting at about 40 years of age. The scatter around the linear regression line was considerable, however, with a median absolute deviation of 15 μs. In the blind group, the fitted regression line corresponds to a threshold increase of only 1.5 μs per decade and the smoother line followed the same trend except for the increase at ages over 65 years (due to the high threshold estimates of the two oldest blind listeners). In general, the large deviations from the linear regression lines were limited to the six listeners with thresholds greater than 25 μs, so the median absolute deviation from the regression line was small (3.0 μs), considerably smaller than for the sighted group. The pattern of steeper linear slopes for sighted compared to blind listeners was also seen for the lead-click (Fig. 5, middle panels) and lag-click ITD thresholds (Fig. 5, lower panels).

(1) The PS comparisons suggested that the blind superiority was more distinct for the ITD than for the ITD thresholds (compare circles with squares in Fig. 3). This was especially pronounced for the lag-click conditions, for which the PS favoring blind over sighted-age-matched listeners was 0.84 for the ILD-lag-click condition compared with 0.63 for the ITD-lag-click condition (these ratios correspond to odds of 5.5 and 1.7 in favor of a random blind listener being better than a random sighted-age-matched listener). The corresponding PSs for the comparison between blind and sighted-young listeners were 0.84 (odds = 5.2) for the ILD-lag-click condition and 0.53 (odds = 1.1) for the ITD-lag-click condition.

(2) The PS comparisons also suggested that the blind-over-sighted superiority followed a different pattern for ILD than for ITD discrimination. For ILD discrimination, the blind superiority over both sighted groups was greater for the lag-click condition than for the single- or lead-click condition. For example, the blind listeners’ superiority over the sighted-young group for the ILD-lag-click condition was 0.84 (odds = 5.2) versus 0.70 (odds = 2.4) for the ILD-single-click condition (compare the rightmost and leftmost circles in Fig. 3, right). For ITD discrimination, the opposite trend was seen, with small blind-over-sighted superiority for the lag-click condition.

Note. Confidence intervals were derived using the bias-corrected and accelerated (BCA) bootstrap method (Efron and Tibshirani, 1994).

### Table 2
Between-group differences in median ITD and ILD threshold (95% confidence interval).

| Between-group difference | ITD (μs) | ILD (dB) |
|--------------------------|---------|---------|
|                          | Single-click | Lead-click | Lag-click | Single-click | Lead-click | Lag-click |
| Sighted-young - Blind    | 3       | 6       | 13       | 0.4       | 0.8       | 3.0       |
| (3–8)                    | (13–14)  | (139–145) |          | (0.1–0.8) | (0.3–1.1) | (1.4–4.2) |
| Sighted-age-matched - Blind | 20     | 43      | 99       | 0.8       | 1.1       | 3.3       |
| (8–28)                   | (13–70)  | (56–261) |          | (0.0–1.4) | (0.4–1.7) | (1.0–4.3) |
| Sighted-age-matched - Sighted-young | 17 | 37 | 112 | 0.4 | 0.3 | 0.3 |
| (6–26)                   | (4–57)   | (11–263) |          | (0.2–1.0) | (0.4–0.8) | (2.1–1.7) |
For the single-click ILD thresholds, the age-related threshold increase was small for both groups (Fig. 6, upper panel). For the age-matched sighted group, the slope of the fitted regression line corresponds to a threshold increase of 0.2 dБ per decade, but the smoother line did not suggest a linear trend. For the blind group, the linear trend corresponds to a threshold increase of only 0.04 dБ per decade. The age-related increase in lead-click (Fig. 6, middle panels) and lag-click thresholds (Fig. 6, lower panels) followed a pattern similar to that of the single-click ILD thresholds (Fig. 6, upper panels).

The early blind listeners (circles in right-hand panels of Figs. 5 and 6) had on average slightly lower thresholds on all conditions than the late blind listeners (squares in right-hand panels of Figs. 5 and 6), this difference being more pronounced for the ILD than the ITD conditions. The same was true for the 16 blind listeners who reported using echolocation “almost always” or “often” (dots in right-hand panels of Figs. 5 and 6) versus the 7 listeners who reported using echolocation “sometimes” or “never”. However, the results of these subgroup analyses should be interpreted cautiously given the small sample sizes.

Finally, we evaluated effects of hearing status by plotting individual threshold estimates against audiometric measures, separately for each listener group and stimulus condition. However, no consistent relationships could be discerned. Furthermore, between-group differences were not much different from those presented above when the blind sample was restricted to listeners with unimpaired hearing (PTA < 10 dB, n = 13).

4. Discussion

This is the first study to directly compare ITD and ILD sensitivities in blind and sighted listeners. The results suggested different patterns of blind-over-sighted advantages for the two binaural cues. Specifically, we demonstrated greater ILD sensitivity for blind listeners than for age-matched and younger sighted listeners. For ITD discrimination, the blind listeners performed better than did the sighted age-matched listeners, but not better than the sighted young listeners. Overall, the blind-over-sighted advantage was most pronounced for the ILD-lag-click condition, which, apart from ILD sensitivity, also relates to the ability to discern (“unsuppress”) ILDs in reflected sound.

The temporal resolving capacity of the auditory system declines with age in the general population (Babkoff et al., 2002; Frisina, 2010; Strouse et al., 1998). However, our results suggest that this may not generalize to blind people: Our blind listeners were as sensitive to ITDs as the considerably younger group of sighted-young listeners, and the relationship between age and ITD thresholds was weaker among the blind than sighted-age-matched listeners. Taken together, these findings suggest that the experience of being blind counteracts the age-related decline in temporal processing observed in the sighted population. This fits well with findings that auditory training programs may reverse age-related neural timing delays (Anderson et al., 2013). Musical training also has been shown to offset age-related declines in auditory temporal processing (Parbery-Clark et al., 2012; Skoe and Chandrasekaran, 2014).

The blind-over-sighted advantage was larger for the ILD than the ITD discrimination tasks, especially for the lag-click conditions. Could this be related to differences in neural plasticity between areas encoding ILDs and ITDs? At first, this seems plausible given that different low-level areas and mechanisms are involved, and that experience-dependent plasticity has been demonstrated in the human auditory brainstem (Skoe and Chandrasekaran, 2014). Encoding ILDs involves integrating ipsilateral excitatory and
contralateral inhibitory input to the lateral superior olive, whereas encoding ITDs involves the coincidence detection of excitatory input from both the ipsi- and contralateral sides to the medial superior olive (e.g., Wang et al., 2014). Studies of the ILD discrimination of tones have reported improvement with training (Constantinides et al., 2003; Kumpik et al., 2009; Wright and Fitzgerald, 2001; Zhang and Wright, 2009), whereas studies of the ITD discrimination of tones have reported both failure (Wright and Fitzgerald, 2001; Zhang and Wright, 2009) and success (Constantinides et al., 2003; Rowan and Lutman, 2006, 2007). The ITD studies used tones with an ongoing ITD but the same onset. It is therefore unclear to what extent they generalize to the present study using ITDs conveyed mainly through onset differences between short clicks. More relevant is a study that used the same single-click stimuli as in the present study and found strong support for perceptual learning of both ITD and ILD discrimination: Improvements on both tasks were seen first on the second day of testing, which speaks in favor of neural consolidation overnight, rather than just procedural learning of the experimental task (Sand and Nilsson, 2014). The empirical evidence therefore suggests that it is equally possible to improve ITD and ILD discrimination, at least for single clicks, which, in turn, speaks against explaining the present results in terms of differential neural plasticity in areas encoding single-click ILDs and ITDs.

Another possibility is that blind listeners may have used monaural cues to a larger extent than sighted listeners. Theoretically, a listener could solve the ILD discrimination task by listening...
to one ear only (e.g., Wright and Fitzgerald, 2001). If a listener focuses solely on the signal in one ear and compares its level on the first interval with its level on the second interval, then this information could be used to solve the ILD task, but not the ITD task, for which no useful monaural strategy is available. Thus, if blind listeners through experience have developed an increased ability to focus on monaural information, this might explain the better performance of the blind compared to the sighted listeners on the ILD task. This could have been circumvented by varying overall levels from interval to interval (level roving), at the cost of a potentially more difficult task due to distraction caused by the roving (Hartmann and Constan, 2002). Studies, however, demonstrate that ILD discrimination thresholds remain fairly constant with or without level roving, suggesting that listeners do not generally use monaural information when discriminating ILDs (Bernstein, 2004; Rowan et al., 2015; Stelmack et al., 2004). In addition, the blind listener’s performance in the present experiment’s lead-click condition was only marginally worse than for the single-click condition. In the lead-click condition, the monaural loudness of the perceptually fused lead- and lag-clicks presumably was strongly influenced by the lagging click, which was the same in both intervals. This speaks against a monaural strategy, unless the system was called upon to ignore the loudness influence of the lagging click when assessing the monaural level of the signal. It is also difficult to see how monaural listening would help blind individuals in their everyday life. On the contrary, integration of binaural information is crucial for auditory space perception, and monaural listening would likely be disadvantageous in most situations where auditory information has to be used to compensate for lack of vision. Still, improved monaural level sensitivity may be a side effect of training on some other, more ecologically relevant ability, such as echolocation, which is discussed next.

A third type of explanation for why the blind-over-sighted advantage was larger for the ILD than the ITD discrimination tasks is in terms of the auditory information available to blind people in their everyday lives. Specifically, localization of direct sound from sources involves both ILD and ITD discrimination, whereas research has suggested that ILDs may be more important than ITDs for the localization of reflected sounds (Rowan et al., 2013). This could explain the greater blind-over-sighted advantage in discriminating ILDs compared with ITDs, an advantage that was most pronounced in the lag-click discrimination task, which, in addition to binaural sensitivity, also taps the ability to discern (“unsuppress”) binaural differences in reflected sound. Many blind people use echolocation actively, whereas others may use reflected sounds unconsciously when navigating the environment (Schwitzgebel and Gordon, 2000). Echolocation involves the use of several types of acoustic information (Kolarik et al., 2014), including changes in sound energy and autocorrelation in detecting the presence of a reflecting object (Schenkman and Nilsson, 2011) and inter-aural differences in determining its location (Dufour et al., 2005). There is evidence that the latter involves mainly ILD discrimination. Rowan et al. (2013) found that sighted listeners who underwent extensive echolocation training used primarily high-frequency information, probably ILDs, from the tested broadband signals. Indeed, performance improved as low frequencies were removed from the sounds, presumably because these conveyed unhelpful ITDs. Schornich et al. (2012) had sighted listeners train in echolocation using self-generated sounds, and found that the sounds produced contained peak frequencies around 6–8 kHz, that is, in a frequency range where ILDs would be much more helpful than ITDs for horizontal sound localization. Although training studies have demonstrated that sighted listeners can improve their echolocation ability (Rowan et al., 2013), they are unlikely to develop this potential in real life, simply because their vision does the job much more efficiently. Moreover, sighted listeners may in general have more experience with ITD-than with ILD-based localization (cf. Wright and Fitzgerald, 2001), because direct sound from many environmental sources, including speech, contains frequency components in the range where ITDs are more useful than ILDs (i.e., below \( \approx 1.5 \text{ kHz} \)).

Our results for the lag-click conditions agree well with the hypothesis that long-term experience of attending to reflected sounds in particular will enhance ILD sensitivity. Performance in the lag-click conditions taps the ability to “unsuppress” lagging sound. The blind-over-sighted superiority in ILD discrimination was greater for the lag-click condition than for the single- or lead-click condition. This was true in both absolute terms (i.e., difference in decibels between group medians) and relative terms (i.e., probability of superiority, PS). For ITD discrimination, the picture was different: The blind listeners’ superiority (PS) over age-matched sighted listeners was less pronounced for the lag-click condition than for the single- or lead-click condition. Moreover, the blind-over-sighted superiority was substantially greater for the ILD-lag-click than the ITD-lag-click conditions. We also compared the performance of the 16 blind listeners who used echolocation “almost always” or “often” with that of the 7 who used echolocation “sometimes” or “never”. The former group had lower thresholds than the latter group on all conditions, the differences in terms of PS being larger on the ILD than the ITD conditions. This is consistent with the hypothesis that ILD sensitivity may benefit from the active use of echolocation, although the small sample sizes limit the support provided by these subgroup analyses. We observed a corresponding pattern of differences between the 13 early-blind (11 of whom used echolocation often or always) and the 10 late-blind (5 of whom used echolocation often or always) listeners. This is consistent with findings suggesting an advantage in spatial hearing of early-versus late-blind listeners (Collignon et al., 2013; Lessard et al., 1998), although other studies have found that late-blind people develop above-normal spatial abilities as well (Fieger et al., 2006; Voss et al., 2004). Again, these results should be interpreted cautiously, given the small sample sizes of our subgroups of blind listeners.

Overall, the analyses presented above suggest that blind people develop an increased ability to unsuppress directional information conveyed by ILDs in lagging sounds, more so than for ITDs in lagging sounds. This conclusion has two implications relevant to research into the precedence effect: (1) It is possible to improve the ability to unsuppress information in lagging sounds, and (2) ILD- and ITD-lag-click suppression may work differently. These implications are discussed next in relation to previous research.

(1) It has been debated whether it is possible to improve the ability to unsuppress the lagging component of sounds (i.e., to “unlearn the precedence effect”, Litovsky et al., 2000). Saberi and Perrott (1990) first suggested that practice may lead to an increased ability to unsuppress ITDs in the lagging clicks of click pairs. However, Litovsky et al. (2000) failed to replicate this in a subsequent study. In response to this, Saberi and Antonio (2003) tested a single listener for about 66 h, and found a decrease in ITD-lag-click threshold that appeared after the first 10–20 h of training, which was the training period of Litovsky et al.’s listeners. Thus, an ability to unsuppress directional information in lagging sound may require extensive practice focusing on the lagging components of sounds, for example, through long-term experience of echolocating objects. Note also that the studies cited above tested only ITD-lag-click discrimination: corresponding perceptual training studies of ILD-lag-click discrimination are lacking. In general, signals containing low-frequency ITD
information seem to evoke stronger precedence effect phenomena than signals lacking robust ITD information (Brown et al., 2015). It is therefore possible that it is easier to learn to unsuppress ILDs than ITDs in lagging sounds. This would imply different mechanisms for ITD and ILD lag-click suppression, as discussed next.

(2) Lag-click suppression is related to processes in areas that act on both ILD and ITD information, particularly the inferior colliculus of the midbrain, but also in areas upstream, including in the auditory cortex (Litovsky et al., 2002). There is evidence that the lateralization dominance of the leading click acts on an integrated ILD and ITD code, as has also been found in studies of other precedence-effect phenomena (Maier et al., 2010). If so, it is not obvious how blind people could develop an increased ability to unsuppress lagging ILD clicks without transfer to ITD-lag-click discrimination. However, there is also evidence of separate ILD and ITD processing related to echo thresholds, that is, the time separation between clicks when the listener starts to hear two clicks rather than one fused click (Brown and Stecker, 2013: Krumbholz and Nobbe, 2002). Our results are consistent with a similar dissociation for lag-click discrimination. Evaluating this hypothesis would require further research involving training in both ITD and ILD-lag-click discrimination.

Finally, note that the blind group also performed better than the sighted groups in ILD-lag-click discrimination, the size of this effect being about the same as for the single-click condition. This result differs from previous findings suggesting that the blind may perform worse than the sighted on tasks in which the suppression of lagging sounds benefits performance (Dufour et al., 2005). It is of course still possible that an increased ability to unsuppress lagging sounds did not interfere with performance on the lag-click discrimination task, in line with the idea that people may change their listening style when locating reflected sounds compared with when locating sound sources (Wallmeier et al., 2013).

In summary, our results suggest that blind people have acquired an enhanced sensitivity to binaural differences and, for ILDs, an increased ability to unsuppress information in lagging clicks. We suggest that these findings are the result of the blind listener's long-term experience of using sounds as their primary source of information for localizing sound sources and sound-reflecting objects. The latter may in particular enhance the sensitivity to ILDs, because this cue may be effective for locating sounds from obstacles in the environment. These findings add to the literature on auditory learning in general and, in particular, to research comparing naïve and expert listeners. The results may guide future research by identifying fundamental auditory abilities in which blind people excel. Such research may have practical implications for the development of training programs for newly blind people, targeting specific auditory abilities susceptible to experience-induced improvement.

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