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Late- but not early-onset blindness impairs the development of audio-haptic multisensory integration

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Abstract

Integrating different senses to reduce sensory uncertainty and increase perceptual precision can have an important compensatory function for individuals with visual impairment and blindness. However, how visual impairment and blindness impact the development of optimal multisensory integration in the remaining senses is currently unknown. Here we first examined how audio-haptic integration develops and changes across the life span in 92 sighted (blindfolded) individuals between 7 and 70 years of age. We used a child-friendly task in which participants had to discriminate different object sizes by touching them and/or listening to them. We assessed whether audio-haptic performance resulted in a reduction of perceptual uncertainty compared to auditory-only and haptic-only performance as predicted by maximum-likelihood estimation model. We then compared how this ability develops in 28 children and adults with different levels of visual experience, focussing on low-vision individuals and blind individuals that lost their sight at different ages during development. Our results show that in sighted individuals, adult-like audio-haptic integration develops around 13–15 years of age, and remains stable until late adulthood. While early-blind individuals, even at the youngest ages, integrate audio-haptic information in an optimal fashion, late-blind individuals do not. Optimal integration in low-vision individuals follows a similar developmental trajectory as that of sighted individuals. These findings demonstrate that visual experience is not necessary for optimal audio-haptic integration to emerge, but that consistency of sensory information across development is key for the functional outcome of optimal multisensory integration.

KEYWORDS
blindness, cross-modal, development, multisensory integration, plasticity

1 | INTRODUCTION

Early sensory input is crucial for the development of perceptual processes. A key method to discover the importance of early sensory input for perceptual development is to compare those who have had a sense, such as vision, impaired at an early developmental age to those who acquire sensory deprivation later in life. For example, comparing humans who became blind early in life to

those who became blind at older ages has revealed the impact of visual experience during development on other aspects of perception and cognition (Bedny, Pascual-Leone, Dravida, & Saxe, 2012; Pasqualotto, Furlan, Proulx, & Sereno, 2018; Wan, Wood, Reutens, & Wilson, 2010, see Scheller, Petrini, & Proulx, 2018 for a review). Reports on early-blind individuals with extraordinary auditory or tactile abilities have nurtured the idea that non-visual perceptual mechanisms improve in order to compensate for the lack of visual information (Goldreich & Kanics, 2003; Gougoux et al., 2004; Kolarik, Cirstea, & Pardhan, 2013; Norman & Bartholomew, 2011; Röder et al., 1999; Vercillo, Milne, Gori, & Goodale, 2015; Voss et al., 2004). For example, it has been shown that the brain of the early-blind allows for changes in perceptual function through cortical reorganization (Amedi, Raz, Pianka, Malach, & Zohary, 2003; Collignon et al., 2015; Ortiz-Terán et al., 2016). Several neuroimaging studies to date revealed structural and functional changes in the blind brain, such as increased fine-tuning of the auditory cortex (Huber et al., 2019), the redeployment of the visual cortex for non-visual tasks such as auditory localization and Braille reading (Gougoux, Zatorre, Lassonde, Voss, & Lepore, 2005; Sadato et al., 1996), or enhanced functional connectivity between uni-sensory and multi-sensory processing areas (Ortiz-Terán et al., 2016). These changes in neural processing, together with enhanced auditory and tactile sensory functioning (Amedi et al., 2003; Collignon et al., 2013), support the hypothesis of cross-modal compensation. That is, the brain adaptively compensates for lacking visual input early during development, leading to enhanced non-visual perceptual functioning. However, a functional adaptation that leads to enhanced tactile or auditory perception is not always present in blindness, but might depend on several factors, such as the sensory experience and proficiency of use of the remaining senses in certain tasks (Grant, Thiagarajah, & Sathian, 2000; Heller & Gentaz, 2013; Sathian & Stilla, 2010; Wong, Gnanakumaran, & Goldreich, 2011), as well as the onset of sensory deprivation (Pasqualotto & Proulx, 2012; Postma, Zuidhoek, Noordzij, & Kappers, 2008). In fact, several previous studies suggest that the enhancement of perceptual functioning in the remaining senses is practice-dependent (Sathian & Stilla, 2010).

Several of the above-mentioned studies highlight that the developmental time point of sensory deprivation determines how well an individual adapts to this perceptual state. That is, while congenitally-blind individuals show enhanced auditory pitch discrimination or horizontal localization abilities, late-blind individuals do not exhibit such perceptual benefits (Gougoux et al., 2004; Voss, Gougoux, Lassonde, Zatorre, & Lepore, 2006; Wan et al., 2010). Furthermore, studies on individuals that were born with dense bilateral cataracts, and who received sight-restoring treatment within the first months of life, showed that even a brief, transient phase of visual deprivation early in life leads to long lasting changes in visual and non-visual information processing (Collignon et al., 2015; Geldart, Mondloch, Maurer, De Schonen, & Brent, 2002; Guerreiro, Putzar, & Röder, 2016; Putzar, Hötting, & Röder, 2010; see Maurer, 2017 for a review). This stresses that sensory experience plays a critical role particularly during early developmental periods, when heightened

Research Highlights

- Audio-haptic integration follows principles of statistical optimality in sighted adults, remaining stable until at least 70 years of life.
- Near-optimal audio-haptic integration develops between 13–15 years in sighted adolescents.
- Blindness within the first 8 years of life facilitates the development of optimal audio-haptic integration while blindness after 8 years impairs such development.
- Sensory consistency in early childhood is crucial for the development of optimal multisensory integration in the remaining senses.

cross-modal plasticity allows the individual to learn about the physical principles of the environment and their relation to their own body through sensory-motor contingencies (de Klerk, Johnson, Heyes, & Southgate, 2015; Nagai, 2019).

The sighted adult brain can integrate multisensory information by weighting the different sensory inputs by their reliability, in order to reduce sensory noise and increase perceptual precision and accuracy (e.g. Ernst & Banks, 2002; Rohde, van Dam, & Ernst, 2016). For example, while one can often easily hold a conversation without directly looking at a conversation partner (e.g. over the phone), this task becomes much more difficult when standing at a busy street. Here, visual information of the partner's mouth movement can greatly enhance understanding of the conversation. However, the ability to optimally integrate sensory information has been found to only emerge late in childhood. While young children already possess the ability to make use of multisensory information (Neil, Chee-Ruiter, Scheier, Lewkowicz, & Shimojo, 2006), they do not perceptually benefit in the same way that adults do until 8–10 years of age (Adams, 2016; Gori, Sandini, & Burr, 2012), or even later (Nardini, Jones, Bedford, & Braddick, 2008; Petrini, Remark, Smith, & Nardini, 2014). For non-visual senses such as touch and sound, the developmental onset of optimal integration has not yet been established, but likely occurs after the age of 11 years (Petrini et al., 2014).

One prominent hypothesis, cross-modal calibration, accounts for this late development of optimal integration by suggesting that in early childhood the senses are kept separate to calibrate each other, thus impeding integration. During this time the more robust sense for a certain task has been suggested to teach (calibrate) the less robust sense about specific features in the environment that are more directly accessible to the former (Burr & Gori, 2012). For example, when trying to estimate the size of a cup by either touching or looking at it, touch provides the more direct estimate of its size, scaling it relatively to the own hand. When perceiving object size visually, on the other hand, the brain needs to take distance, perspective, shading, and other information that is inherent to the visual modality into account. Touch is therefore considered the more robust sense for estimating object size (Gori, Del Viva, Sandini, & Burr, 2008; Petrini

et al., 2014). Vision, on the other hand, can be considered the more robust sense for estimating object orientation, and has been shown to calibrate the other senses in object orientation estimation (Gori et al., 2008). In support of the cross-modal calibration hypothesis Gori and colleagues demonstrated the role that touch and vision play for the perception of object size and object orientation. In a first study, they tested how the absence of visual experience early in life affects haptic orientation and size discrimination in a group of non-sighted children and adolescents aged 5–19 years. They found that, while haptic size discrimination performance in non-sighted children and young adults was similar to that of a sighted, age-matched control group, haptic orientation discrimination performance resulted impaired (Gori, Sandini, Martinoli, & Burr, 2010). The authors concluded that this was because vision could not calibrate touch about estimating object orientation accurately. In a second study, the authors tested a group of 5- to 18-year-olds with motor impairments on a visual version of the same object size and orientation tasks. The results showed the opposite pattern: visual size discrimination performance was impaired, while visual orientation discrimination was intact (Gori, Tinelli, Sandini, Cioni, & Burr, 2012). What this further demonstrates is that cross-modal processes are not only domain-specific (spatial/temporal) but also task-dependent. While orientation and size both form spatial object features, the functional outcome of cross-modal calibration differs depending on the robustness of the calibrating sense. Further evidence, accumulated in the last two decades, supports this cross-calibration theory by showing that perceptual functions in the remaining senses of blind individuals are severely compromised (Cappagli, Cocchi, & Gori, 2017; Cappagli, Finocchietti, Baud-Bovy, Cocchi, & Gori, 2017; Vercillo, Burr, & Gori, 2016; Zwiers, Van Opstal, & Cruysberg, 2001) when accurate performance depends on high resolution visual input (Coluccia, Mammarella, & Cornoldi, 2009; Gori, Sandini, Martinoli, & Burr, 2014; Pasqualotto et al., 2018; Pasqualotto & Proulx, 2012; Vercillo et al., 2016).

Most of the aforementioned studies on cross-modal compensation and cross-modal calibration assessed how visual impairment influences perception in the remaining, single senses. For example, Cappagli, Cocchi, et al. (2017) showed that early-blind children and adults are severely compromised in the reproduction of hand pointing movements using proprioception, and struggle with extracting distance information from sound (Cappagli, Cocchi, et al., 2017), indicating that unisensory processing in the remaining senses seems to depend on visual calibration early in development. However, much less is known about whether multisensory processes are affected by visual impairment in a similar way, although few studies tried to address this research question previously (Hötting and Röder, 2004; Champoux et al., 2011). It is still unknown how visual impairment affects optimal multisensory integration of the intact senses (e.g. audio-haptic optimal integration), and whether the onset and severity of visual impairment have a modulatory effect on it. As the visually impaired rely heavily on their remaining senses such as touch and hearing, it is crucial to understand when the ability to increase perceptual precision through optimal multisensory integration of the

remaining senses is achieved. This knowledge would allow for the development of more effective sensory rehabilitation techniques that are functionally beneficial and meet the needs of the visually impaired individual (Ben Porquis et al., 2017; Gori, Cappagli, Tonelli, Baud-Bovy, & Finocchietti, 2016; Luo & da Cruz, 2016; Meijer, 1992, see Scheller et al., 2018 for a review).

Here we used an optimized version of the audio-haptic size discrimination task from Petrini et al. (2014) to examine to what extent sighted and visually impaired adults and children reduce perceptual uncertainty by integrating sensory information from touch and hearing. We chose an object size discrimination task as haptic information tends to be the most robust sense for it, even in sighted children (Gori et al., 2008; Petrini et al., 2014) and thus should allow for an unbiased comparison that is not driven by differences in task difficulty and familiarity between the different vision groups. Based on the cross-modal compensation hypothesis, whereby intact senses compensate for impaired ones, an increased use of the non-visual senses would predict an earlier developmental onset of audio-haptic integration in low vision and blind individuals compared to sighted individuals. Furthermore, due to increased developmental plasticity early in life (Cappagli, Cocchi, et al., 2017; Collignon et al., 2013) we would predict that congenitally- and early-blind adults benefit more from integrating audio-haptic information, compared to late-blind individuals. Based on the cross-modal calibration hypothesis, we would predict similar development of optimal audio-haptic integration in sighted, low vision, and blind individuals (independent of when vision was lost) as vision is not the most robust sense for this task and thus does not need to calibrate the other senses to achieve a more precise performance. Lastly, since recent findings (Cappagli, Finocchietti, Baud-Bovy, et al., 2017; Cappagli, Finocchietti, Cocchi, & Gori, 2017) have shown that children with low vision perform more similar to sighted than to blind children on different perceptual tasks, we predict that children and adults with low vision integrate audio-haptic information similar to sighted children and adults.

2 | METHODS

2.1 | Participants

A total of 120 participants were recruited for this study. Of these, 46 were sighted adults (28 female, 41.6 ± 18.2 years of age) and 46 sighted children (32 female, 11.5 ± 2.5 years of age). They were grouped into five age groups in order to assess changes in multisensory integration across development. These age groups comprised of younger children (7–9 years), older children (10–12 years), adolescents (13–17 years), younger adults (18–44 years), and older adults (45–70 years). For more details see Supplementary Material S1.

Furthermore, three adults (two female, 30 ± 16.8 years of age) and 11 children (six female, 10 ± 2.1 years of age) with low vision, as well as nine totally blind adults (three female, 36 ± 19 years of age), and five totally blind children (all male, 12.6 ± 2.9 years of age) participated in the study. This sample size is similar to other studies

TABLE 1 Clinical and demographic information for blind and low vision adult participants

Participant	Sex	Age	Handedness	Age of Onset	Vision status	Diagnosis	Visual Acuity (Right Eye; Left Eye) [logMAR]	Vision group
VIa1	Female	18	Right	Birth	Congenitally blind	Bilateral retinoblastoma, cataract, right enucleation	R = –; L = 2.8	CB
VIa2	Male	59	Right	Birth	Congenitally blind	Glaucoma	R > 3; L > 3	CB
VIa3	Male	21	Right	Birth	Congenitally blind	Congenital bilateral cataracts (until 9 years), Glaucoma, Retinal detachment		CB
VIa4	Male	33	Right	5.5 years	Early blind	Glaucoma	R > 3; L > 3	EB
VIa5	Female	18	Right	6 years	Early blind	Retinitis pigmentosa	R > 1.8; L > 1.8	EB
VIa6	Female	19	Right	7 years	Early blind	Stargardt disease	R = 2.8; L = 2.8	EB
VIa7	Male	60	Right	10 years	Late Blind	Leber's optic neuropathy	R = 1.5; L = 1.5	LB
VIa8	Male	61	Right	11 years	Late Blind	Stargardt disease	R = 2.8; L = 2.8	LB
VIa9	Male	35	Right	25 years	Late Blind	Macular degeneration, retinopathy	R > 3; L = 2.8	LB
VIa10	Female	49	Right	41 years	Low vision	Pathological myopia, choroidal neovascularization	R = 1.1; L = 0.8	LV
VIa11	Female	19	Right	Birth	Low vision	Cataracts, aniridia, macular hypoplasia, underdeveloped cornea	R = 1.1; L = 1.1	LV
VIa12	Male	21	Right	Birth	Low vision	Ocular albinism, nystagmus	R = 0.7; L = 0.7	LV

assessing perceptual functioning in children and blind individuals (Cappagli, Cocchi, et al., 2017; Cappagli, Finocchietti, Baud-Bovy, et al., 2017; Garcia, Petrini, Rubin, Da Cruz, & Nardini, 2015; Gori et al., 2010, 2014). Details of visually impaired (VI) participants are depicted in Table 1 and 2. The difference of interest between these groups is the presence or absence of visual experience during and after the first 8 years of life. Eight years was chosen as a cut-off age as this has been shown to be the earliest age at which (sighted) children integrate size information across two senses (Gori et al., 2008). Several previous studies have further suggested that cross-modal calibration ends around 8 years of age (Burr & Gori, 2012; Cappagli, Cocchi, et al., 2017). Therefore, our grouping can be understood as early and late blindness, relative to the onset of the mechanism of interest (optimal multisensory integration).

All participants had normal hearing. Cognitive abilities were not explicitly assessed within this study. However, inclusion criteria set out at the start specified that participants were required to not have any other cognitive or developmental disorders that are frequently associated with visual impairment (e.g. Attentional Deficit Hyperactivity Disorder, Autism Spectrum Disorder). Data from one blind child (VIc16) were excluded from the analysis due to inability to pay attention and complete the task due to hyperactive behaviour, leaving data of four blind children. Handedness was assessed using the Oldfield Edinburgh Handedness Inventory (Oldfield, 1971). All adults and parents of sighted and visually

impaired children gave informed consent before participating in the study, which received ethical approval from the University of Bath Ethics Committee (ref # 15-211) and the National Health Research Authority (IRAS ref # 197917). Sighted adults and children were recruited through local schools, University advertisements, and Research Participation Panels. Visually impaired individuals were recruited through Moorfields Eye Hospital, Bristol Eye Hospital, local charities for the visually impaired, word of mouth, and University advertisements.

2.2 | Stimuli

Stimuli development was based on a standardized and validated method by Petrini et al. (2014). The stimuli consisted of 17 white, 3D-printed plastic balls of different sizes, ranging from 41 to 57 mm in diameter with an increment size of 1 mm. The median ball size with a diameter of 49 mm was chosen as standard stimulus, leaving eight comparison stimuli bigger than the standard ball (50–57 mm) and eight smaller comparison stimuli (41–48 mm). A sound recorded from the standard ball with 49 mm diameter was used to create the comparison balls sound. Praat software (Boersma, 2001) was used to modulate the sound in amplitude to match the sizes of all comparison balls, resulting in sixteen comparison sounds ranging from 71 to 79 dB. The increment size for auditory stimuli was 0.5 dB and

TABLE 2 Clinical and demographic information for blind and low vision child participants

Participant	Sex	Age	Handedness	Age of onset	Vision status	Diagnosis	Visual Acuity (right eye; left eye) [logMAR]	Vision group
VIc1	Male	13	Right	Birth	Congenitally Blind	Bilateral microphthalmia, sclerocornea	R = 2.3; L = 2.3	Blind (EB/CB)
VIc2	Male	12	Right	Birth	Congenitally Blind	Retinal dystrophy; Leber's congenital amaurosis	R > 3; L > 3	Blind (EB/CB)
VIc3	Male	17	ambi./right	4 years	Early Blind	Retinal dystrophy	R > 3; L > 3	Blind (EB/CB)
VIc4	Male	9	Left	6 years	Early Blind	Glaucoma	R > 1.8; L > 3	Blind (EB/CB)
VIc5	Female	7	ambi./right	Birth	Low vision	Oculocutaneous albinism; hypermetropia	R = 0.88; L = 0.76	LV
VIc6	Male	11	Right	Birth	Low vision	Red cone dystrophy	R = 0.7; L = 0.8	LV
VIc7	Male	12	Right	Birth	Low vision	Bilateral juvenile retinoschisis	R = 0.76; L = 1.3	LV
VIc8	Female	13	Right	Birth	Low vision	Stargardt disease	R = 1.0; L = 1.0	LV
VIc9	Male	12	Right	Birth	Low vision	Cone dystrophy	R = 0.58; L = 0.94	LV
VIc10	Male	9	Right	Birth	Low vision	Stargardt disease	R = 1.0; L = 1.0	LV
VIc11	Female	7	Right	Birth	Low vision	Stargardt disease	R = 1.0; L = 1.0	LV
VIc12	Female	11	Right	Birth	Low vision	Stargardt disease	R = 1.04; L = 1.04	LV
VIc13	Male	11	Right	11 years	Low vision	Neuromyelitis optica	R = 1.5; L = 0.3	LV
VIc14	Female	9	Right	3.5 years	Low vision	Bilateral optic atrophy and nystagmus	R = 1; L = 1.3	LV
VIc15	Female	8	Right	4 years	Low vision	Stargardt disease	R = 0.4; L = 0.3	LV
VIc16[a]	Male	12	Right	Birth	Low vision	Congenital glaucoma, left enucleation	R = 1.1; L = −	Blind (EB/CB)

[a]Data from this individual had to be excluded.

has been matched to the haptic stimuli in accordance with Petrini et al. (2014), in which 2 mm haptic size increment were used with 1 dB sound amplitude increments. Pilot tests confirmed the audio-haptic stimulus pair to be well adjusted.

2.3 | Procedure

The participant was blindfolded and seated comfortably in a chair in front of a table and was blindfolded in order to eliminate any visual cues during the experiment. The set up on the table comprised of a touch screen panel on which the haptic stimuli (plastic balls) were placed during the experiment, one at a time (see Figure 1). A thin layer of foam between the ball and touch screen prevented the stimuli from generating impact sounds when being placed down. The participant's dominant hand rested on a soft foam block, which was positioned next to the touch screen. During each trial, a ball was placed on the touch screen in front of the participant, who was then asked to briefly tap the ball with the straight and flat palm of their dominant hand. As the participant was blindfolded, their hand was guided by the experimenter. Once pressure was sensed on the touch

screen the corresponding sound, which provided the auditory size information, was played back through headphones. After tapping the ball, the hand was returned to the soft foam block and the same procedure was repeated with a second stimulus. After two stimuli (unimodal) or two stimuli-pairs (bimodal) were presented, the participant was asked to indicate whether the first or the second object was bigger. Before each experimental block (condition), participants received training on at least four practice trials in order to indicate whether they were able to do the task and to familiarize them with the stimuli.

During each trial, the standard stimulus (49 mm ball, 75 dB sound) was compared to either a bigger or a smaller stimulus. The order in which standard or comparison stimuli were presented was random—with the standard being either first or second. The following stimulus conditions were grouped into blocks of 30 trials in a counter-balanced order: (a) audio only, (b) haptic only, (c) bimodal congruent, and (d) bimodal incongruent. In the audio-only condition, participants only discriminated between object sizes based on the sounds they heard through headphones. Sounds were triggered by participants tapping on the touch screen with a pen. Their hand was guided by the experimenter in order to match the timing of arm
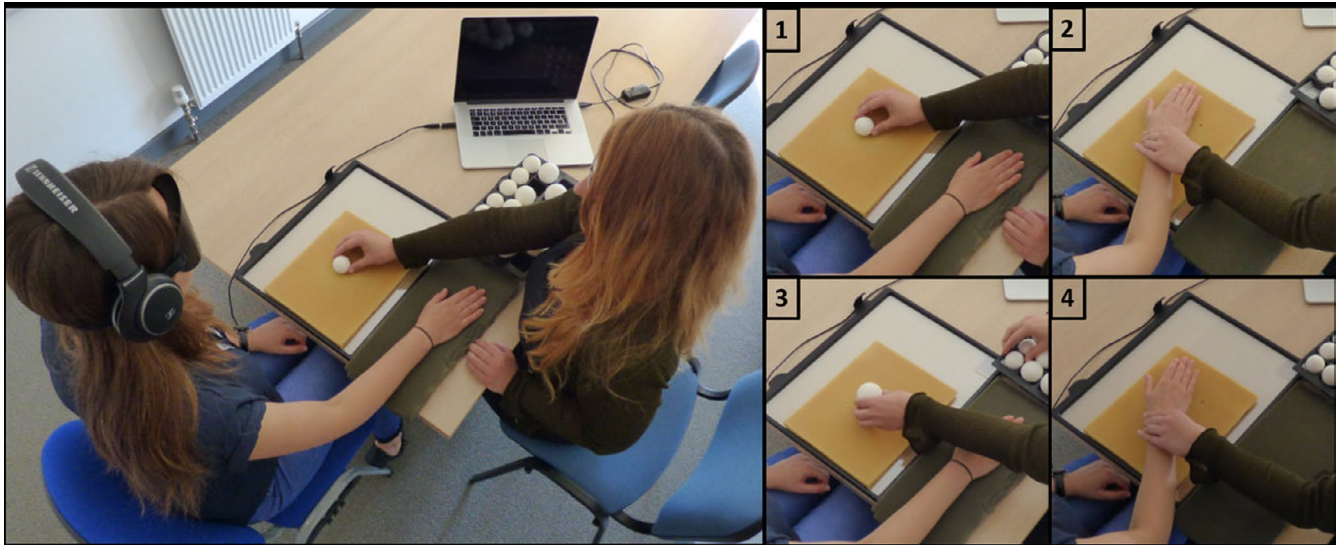
FIGURE 1 Experimental set up and procedure. All participants were blindfolded and sat in front of the set up with their dominant hand resting on a semi-soft foam surface. (1) Haptic stimuli were positioned in a pre-defined location on a thin foam surface that was placed on a touchscreen in front of the participant. (2) Their dominant hand was guided to the location of the stimulus, which they briefly tapped with the flat and straight hand. In the haptic condition, only information from touch was available. In the bimodal conditions, the pressure that was sensed by the touch screen elicited the size-corresponding sound to be played back through headphones. In the audio only condition, participants held a pen, which they used to tap on the touch screen to trigger the sound. In this condition their hand was guided as well. (3, 4) The same procedure repeated for a second stimulus. Participants were then asked to judge which of the two objects was bigger

movement in the other blocks. Triggering the sound through tapping was used to allow comparison between blocks that all used active arm movement and to control for attentional shift due to expected sound onset. In the haptic only condition, participants tapped the ball, but the sound was not played back. Bimodal congruent presentations played the corresponding sound when the ball was tapped. In the bimodal incongruent condition sound and touch gave conflicting size information i.e. a bigger ball (53mm) was presented with the sound of a smaller ball (73 dB = 45 mm), together averaging on the standard stimulus size (49 mm). This cross-modal conflict between haptic and auditory information can be used to determine the degree of perceptual bias towards one of the two cues, and with that the relative reliability (or attributed weight) of the two modalities for this task. We used only one incongruent condition, as Petrini et al. (2014) reported no differences between incongruent pairings. Limiting the length of the experiment is especially important with respect to testing children and individuals with shorter attention spans. Responses were used to calculate discrimination thresholds for each condition, which serve as a measure for perceptual precision. Lower discrimination thresholds indicate a higher perceptual precision. For further information on the procedure and data analysis, see the Supplementary Material S2.

3 | RESULTS

Size discrimination thresholds were used as a measure of precision and were estimated for all participants and conditions separately. All data were assessed for normality, homogeneity of variances and outliers before appropriate tests were chosen. Test assumption checks are reported in the Supplementary Material S3.

To assess how size discrimination thresholds for audio, haptic, and audio-haptic stimuli differ between age groups we carried out a mixed factorial ANOVA, using the three conditions as within-subjects factor and age group as between-subjects factor. The analysis indicated significant main effects for age ($F(4,87) = 8.975$, $p < .001$) and condition ($F(2,174) = 12.93$, $p < .001$), as well as a significant interaction between age group and condition ($F(8,174) = 2.856$, $p = .005$). Bonferroni-corrected, paired t-test were used to compare discrimination thresholds between age groups. Below, we report corrected p-values. Effect sizes were computed as Hedges g with correction for small sample sizes ($d_{unbiased}$, Cumming, 2012). Younger adults performed significantly better in the audio-haptic bimodal condition than with either auditory ($t(29) = 4.85$, $p < .001$, $d_{unb} = 0.874$) or haptic ($t(29) = 2.28$, $p = .015$, $d_{unb} = 0.411$) information alone. Similarly, the older adults performed significantly better in the bimodal condition than in either the auditory ($t(14) = 4.06$, $p = .002$, $d_{unb} = 1.018$) or haptic ($t(14) = 4.10$, $p = .002$, $d_{unb} = 0.703$) condition. In both, the young and older children groups, thresholds in the bimodal condition did not differ from either the auditory-only (7–9 year olds: $t(7) = 0.239$, $p = 1$, $d_{unb} = 0.153$; 10–12 year olds: $t(21) = 1.15$, $p = .394$, $d_{unb} = 0.241$) nor haptic-only (7–9 year olds: $t(7) = 0.45$, $p = 1$, $d_{unb} = 0.203$; 10–12 year olds: $t(21) = 2.32$, $p = 1$, $d_{unb} = 0.485$) condition. In adolescents, bimodal discrimination thresholds were significantly lower than in the auditory-only condition ($t(14) = 3.01$, $p = .014$, $d_{unb} = 0.756$), but only marginally lower than in the haptic-only condition ($t(14) = 2.32$, $p = .054$, $d_{unb} = 0.584$) condition. The results are depicted in Figure 2, showing a clear
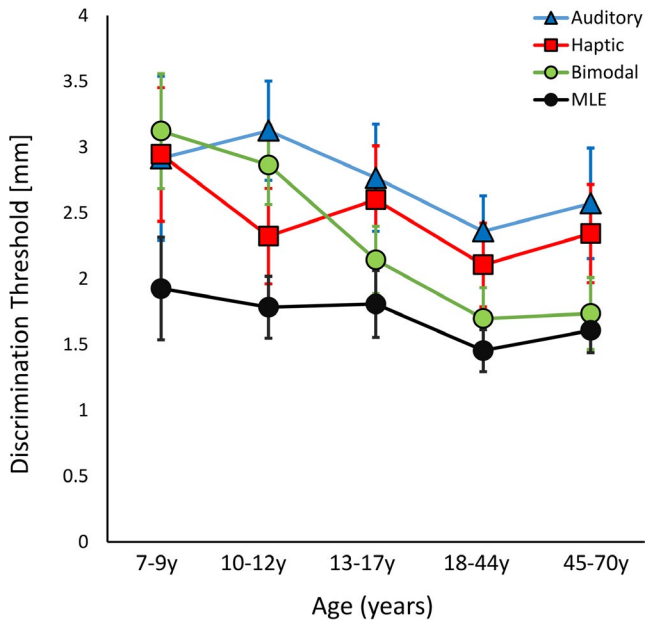
FIGURE 2 Unimodal and bimodal discrimination thresholds of sighted individuals of different ages. Average size discrimination thresholds for all conditions across five age groups. Measured discrimination thresholds for auditory-only (blue triangles), haptic-only (red squares), as well as bimodal (green circles) conditions plotted for five age groups, including younger children, older children, adolescents, as well as younger and older adults. Black circles represent the average discrimination thresholds predicted by Bayed optimal prediction (MLE) and were calculated as a weighted combination of the two unimodal estimates for each individual. Error bars represent 95% CIs

trajectory of the improvement of size discrimination performance with age. In order to compare discrimination performance in the multisensory condition with Bayes-optimal integration performance, we calculated predictions for discrimination thresholds based on maximum likelihood estimation (MLE, see equation 1.3 and 1.4 in Supplementary Material S2) for each individual separately. Averages for predicted bimodal thresholds are depicted in Figure 2 as black circles. For more details on individual integration performance see Supplementary Material S4. Comparing the bimodal threshold to MLE prediction, we found that only in the two adult groups discrimination thresholds did not differ from MLE prediction (18–44 year-olds: $t(29) = 2.1$, $p = .133$, $d_{unb} = 0.379$; 45–70 year-olds: $t(14) = 0.94$, $p = 1$, $d_{unb} = 0.229$). Sensory weights for auditory and haptic cues indicated that all groups, apart from older adults, weighted haptic cues stronger than auditory cues. For more details on cue weighting see Supplementary Material S5.

To examine the extent to which the development of audio-haptic integration depends on visual input, we assessed audio-haptic discrimination performance in adults and children with different levels of visual experience. Thereby we focused on individuals with reduced visual input (low vision, logMAR < 1.3, $n = 15$) and no functional visual input (blind, logMAR ≥ 1.3; $n = 14$) separately. The grouping was based on the WHO definition of blindness using individual visual acuity measures (World Health Organization, 2018).

In the low vision group, integration performance was compared between adults and children to assess whether a reduction in visual input affects how audio-haptic integration develops. To assess how the absence of vision and the developmental time point of vision loss affect audio-haptic integration, we then compared integration performance between blind adults with three different onsets of vision loss: congenitally blind, early blind, and late blind. We chose eight years as a developmental cut-off age to differentiate between the early and the late blind, as this has been identified as the earliest age at which adult-like multisensory integration emerges in sighted children when using vision (Adams, 2016; Gori et al., 2008; Nardini et al., 2008, see Figure 9 in discussion). Furthermore, it has been proposed that vision-driven cross-modal calibration takes place within the first eight years of life (Cappagli, Cocchi, et al., 2017;). In cases where both eyes were affected differently (e.g. participant VIc13) the visual function of the better eye was used as an approximation of best visual function. Non-parametric tests were applied for all analyses including visually impaired individuals as the sample size was small in all sub-groups. Bonferroni-corrected Mann–Whitney U tests were used for group comparisons, while Crawford-Howell case–control comparisons (Crawford, Garthwaite, & Porter, 2010) were used for individual-based performance comparisons.

The influence of reduced visual input on audio-haptic integration was examined by comparing discrimination thresholds of children and adults with low vision against the respective developmental group of sighted participants. Comparing children with low vision (aged 7–12 years) to typically sighted children (aged 7–12 years) showed that discrimination thresholds did not significantly differ between groups in neither auditory-only ($U = 151$, $p = 1$, $r = .04$), haptic-only ($U = 158$, $p = 1$, $r = .10$), nor audio-haptic ($U = 171$, $p = 1$, $r < .01$) conditions. Furthermore, there was no difference between adults with low vision and adults with typical sight in either condition (auditory: $U = 74$, $p = 1$, $r = .04$; haptic: $U = 39$, $p = .674$, $r = .18$; audio-haptic: $U = 43$, $p = .890$, $r = .15$, see Figure 3).

The influence of functional visual input on audio-haptic integration was assessed by comparing discrimination thresholds of typically sighted children and adults to that of blind children and adults with different onsets of blindness (congenitally, early, and late blind). Each individual blind child was compared to the respective age group described in the sighted section above (7–9, 10–12, 13–17 years) using Crawford-Howell t-tests for case-control comparisons. Most comparisons did not reach significance ($p > .05$), however, the 9-year-old early-blind child showed a significantly lower discrimination threshold only in the bimodal condition, compared to sighted 7- to 9-year-olds ($t = 3.47$, $p = .025$, $zCC = 3.66$, see Figure 4).

Discrimination thresholds of blind adults were assessed, similar to low vision adults, on the basis of group comparisons using Bonferroni-corrected Mann–Whitney U-tests. There were no significant differences between the congenitally-blind, nor the early-blind individuals and sighted adults in either the auditory (CB: $U = 47$, $p = 1$; EB: $U = 83$, $p = 1$), haptic (CB: $U = 35$, $p = .499$; EB: $U = 67$, $p = 1$), or audio-haptic conditions (CB: $U = 91$, $p = .951$; EB: $U = 82$, $p = 1$). However, the late-blind individuals differed from sighted adults in

the audio-haptic condition, showing higher discrimination thresholds ($U = 9$, $p = .038$, $r = .36$, see Figure 4), while they did not differ in either auditory ($U = 108$, $p = .254$) or haptic thresholds ($U = 91$, $p = .951$).
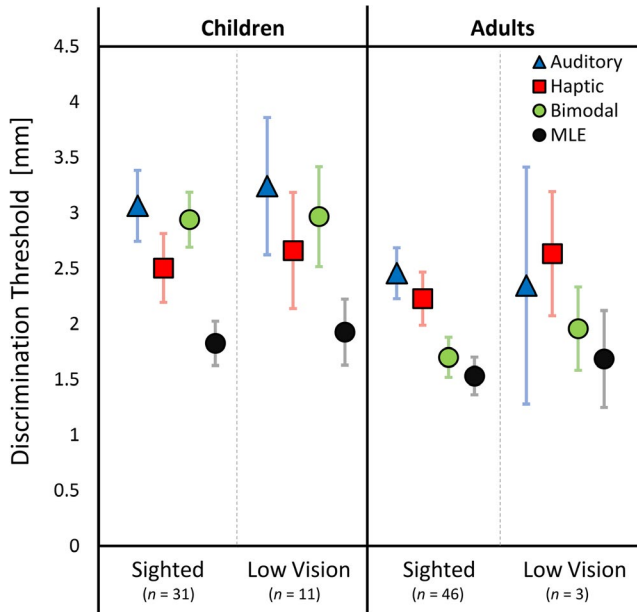

FIGURE 3 Unimodal and bimodal discrimination thresholds of sighted and low vision individuals. Average size discrimination thresholds of both unimodal and bimodal conditions, as well as Bayes optimal prediction (MLE). Left panel shows average thresholds for children, while the right panel shows discrimination thresholds for adults, with the sighted group averages plotted as reference. Error bars represent 95% CIs

3.1 | Multisensory benefit

We next computed the differences between bimodal discrimination thresholds and MLE predictions $\Delta_{measured-predicted}$ for each individual. This measure provides a quantified estimation of the perceptual benefit that is gained through multisensory integration. Differences between bimodal threshold and MLE prediction across the developmental age range are depicted for sighted individuals in Figure 5, and for low vision and blind individuals in Figure 7.

Comparing the multisensory benefit of young adults with the different developmental age groups, we found young adults and older adults did not differ from each other ($t(29) = 0.33$, $p = 1$, $d_{unb} = 0.101$). Furthermore, the multisensory benefit of adolescents aged 13–17 years did not differ from that of young adults either ($t(35) = 1.23$, $p = .568$, $d_{unb} = 0.357$). Contrastingly, the two youngest age groups significantly differed from young adults in the perceptual benefit gained through multisensory integration (7–9 year olds: $t(9) = 2.81$, $p = .039$, $d_{unb} = 1.319$; 10–12 year olds: $t(35) = 4.19$, $p < .001$, $d_{unb} = 1.231$; see Figure 5).

To assess how integration performance develops in low vision individuals we compared the multisensory benefit $\Delta_{measured-predicted}$ between sighted and low vision children, and between sighted and low vision adults. Average scores were not significantly different between sighted and low vision individuals. This was true for both children ($U = 158$, $p = .735$, $r = .10$) and adults ($U = 83$, $p = .543$, $r = .02$, see Figure 6).

Comparing the average $\Delta_{measured-predicted}$ between individual blind children and the age-matched sighted children (7–12 years) or adolescent (13–17 years) groups indicated that the congenitally-blind 9-year-old benefitted from integrating audio-haptic
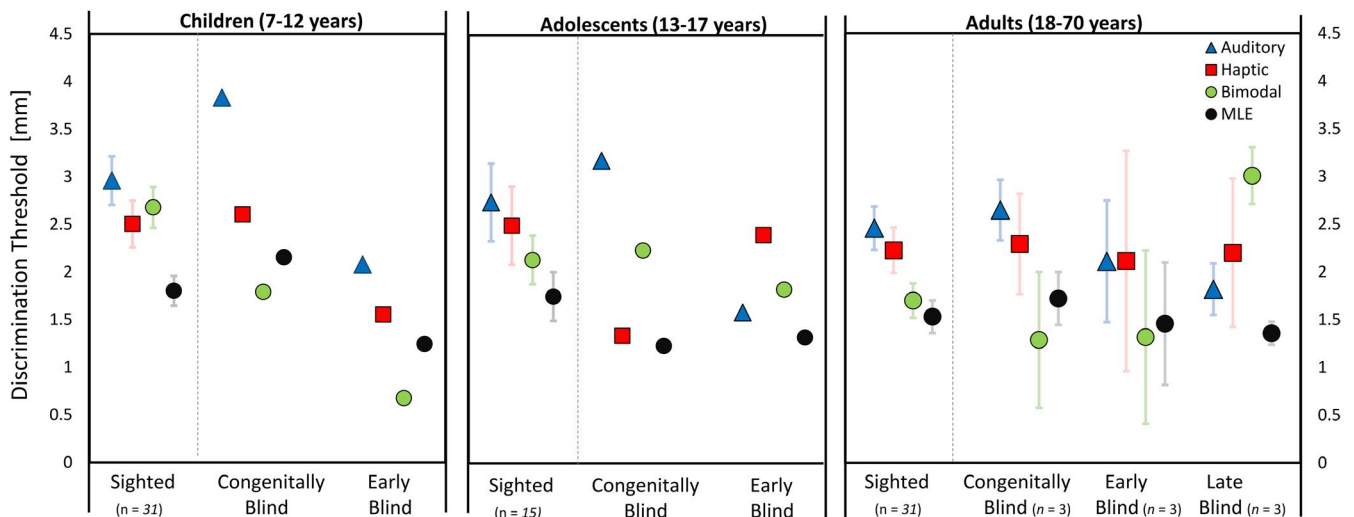

FIGURE 4 Discrimination thresholds for unimodal and bimodal performance for sighted and blind individuals. Average size discrimination thresholds for both unimodal and bimodal conditions, as well as Bayesian model prediction (MLE). Panel (a) shows thresholds for two blind children aged 12 and 9 years, as well as the average thresholds for children aged 7–12 years. Panel (b) shows thresholds for two blind adolescents aged 13 and 17, together with the average thresholds for 13- to 17-year-old sighted adolescents. Panel (c) shows average thresholds for adults with congenital, early, or late blindness onset, as well as the sighted adult thresholds for reference on the left. Early blindness is defined as having an onset within the first 8 years of life, while late blindness is defined by an onset after 8 years of life, in line with the duration of cross-modal calibration (Burr & Gori, 2012). Black circles represent the average discrimination thresholds predicted by maximum likelihood estimation based on a weighted combination of the two unimodal estimates. Error bars represent 95% CIs

information significantly more than sighted children (t = 1.92, p = .032, zCC = 1.96). For the 12-year-old early-blind individual, there was a marginal difference (t = 1.69, p = .051, zCC = 1.72), suggesting that this individual also reduced uncertainty more than sighted children. We did not find any differences between the 17-year-old congenitally-blind individual and sighted adolescents (t = 0.25, p = .105, zCC = 1.36), nor between the 13-year-old early-blind individual and sighted adolescents (t = 0.25, p = .403, zCC = 0.26). Next, we compared sighted adults with blind adults in three different blindness onset groups (congenitally, early, late blind). Congenitally-blind individuals integrated audio-haptic information optimally, or even super-optimally (see Figure 6). This group differed from sighted adults only marginally (U = 112, p = .059, r = .24). Discrimination thresholds of early-blind individuals did not differ significantly from that of sighted adults (U = 92, p = .322, r = .07). Lastly, late-blind individuals showed significantly higher $\Delta_{measured-predicted}$ scores compared to sighted individuals (U = 5, p = .002, r = .448), indicating reduced integration performance. Figure 4 shows late-blind adults exhibit similar auditory and haptic thresholds as the other adult groups. Differences between bimodal threshold and MLE prediction for blind children and adults, as well as the respective sighted age groups, are depicted in Figure 6. For an overview of individual scores for adults and children from all vision groups across the developmental age range see Figure 7.

4 | DISCUSSION

The brain's ability to enhance perceptual precision by integrating input from multiple senses develops late in sighted individuals (Adams, 2016; Gori et al., 2008; Nardini et al., 2008; Petrini et al., 2014). Early blindness has been shown to impact on non-visual perception in two ways: on the one hand, neural plasticity allows the individual to cross-modally compensate for missing sensory input, for example through enhanced tactile discrimination or auditory localization (Amedi et al., 2003; Collignon et al., 2013). On the other hand, blindness precludes the calibration of the non-visual senses through vision. This has been shown to lead to impaired auditory or proprioceptive spatial perception (Cappagli, Cocchi, et al., 2017; Gori et al., 2014). However, as most of our environment is multisensory, and as visually impaired individuals rely more heavily on other senses such as touch and hearing, the functional outcomes of visual deprivation on the benefits of
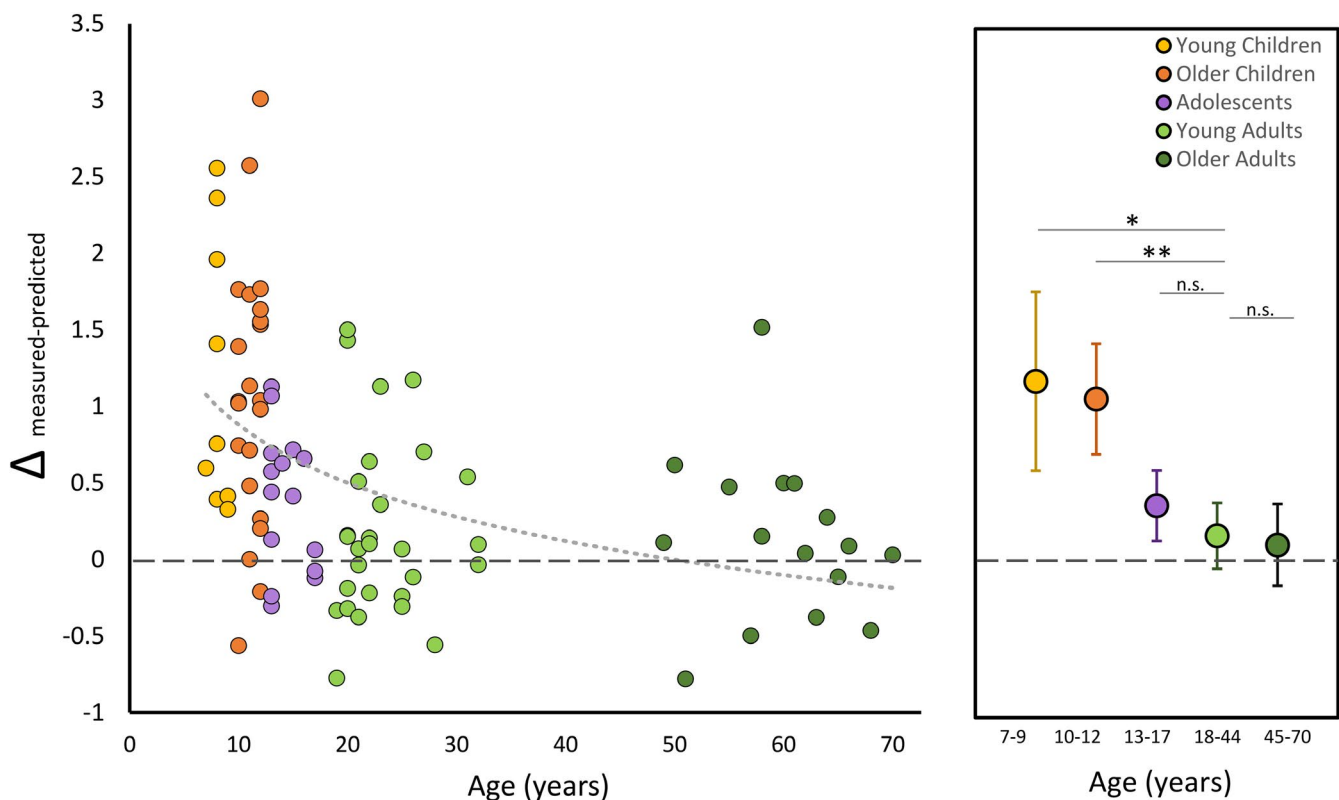

FIGURE 5 Integration performance of typically sighted individuals. Left panel shows individual threshold differences between predicted and measured discrimination thresholds for audio-haptic bimodal stimulus presentation across all ages. The dashed line at y = 0 indicates optimal performance predicted by MLE, which is based on the auditory and haptic unisensory estimates. Data below this line indicate an increase in precision that is better than predicted by the model. Different colors correspond to the different age groups: young children (7–9 years), older children (10–12 years), adolescents (13–17 years), younger adults (18–44 years), and older adults (45–70 years). Light gray trend line indicates the line of best fit. The right panel shows means for discrimination threshold difference scores (Δ) for each age group separately. Error bars indicate 95% CI. *p < .05; **p < .01; n.s. = not significant
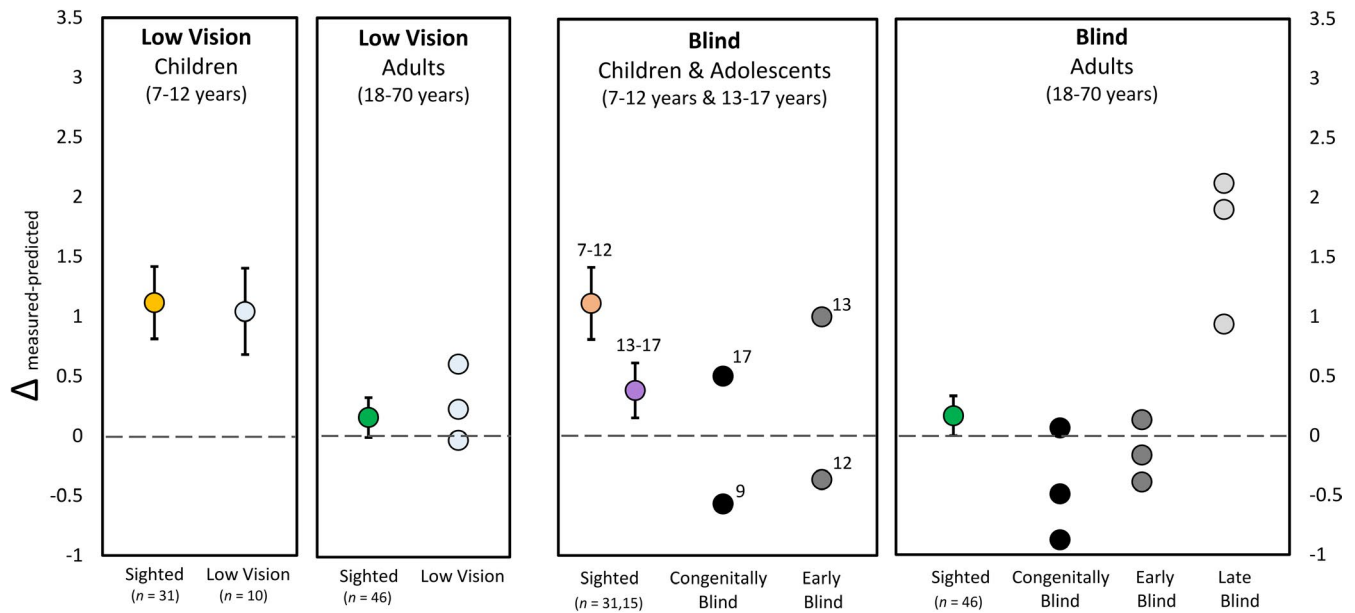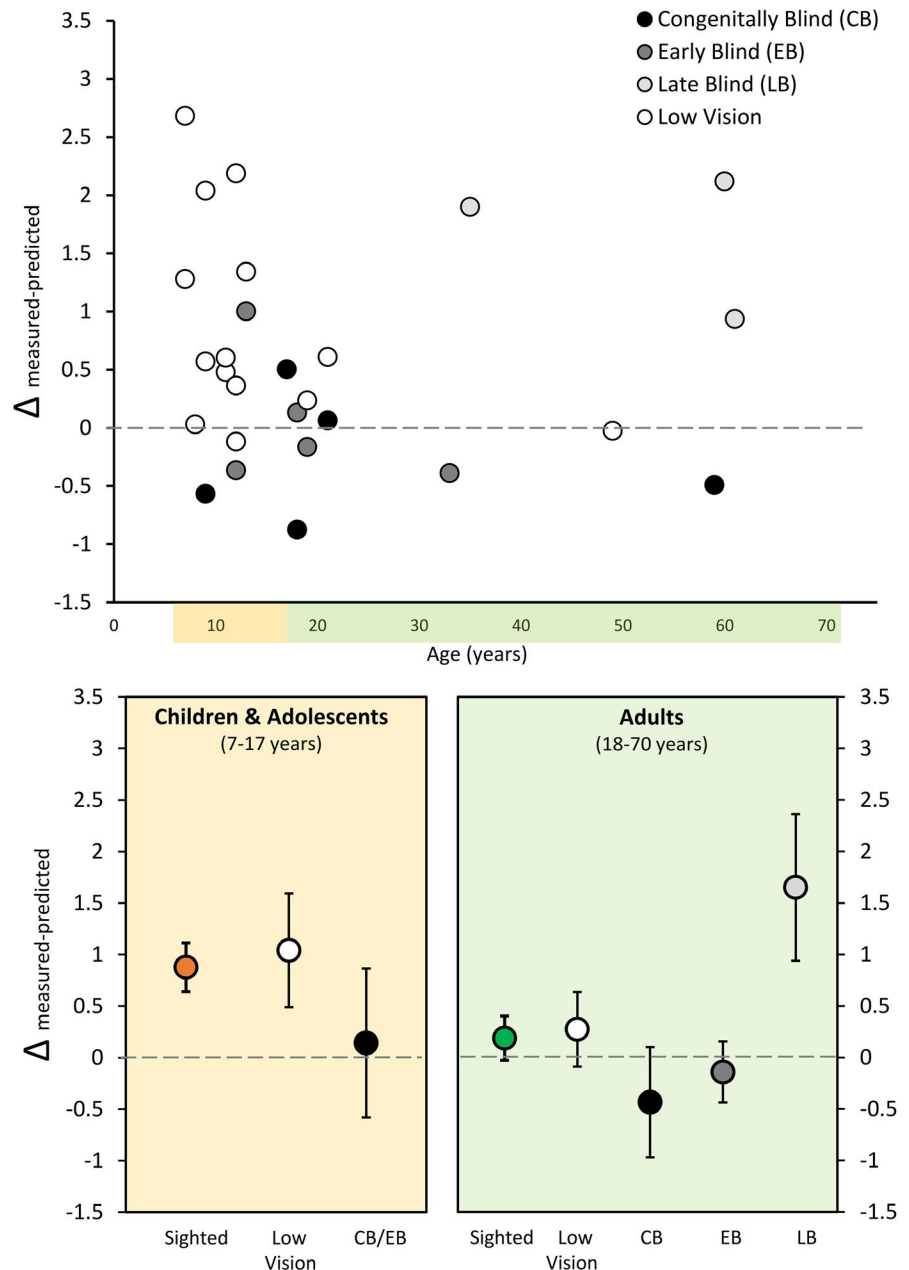
FIGURE 6 Integration performance of low vision and blind individuals. Differences between predicted and measured discrimination thresholds for bimodal stimulus presentation. Panel (a) show average multisensory benefit scores for children, and individual multisensory benefit scores for adults with low vision (light circles). The average multisensory benefit scores of the respective, age-matched sighted groups are plotted as references. Panel (b) show multisensory benefit for individual congenitally-blind (black), early-blind (gray), and late-blind (light gray) individuals. Early and late blindness are defined by the onset of blindness either before or after the age of 8 years. For the children and adolescents, individual ages and age ranges are indicated next to the data points to allow for a direct comparison. The dashed line at y = 0 indicates MLE model prediction based on the auditory and haptic unisensory estimates, while data below this line indicates an increase in precision that is better than predicted by the model. Error bars indicate 95% CI

audio-haptic integration (reducing sensory uncertainty by combining sensory information) are of fundamental importance.

Here we report, for the first time, that while congenitally- and early-blind (EB) adults show similar or even marginally better audio-haptic integration performance than sighted adults, this integration performance is impaired in late-blind adults. As expected, the developmental period during which visual experience influences the development of audio-haptic integration extends until 8–9 years of life. This falls in line with the previously proposed period of cross-modal calibration through vision (Cappagli, Cocchi, et al., 2017; Gori et al., 2014). Based on the idea that during development the more robust sense calibrates the less robust senses, we expected that the presence or absence of visual experience would not affect the performance on our audio-haptic size discrimination task. This is because touch is the more robust sense for assessing size information, compared to audition (Petrini et al., 2014; *present study*) or vision (Gori et al., 2008; Gori, Tinelli, et al., 2012). Indeed, we find that blindness early in life does not affect audio-haptic integration later in life, which would therefore support the idea that the more robust sense, here haptics, teaches the less robust sense and that vision is not necessary for the development of audio-haptic integration. Furthermore, haptic precision seems to be more stable across individuals with different levels of developmental vision, while auditory precision and the propensity to integrate both types of information changes (Figures 3 and 4). This would further support that touch is the more robust sense on this specific task, and is in line with previous findings showing that tactile

performance in the blind is not overall enhanced, but improves due to practice (Grant et al., 2000; Wong et al., 2011). Interestingly, however, we also find that early blindness seems to lead to an earlier developmental onset of optimal audio-haptic integration, supporting the idea of cross-modal compensation. That is, an increased use of the remaining senses leads to an enhanced recruitment of presumptive "visual" areas in the brain to process non-visual information. Thereby the integration of audio-haptic information is facilitated already at an age at which sighted children typically start to integrate visuo-haptic information optimally (Amedi et al., 2003; Collignon et al., 2013; Gori et al., 2008). Note here that the present findings, as well as other previous findings showing functional compensation in the sensory deprived, depend on the nature of the perceptual task and the relative sensory robustness of the senses for this task during development (Cappagli, Cocchi, et al., 2017; Gori, Sandini, et al., 2012; Gori et al., 2010; Gori, Tinelli, et al., 2012). Generalization of such findings to other spatial tasks would therefore be subject to replication with these tasks or require a strong theoretical foundation, which is offered by the idea of relative differences in sensory robustness as stipulated in the cross-modal calibration hypothesis. In contrast to both hypotheses, however, we find that late blindness, which includes the presence of visual experience during early development, leads to a disruption in audio-haptic integration performance. Notably, while the presence of visual experience early in life reduces audio-haptic integration performance in the late blind, it does not reduce integration performance in the sighted. These findings cannot be explained by

FIGURE 7 Overview of multisensory integration performance in low vision and blind individuals. Upper panel shows individual difference scores for measured versus predicted discrimination thresholds as a function of age. Difference scores are inversely proportional to the multisensory benefit. Predicted threshold, indicated by the gray dashed line at y = 0, is based on the Bayesian integration model indicating optimal integration performance. Model predictions have been calculated for each participant separately and are based on the individual auditory and haptic unisensory thresholds. Individuals are color-coded based on different amounts of visual experience. Bottom left panel shows average scores for low vision and blind children and adolescents, with the sighted children and adolescent groups as reference. Bottom right shows average scores for low vision and blind adults, depending on the age of blindness onset. Average scores for sighted adults are plotted as a reference. Error bars indicate 95% CI

either cross-modal calibration or sensory compensation alone. A summary of these findings can be seen in Figure 8.

Previous studies that reported perceptual differences between individuals with different levels of visual experience showed that congenitally-blind individuals performed significantly worse than sighted individuals on different auditory and proprioceptive spatial perception tasks. At the same time, late-blind individuals and those with low vision performed similar or even better than sighted individuals (Cappagli, Cocchi, et al., 2017; Cappagli, Finocchietti, Baud-Bovy, et al., 2017). These findings suggest that the mere presence or absence of visual input early in life can affect spatial processing in the remaining senses. Interestingly, the effect of visual deprivation shows the opposite pattern in our study. A possible explanation for this opposing trend is that the task used in the present study is targeting different processes. While Cappagli, Cocchi, et al. (2017) used

a task for which vision was the most robust sense and examined the effect of visual experience on proprioception and audition separately, our study used a task for which touch was the most robust sense and we examined the effect of visual experience on the integration of touch and audition. Therefore, if vision was the most robust sense for a task, only early, but not late blindness, would affect non-visual processing later in life (Cappagli, Cocchi, et al., 2017). If touch, on the other hand, was the more robust sense for a task, early blindness should not affect non-visual processing later in life. Late blindness could, however, still affect non-visual processing if the perceptual process (e.g. non-visual multisensory integration) is dependent on the developmental consistency of sensory experience. Our results therefore support both cross-modal compensation and cross-modal calibration. However, they also suggest that these processes serve an adaptive purpose by allowing early sensory experience to imprint
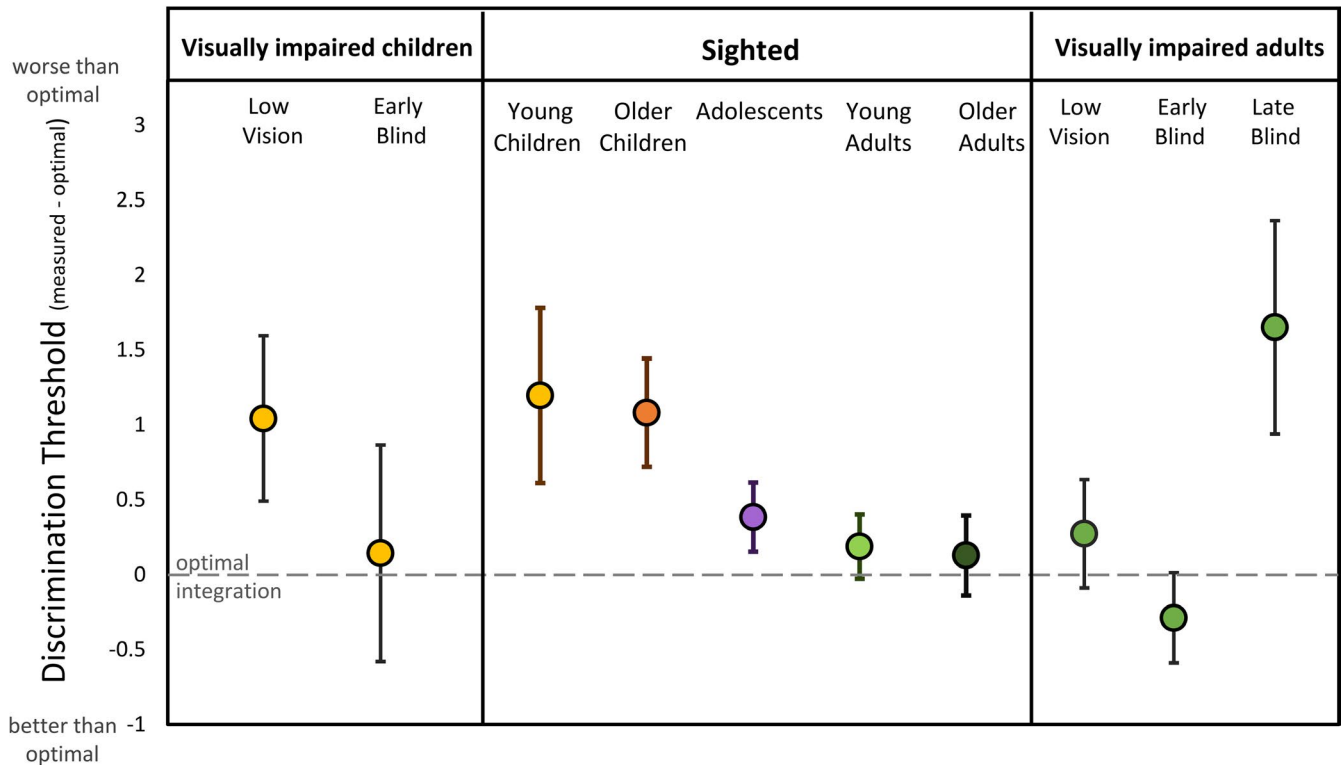
FIGURE 8 Overview figure summarizing main effects. Optimal audio-haptic integration develops across adolescence in sighted individuals. Low vision does not affect this development. Congenital and early blindness lead to an earlier development of optimal audio-haptic integration, while late blindness disrupts optimal integration

on the developing brain and to prepare the developing individual for the sensory environment they are likely to experience later in life. That is, throughout the first 8 years in life, the system accumulates sensory experience in order to gauge the reliability of the different sensory modalities that they will likely require later, and to distribute modality-specific weights accordingly (Noppeney, Ostwald, & Werner, 2010; Rohe, Ehlis, & Noppeney, 2019). If the early sensory environment (e.g. typical sight) does not match up with the environment that the individual experiences later in life (e.g. blindness), the system might attribute higher weights to the wrong (i.e. impaired) sensory modality.

The second aim of this study was to provide a comprehensive trajectory of the development of audio-haptic integration across the life span in sighted humans. To the best of our knowledge, only one study (Petrini et al., 2014) so far assessed how optimal audio-haptic integration develops between middle childhood (5–11 years) and young adulthood (19–35 years). The authors found that audio-haptic multisensory integration is not yet fully developed by the age of 11 years, with the onset of optimal integration remaining unknown. Our results replicate these findings, but also show that audio-haptic integration becomes more adult-like at around 13–15 years in typically sighted individuals. This is evidenced by a similar weighting of sensory cues, and a reduction in sensory uncertainty between adolescents and young adults. Arguably, the maturation of this process is still ongoing for several individuals at this age, while the majority of adolescent participants in our study benefitted

from having both sensory cues available. This likely explains why the adolescent group showed a reduction of uncertainty in the audio-haptic condition compared to auditory-only or haptic-only conditions, but still differed in measured and predicted discrimination thresholds (for individual data and discussion see Supplementary Materials S4 and S4.2; Jonas, Spiller, Hibbard, & Proulx, 2017; Murray, Thelen, Ionta, & Wallace, 2018; Peterzell, 2016). Finally we found that, overall, the haptic information dominated object size perception, confirming the haptic dominance for this task over other senses, which is in line with the findings of previous developmental studies (Gori et al., 2008, 2010; Petrini et al., 2014).

The summary shown in Figure 9 suggest that the onset of adult-like integration and possibly the end of cross-modal calibration (Burr & Gori, 2012) may differ for the different senses and tasks (see also Figure 3 in Stanley, Chen, Lewis, Maurer, & Shore, 2019). For example, the perception of temporal properties (Adams, 2016; Gori, Sandini, et al., 2012; Gori, Tinelli, et al., 2012) proceeds the integration of spatial characteristics (Gori Sandini, & Burr, 2012; Gori, Tinelli, et al., 2012). This is also in line with a number of studies showing that audio-visual, visuo-tactile, and audio-tactile simultaneity perception develops adult-like characteristics before the respective spatial information is integrated (Chen, Lewis, Shore, Spence, & Maurer, 2018; Chen, Shore, Lewis, & Maurer, 2016; Stanley et al., 2019), suggesting that temporal simultaneity perception is a prequisite for the integration of spatial information. However, the onset of optimal multisensory
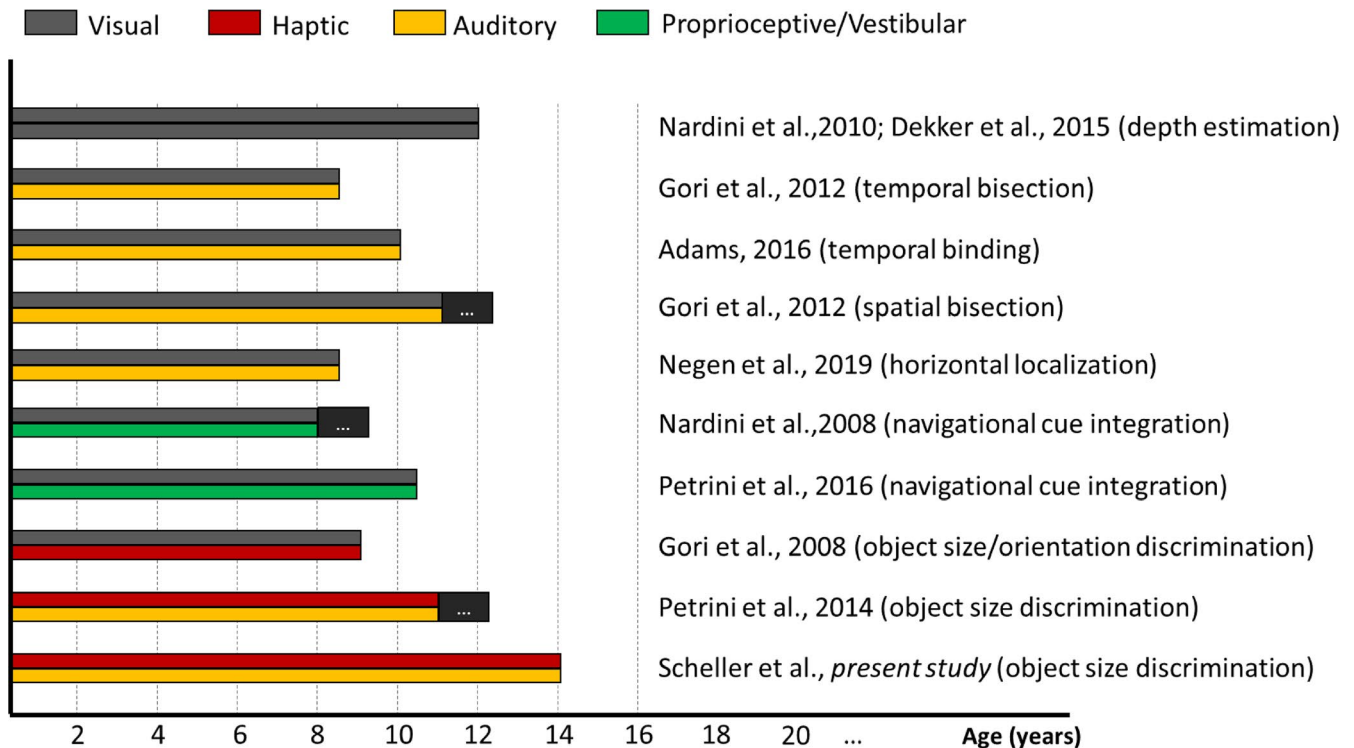
FIGURE 9 Developmental onset of adult-like multisensory integration. Reported age of onset of adult-like multisensory integration for different sensory systems. Color combinations indicate the sensory combinations that have been tested by respective studies and tasks. All identified ages of onset fall within a period of 8–14 years, coinciding with major developments in fronto-parietal networks (Giedd et al., 1999; Gogtay et al., 2004) governing multisensory weighting (Cao et al., 2019; Rohe et al., 2019). Black boxes at the right end of the developmental trajectory indicate that multisensory integration performance has not yet reached adult-like levels at this age, but is likely to develop later (indicating the upper boundary of the age range tested in each respective study). Note that several studies did not report a concrete age of onset, but an age range during which this ability develops. The figure presents mean age of these age ranges.

integration also seems to depend on the sensory modality pairing that is involved in the task. For example, while audio-visual optimal integration seems to develop between 8 and 12 years of age (Adams, 2016; Gori et al., 2008; Gori, Sandini, et al., 2012; Nardini, Bedford, & Mareschal, 2010; Petrini, Caradonna, Foster, Burgess, & Nardini, 2016), the integration of non-visual information does not emerge until later (Petrini et al., 2014; *present study*).

The late maturation of optimal integration consistently shown by several studies (Figure 9) could be a consequence of the late maturation of the substrates that subserve optimal multisensory integration. While low-level sensory processing areas mature relatively early in childhood, frontal and parietal regions have been shown to develop last, with maturational peaks around late childhood and adolescence (Giedd et al., 1999; Gogtay et al., 2004; Sowell et al., 2003). Notably, there has been long-standing evidence of the modulatory involvement of a fronto-parietal network in the optimal integration of multisensory information (Engel, Senkowski, & Schneider, 2012; Jones & Powell, 1970; Ma, Beck, Latham, & Pouget, 2006). However, specific evidence for the neural basis of multisensory reliability weighting in frontal (Cao, Summerfield, Park, Giordano, & Kayser, 2019) and parietal (Boyle, Kayser, & Kayser, 2017; Rohe et al., 2019) areas has only been provided recently. Taken together with the findings summarized in Figure 9, this might suggest that the functional onset of optimal multisensory integration depends on the maturation of

these networks, leading to a sensory-specific onset in late childhood and early adolescence. Evidence for a link between optimal cue integration within one modality and maturational changes in their processing substrate has previously been provided by Dekker and colleagues (2015).

4.1 | Limitations

A limitation to the generalization of the findings reported here, however, is the small sample size of blind individuals. While the sample size is similar to other studies that assessed perceptual functioning in blind adults and children (e.g. Cappagli, Cocchi, et al., 2017; Cappagli, Finocchietti, Baud-Bovy, et al., 2017; Garcia et al., 2015; Gori et al., 2010, 2014), sub-groups of congenitally-, early-, and late-blind adults consist of few individuals. It is worth emphasizing, however, that the design and nature of the study, similar to other psychophysical studies measuring optimal multisensory cue combination, typically lends high statistical power on the individual level and high inter-individual robustness (Rohde et al., 2016). Furthermore, a sensitivity analysis (Supplementary Material S4.3), comparing subsamples of age- and sex-matched sighted controls with blind adults and children confirms the findings of a disruption in optimal audio-haptic integration in the

late-blind, and an earlier onset of optimal audio-haptic integration in the early-blind. Nevertheless, while the present study provides an overview of the effects of different levels of visual experience on the development of non-visual multisensory integration, our finding of disrupted integration performance in late-blind individuals would require replication before more general conclusions can be drawn.

Linked to the first limitation discussed above, the number of children in each sub-group is not homogenous. Similar to previous studies (e.g. Gori et al., 2008; Petrini et al., 2014) the number of participants in our sub-groups varies. This was intentional and based on previous findings using the same task with a sighted population. Using the same task, Petrini et al. (2014) found that sighted children under the age of 11 years do not integrate audio-haptic information in an adult-like (statistically optimal) fashion. We would have therefore expected to see a progression and onset of multisensory integration within the age group 10–12 or older. Hence, the large sample size of the 12- and 13-year-olds would have allowed to test when audio-haptic multisensory integration occurred. In fact, despite the smaller sample size of the younger developmental age groups and the adaptation of methodology—using an adaptive staircase procedure instead of constant stimuli—we replicated the developmental results and trends of Petrini et al. (2014). This shows that the results for sighted children up to 11 years are very consistent across studies and consequently robust and replicable. Following this, we were now able to confirm that optimal audio-haptic integration emerges largely from 13 years of age onwards.

5 | CONCLUSION

Our results show that the ability to combine audio-haptic sensory input in an optimal way does not develop before adolescence (13–17 years) in typically sighted individuals. The data further provide empirical evidence that visual experience is not necessary for non-visual optimal multisensory integration to emerge, but that consistency of sensory experience plays an important role in setting up the rules under which information is integrated later in life. They highlight that the adaptiveness of cross-modal plasticity lies in preparing the developing individual for the sensory environment they are likely to experience later in life. That is, during development, the system accumulates sensory experience in order to gauge the reliability of the different sensory modalities, and to distribute modality-specific weights accordingly. If the early sensory experience (e.g. sighted) does not match up with what the individual experiences later in life (e.g. blindness), the system might attribute higher weights to the wrong (lost or impaired) sensory modality. Our results further suggest that the calibration of the perceptual weighting system is taking place during approximately the first 8–9 years of life, highlighting the important role of early multisensory experience during this developmental period.

CONFLICT OF INTEREST
The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are openly available within the Open Science Framework at Scheller (2020) http://doi.org/10.17605/OSF.IO/7XSF3

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