



Spatial modulation of motor-sensory recalibration in early deaf individuals



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ABSTRACT

Audition dominates other senses in temporal processing, and in the absence of auditory cues, temporal perception can be compromised. Moreover, after auditory deprivation, visual attention is selectively enhanced for peripheral visual stimuli. In this study, we assessed whether early hearing loss affects motor-sensory recalibration, the ability to adjust the timing of an action and its sensory effect based on the recent experience. Early deaf participants and hearing controls were asked to discriminate the temporal order between a motor action (a keypress) and a visual stimulus (a white circle) before and after adaptation to a delay between the two events. To examine the effects of spatial modulation, we presented visual stimuli in both central and peripheral visual fields. Results showed overall higher temporal JNDs (Just Noticeable Difference) for deaf participants as compared to hearing controls suggesting that the auditory information is important for the calibration of motor-sensory timing. Adaptation to a motor-sensory delay induced distinctive effect in the two groups of participants, with hearing controls showing a recalibration effect for central stimuli only whereas deaf individuals for peripheral visual stimuli only. Our results suggest that auditory deprivation affects motor-sensory recalibration and that the mechanism underlying motor-sensory recalibration is susceptible to spatial modulation.

1. Introduction

After long-term auditory deprivation, the brain undergoes complex dynamic changes that rearrange the functional properties of the auditory areas and the anatomical connections between them and other cortical regions. The brain areas serving the auditory modality can develop the ability to process visual and/or tactile stimuli (Finney et al., 2003; Finney, 2001; Levänen et al., 1998) and the cortical regions supporting the remaining senses may also acquire enhanced functional and processing competences (Bavelier et al., 2000; Neville and Lawson, 1987; Neville et al., 1983; Scott et al., 2014). Consequently, deaf individuals can operate effectively within their environment.

Most of the psychophysical studies that have investigated the effects of early auditory deprivation on visual and tactile perception report similar performance between deaf and hearing individuals (see Pavani and Bottari, 2012 for a review). Enhanced abilities in deaf individuals have been reported only for the processing of visual features that are typically handled by the magnocellular system. For example, functional neuroimaging revealed that the recruitment of the motion selective area MT/MST by moving stimuli is higher in deaf than in hearing individuals (Bavelier et al., 2000) and that motion stimuli evoked significant responses in the auditory cortex of deaf subjects, but not in hearing controls (Fine et al., 2005). Moreover, it has been observed that compared to hearing controls, deaf participants are better at detecting

changes in a moving pattern when stimuli are located in the peripheral, rather than central, visual field (Bavelier et al., 2000, 2001; Neville and Lawson, 1987) and that they show faster responses for targets appearing at peripheral locations (Loke and Song, 1991). Since the auditory system most importantly provides information about events occurring outside the central visual field, it has been hypothesized that, in the absence of audition, visual processing might adjust to favor peripheral vision to better organize orienting responses to distal events (Loke and Song, 1991; Neville and Lawson, 1987; Parasnis and Samar, 1985). In deaf individuals, the increased reliance on the visual periphery can affect the distribution of visual attention. Indeed, compared to hearing individuals, deaf people are more affected by peripheral, rather than foveal, distractors (Parasnis and Samar, 1985; Proksch and Bavelier, 2002). These results suggest that the representation of peripheral space is more susceptible to early auditory deprivation than is the representation of the foveal, central visual space.

Besides the compensatory advantages in the peripheral visual processing reported above, other studies have suggested that the premature and substantial deficit in the auditory modality might affect the development and organization of the other sensory systems. Specifically, as the auditory modality dominates other senses in temporal processing (Gori et al., 2012; Morein-Zamir et al., 2003; Recanzone, 2003; Repp and Repp, 2003; Shams et al., 2000), it has been hypothesized that the absence of auditory information may undermine normal development

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of temporal perception. As suggested by Conway et al. (2009), sound might provide a “scaffolding” that the brain uses to learn how to interpret and process sequential information (Conway et al., 2009). In particular sound, as music or speech, is a sequential signal containing strong temporal patterning that requires rapid temporal analysis. For this reason, auditory experience might play a critical role in developing accurate and effective temporal processing. In support of this idea, Heming and Brown (2005) reported higher perceptual thresholds in deaf individuals as compared to hearing controls for tactile and visual temporal tasks. Similarly, Kowalska and Szelag (2006) and Bolognini et al. (2012) reported an impairment for deaf individuals in the discrimination of the temporal duration of touches, but not in the discrimination of their spatial length. Bolognini et al. (2012) also showed that the auditory association cortex is involved in tactile temporal processing in both hearing and deaf individuals, despite a different chronometry. Nevertheless, other studies showed that the deaf individuals’ deficit in the temporal processing might be task-dependent and that temporal precision might not be affected by stimulus eccentricity (Nava et al., 2008; Poizner and Tallal, 1987). The importance of audition for temporal perception and its dependence on stimulus location, therefore, are still under debate.

In the current study, we investigated the effect of early deafness on sensory-motor temporal processing and on the spatial modulation of this processing. Encoding the temporal order between a self-produced motor action and a sensory event is extremely important in everyday life for understanding causal relationships between action and perception. The mechanism responsible for this temporal processing has to be flexible and adaptable to overcome environmental changes in the physical propagation of external stimuli (for example a slowly responding computer). Indeed, previous studies reported that after adaptation to a delayed sensory feedback from a self-produced action, the brain can adjust the perceived time of the sensory event relative to the perceived time of the action in a motor-sensory recalibration process, to keep causality assessment accurate (Heron et al., 2009; Keetels and Vroomen, 2012; Stetson et al., 2006; Sugano et al., 2010). In the current study, we investigated the effect of early deafness on sensory-motor temporal recalibration. We also tested whether stimulus eccentricity affects motor-sensory recalibration in deaf and hearing participants. Our hypothesis was that the lack of auditory temporal calibration early in life might reduce temporal precision and impair motor-sensory recalibration in deaf individuals. We also expected that the differences in motor-sensory recalibration between deaf and hearing participants might depend on the spatial locations of the visual stimulus.

2. Methods

Nine early deaf signers (mean age: 39 ± 3.5 years, 8 females and 1 male) and eleven hearing non-signers (mean age: 31 ± 3.3 years, 10 females and 2 males) participated in the study. Deaf participants lose their hearing before the second year of age. Individual information about deaf participants are reported in the supplemental material Table S1. We found no significant age difference between the two groups (independent samples *t*-test, $t_{19} = 1.86$, $P > 0.05$). Participants were right-handed and had normal or corrected-to-normal sight. Control participants had normal hearing. All the deaf participants learned American Sign Language during early childhood (additional information about deaf participants are reported in Table S1). For deaf participants, a sign language interpreter was present during the experiment, to provide instructions and to mediate participants’ responses. Informed consent was obtained from all subjects. Methods and procedures of the experiment were approved by the local ethics committee at the University of Nevada, Reno and followed the principles of the declaration of Helsinki.

Methods and procedures were adapted from Vercillo et al. (2014). Participants sat in a silent and dark room at 57 cm from the computer screen. Stimuli were presented through a Display ++ LCD monitor and

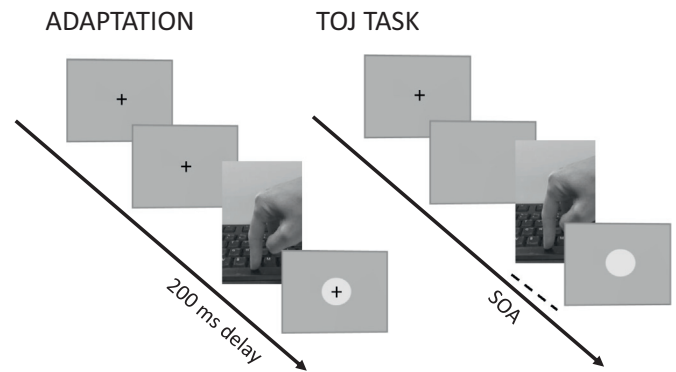


Fig. 1. Methods and procedures. Adaptation (left panel) and TOJ task trials (right panel). In the adaptation trials participants pressed a button and received a visual feedback after 200 or 500 ms. In the TOJ trials participants pressed a button after the fixation cross disappeared and judged whether a visual stimulus appeared before or after their own action. The distribution of the stimulus latency was centered on individual average reaction times.

motor actions were recorded through a CB6 response box that interfaces directly with Bits# via an infra-red link, and supports a high-resolution counter to measure reaction times. Together, these Cambridge Research System devices ensured high precision timing and sensory-motor synchronization. The visual stimulus was a 6° diameter white circle presented on a grey background. A black fixation cross was displayed at the center of the screen and the visual stimulus was presented in three possible locations depending on the experimental condition: at fixation, 10° to the left, and 10° to the right. Hearing participants listened to white noise delivered through headphones at 65 dB for all the duration of the experiment to isolate the sound produced by the button press.

A Temporal Order Judgment (TOJ) task was used to measure the perception of sensory-motor synchrony (Fig. 1, right panel). In the TOJ task, participants performed a voluntary action pressing the button on the response box as soon as the fixation cross on the screen disappeared. A visual stimulus was displayed before or after the button press. Participants reported verbally (deaf participants signed) whether the visual stimulus occurred before or after their button press, thus making a temporal order judgment between the button press and the visual event.

The latencies of the visual stimulus were partially determined by individual average reaction times (RTs). After each experimental block, we recalculated the average RTs and updated the value for the next block. The stimulus latencies (Stimulus Onset Asynchrony – SOA) were: ± 100 ms, ± 80 ms, ± 60 ms, ± 40 ms, ± 20 ms, and 0 ms, where negative values indicate that the visual stimulus was presented before the motor action and positive values indicate that it was presented after. Each latency was repeated 10 times in a constant stimuli algorithm. Note that because of individuals’ RT variability, the effective SOA values diverged from the SOA values that we originally selected, and were slightly different across participants. For example, if in a particular trial the participant’s RT was slower than the average RT and the SOA value was supposed to be 0 (synchrony between the motor action and the visual stimulus), the visual stimulus could have not been delivered in synchrony with the motor action, but rather before, resulting in a negative SOA value. For this reason, we decided to fix latencies within a small temporal window (from -100 to $+100$ ms) and take advantage of the variability in the reaction times. Because of this strategy, we were able to deliver the stimulus as much as 300 ms before and 300 ms after the button press. Following a recent study that investigated the role of SOA distribution on perceptual synchrony (Lupo and Barnett-Cowan, 2017), we reported distributions of SOA values in the Supplemental material showing similar patterns across participants and across conditions (Figs. S1 and S2).

During adaptation, participants were exposed to a 200 ms delay between the motor action and the visual feedback (Fig. 1 left panel).

Participants fixated at the center of the screen and pressed the button at their own will without any additional prompting cue. After each press, they received a visual feedback with a 200 ms delay. To ensure participants' attention and to avoid short inter-press intervals, we randomly presented catch trials with a deviant stimulus (a dark grey circle). Participants were asked to count the number of deviant stimuli during adaptation and report this number at the end of the adaptation phase. The number of catch trials was randomly selected from a range of 30–50 by the experimenter.

At the beginning of the experiment, we ran a training session to familiarize participants with the TOJ task. The training consisted of 30 trials. At the end of each trial, we provided a feedback on participants' response to facilitate the learning process. During the training, average RTs were fixed at 250 ms. The average RTs measured at the end of the training session were used for the first baseline block.

After the training, participants performed six experimental blocks: two blocks where the visual stimulus was displayed at fixation, two blocks with the stimulus in the right periphery of the visual field, and two blocks with the stimulus in the left. At each stimulus location, participants performed a baseline block and then an adaptation block. Baseline blocks consisted of 110 TOJ trials while adaptation blocks consisted of 100 adaptation trials followed by 110 TOJ trials. The order of stimulus location was counterbalanced across participants. Baseline blocks were always performed first to avoid any effect of adaptation in this measurement. After each block, we recalculated average RTs and updated the value for the next block.

For each block, the proportion of trials where the visual stimulus was perceived after the motor action was computed for each effective SOA value and fitted with cumulative Gaussian functions for each participant (like those shown in Fig. 2). From this psychometric function, we calculated the Point of Subjective Simultaneity (PSS), the 50% point of the function that represents the perceived simultaneity

between the motor action and the visual stimulus, and the JND (Just Noticeable Difference), the standard deviation of the function that is an index of the precision in the task. Specifically, JND represents the minimum temporal delay between the motor action and the visual feedback required to produce a just noticeable difference in temporal perception. JNDs were calculated as half the distance between the stimuli that elicits 0.75 and 0.25 of responses of “vision after key-press”. Standard errors for the PSS and threshold estimates were obtained with a bootstrap procedure (Efron and Tibshirani, 1993). Trials from the training session were excluded from the analysis.

A temporal delay of 200 ms was used in the main adaptation condition (as suggested by Stetson et al., 2006, the most effective delay for motor-sensory recalibration is around 130–200 ms). After the main adaptation condition was completed by all participants, we decided to add another adaptation condition as a control in which participants were adapted to a 500 ms delay between the motor action and the visual feedback. A longer temporal delay was used in the control condition to ensure that participants perceived the asynchrony during adaptation. Procedures and data analyses for the 500 ms adaptation condition were the same as those for the 200 ms adaptation condition described above.

3. Results

Fig. 2 shows results from the main adaptation condition in which the delay between the motor action and the visual feedback was 200 ms. The figure shows data from two representative participants, one from the control group (black lines and symbols) and one from the deaf group (grey lines and symbols), for the central and peripheral conditions (left periphery, center, right periphery). The solid lines show participants' performance in the baseline block while the dashed lines show the performance after adaptation to a 200 ms delay. A PSS equal

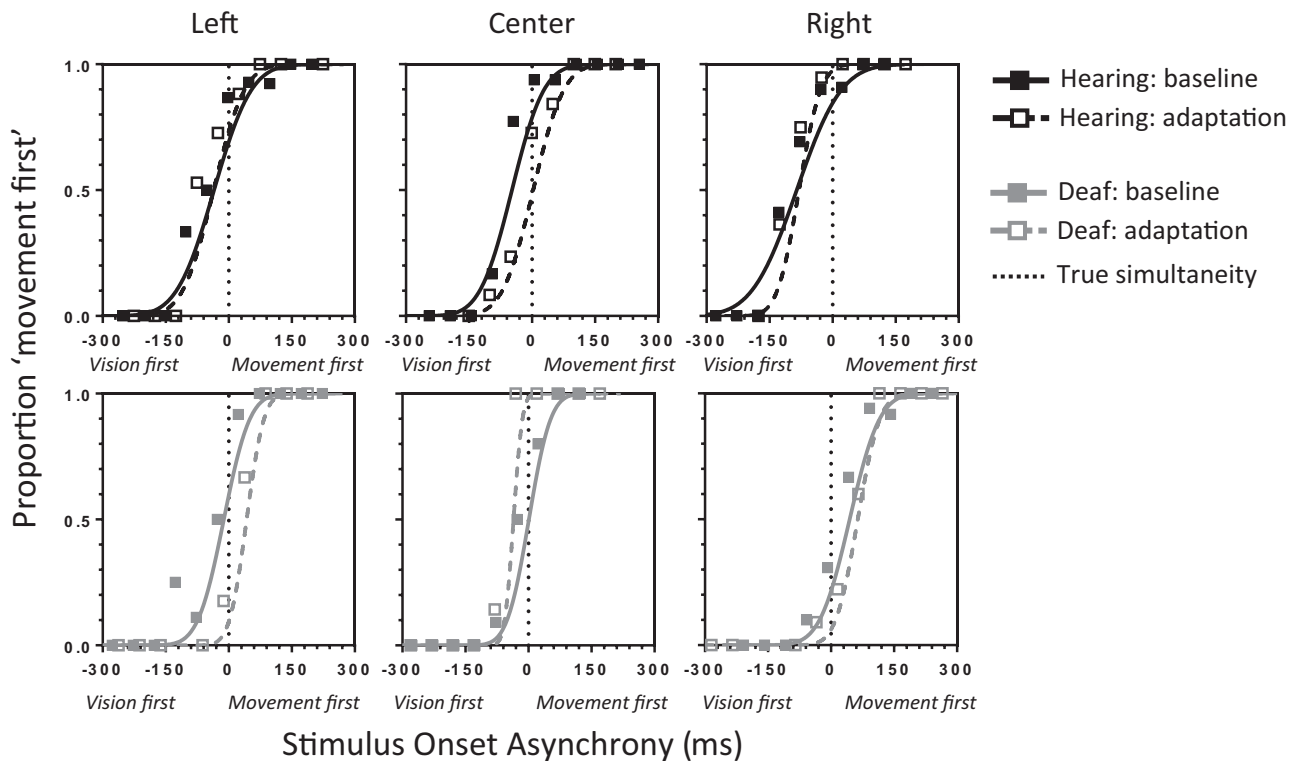


Fig. 2. Psychometric functions for the 200 ms condition from a representative hearing controls (black curves) and deaf participants (grey curves) for all the spatial conditions. The curves show the proportion of trials where the visual stimulus was perceived as occurring after the movement as a function of the motor-sensory stimulus onset asynchrony (SOA). Positive values of the SOA indicate that the motor action occurred first, while negative values that the stimulus appeared before the action. The solid curves show data for the baseline condition while dashed curves the adaptation condition. Columns show the different spatial conditions. The dotted line show the physical simultaneity between the motor action and the visual stimulus.

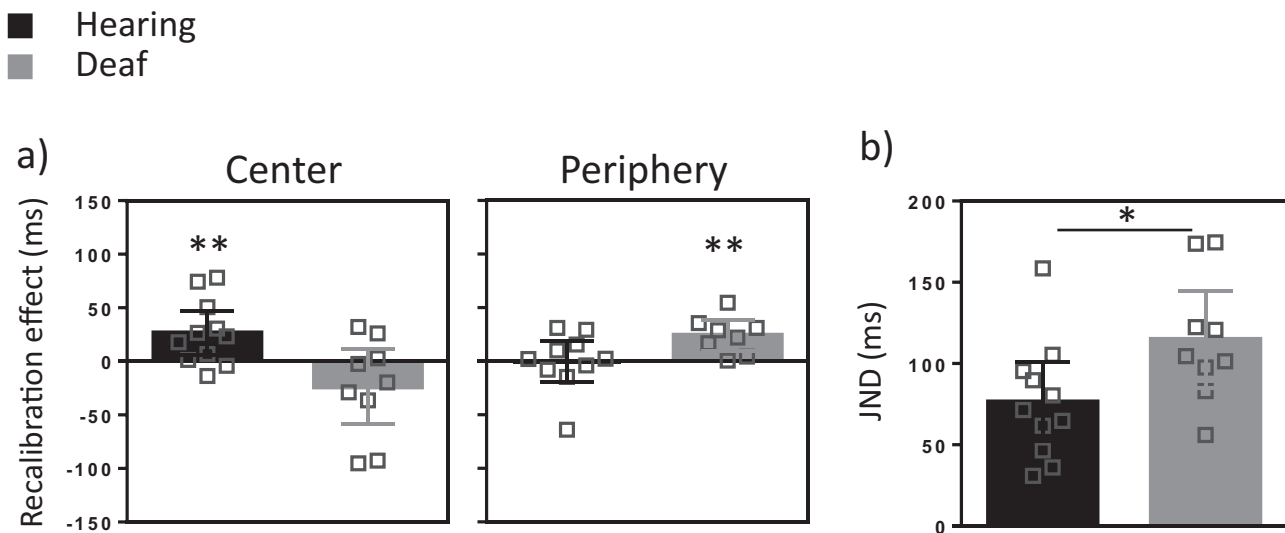


Fig. 3. a) Average recalibration effect after 200 ms delay for hearing controls (black bars) and deaf participants (grey bars); symbols represent individual data. b) Average JNDs for hearing controls (black bars) and deaf participants (grey bars) for all the spatial locations of the visual stimulus. Individual thresholds are calculated as the average JNDs across conditions.

to 0 indicates that the motor action and the visual stimulus are perceived synchronous when the two events are physically simultaneous. On the other side, a positive PSS value indicates that the motor action and the visual stimulus are perceived synchronous when the visual stimulus occurs after the button press (as during adaptation). A shift to the right (toward positive values) of the dashed curve indicates a recalibration effect. In the central condition, hearing controls showed a positive shift of the psychometric functions denoting motor-sensory recalibration. Deaf participants did not show any positive shift when the stimulus was presented in the center of the screen. Conversely, when the stimulus appeared in the peripheral visual field, deaf participants showed motor-sensory recalibration whereas hearing controls did not.

The average recalibration effect, calculated as the average difference between the PSS measured after a 200 ms delay adaptation and the PSS in the baseline block, is reported in Fig. 3a. Since we did not find any significant difference in the recalibration effect between the two peripheral conditions (2-tailed paired t -test with Bonferroni correction for multiple comparison; controls: $t_{10} = 0.06$, $P = 0.95$; deaf: $t_8 = 1.19$, $P = 0.27$) we averaged values from the “right” and “left” spatial condition. The two different colors represent the two groups of participants (black: hearing; grey: deaf) and square symbols represent individual data. Consistent with previous findings (see Stetson et al., 2006), the recalibration effect for the hearing group was $(21.8 \pm 10$ ms), significantly different than 0 when the visual stimulus was presented in the center of the visual field (one sample 2-tailed t -test with Bonferroni correction for multiple comparison, $t_{10} = 2.9$, $P = 0.01$). No significant recalibration occurred for peripheral location, with an average recalibration of 0.06 ± 8 ms for (one sample 2-tailed t -test with Bonferroni correction for multiple comparison, $t_{10} = 0.008$, $P = 0.9$). The recalibration effect for the deaf group in the periphery was 24.26 ± 6 ms, significantly different from 0 (one sample 2-tailed t -test with Bonferroni correction for multiple comparison, $t_8 = 3.93$, $P = 0.006$). We found no significant effect for the deaf group in the central visual field (one sample 2-tailed t -test with Bonferroni correction for multiple comparison, $t_8 = -1.5$, $P = 0.15$). A repeated measure ANOVA (within factor: spatial stimulus location; between factor: group) revealed a significant interaction between group and spatial stimulus location ($F_{1,1} = 10.27$, $P = 0.006$, partial $\eta^2 = 0.39$).

To ensure that the spatial location of the stimulus and/or the effect of adaptation did not affect participants’ precision in the task, for each group of participants we compared the JND before and after adaptation

for all the spatial conditions. As a repeated measure ANOVA (within factor: spatial stimulus location, experimental condition) showed no differences in both groups of participants (all P -values > 0.15) we averaged JNDs across conditions for each group. In the supplemental material Fig. S3, we reported average JNDs for all the experimental conditions. Fig. 3b shows the average JND for hearing (74.5 ± 11) and deaf participants (114.9 ± 13). JNDs for the deaf group were higher compared to those for the hearing group (two sample 2-tailed unpaired t -test, $t_{19} = -2.29$, $P = 0.03$).

In a control experiment, we measured the recalibration effect after adaptation to a 500 ms delay. Similarly, we found no significant difference in the recalibration effect between the two peripheral conditions (2-tailed paired t -test with Bonferroni correction for multiple comparison; controls: $t_{10} = 2.065$, $P = 0.07$; deaf: $t_8 = 0.69$, $P = 0.5$) and we averaged values from the “right” and “left” spatial condition. As mentioned above, we included 500 ms adaptation condition as a control to ensure that participants perceived the asynchrony during adaptation. Fig. 4a shows the recalibration effect produced by adaptation to a temporal delay of 500 ms between the motor action and the sensory feedback, for hearing controls (black bars) and deaf participants (grey bars). The recalibration effect did not change significantly across the two adaptation conditions for either of the participants groups. We ran a repeated measure ANOVA, with two within-subjects factors: temporal delay (200/500 ms) and stimulus location (center/periphery); and one between-subjects factor: group (hearing/deaf), and again we found a significant interaction between group and stimulus location ($F_{(1,1)} = 10.83$, $P = 0.005$, partial $\eta^2 = 0.4$), but no effect of delay and any other interaction (all $P > 0.14$). However, the recalibration effect in the 500 ms was not significantly different from 0 in any spatial condition and for any of the two groups (2-tailed paired t -test with Bonferroni correction for multiple comparison; all $P > 0.17$).

Also for the 500 ms condition we analyzed eventual difference in the JND, for each group and found no differences (repeated measure ANOVA, within factor: spatial stimulus location, experimental condition; all P -values > 0.15) and we averaged JNDs across conditions for each group. Fig. 4b shows average JNDs for the 500 ms adaptation condition, for hearing controls (black bars) and deaf participants (grey bars). Also in this condition, deaf participants showed higher JNDs compared to hearing participants (two sample 2-tailed unpaired t -test, $t_{19} = -2.87$, $P = 0.01$).

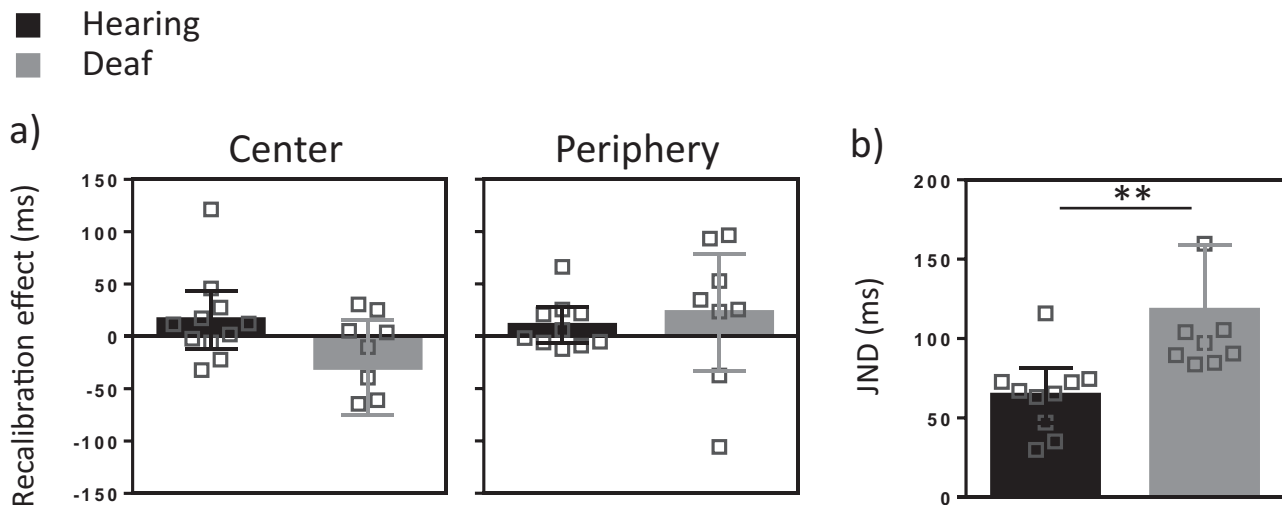


Fig. 4. a) Average recalibration effect after adaptation to 500 ms delay, for hearing controls (black bars) and deaf participants (grey bars), in the two spatial conditions (center vs. periphery). b) Average JNDs for the 500 ms condition, for the two groups of participants.

4. Discussion

In the current study, we showed that early auditory loss affects motor-sensory integration. Results revealed that after experiencing a delay in the time between the initiation of an action and the arrival of a sensory feedback presented in the central visual field, deaf individuals did not recalibrate the temporal sequence of the two events to create a more veridical causal experience. The plasticity of motor-sensory delay compensation, which is considered crucial to perceive causality between motor and sensory events, may be affected by auditory loss, compromising one's ability to compensate for atypical temporal delays. In agreement with our results, previous studies suggest that the lack of audition during the critical period might indeed challenge the normal development of temporal perception (Conway et al., 2009; Gori et al., 2012; Morein-Zamir et al., 2003; Shams et al., 2000) and that deaf individuals sometimes have a deficit in the temporal processing of visual and tactile stimuli (Bolognini et al., 2012; Heming and Brown, 2005; Kowalska and Szlag, 2006).

The lack of motor-sensory recalibration in deaf individuals depended on stimulus eccentricity. Our results showed a double dissociation in the motor-sensory recalibration effect between hearing and deaf participants. On one side, early auditory deprivation impaired temporal recalibration when stimuli were presented in the center of the visual field. On the other side, deaf individuals showed an effect of recalibration when the visual feedback appeared in the peripheral visual field. Hearing controls showed the opposite pattern of results with a significant recalibration effect only observed in the central visual field. Our results suggest that in the absence of auditory information, the mechanism of visuo-motor temporal integration might have been strengthened and made more flexible in the peripheral visual field. Moreover, this different pattern of temporal integration shaped by auditory deprivation seems to benefit peripheral events to the detriment of the central ones. While in hearing individuals the center of the visual field represents the main focus of attentional resources, deaf people might have developed a more alert peripheral vision to improve orienting responses to distal events that are usually detected by the auditory system (Parasnis and Samar, 1985). Indeed, it has been shown that, as compared to hearing controls, deaf individuals have faster reaction time for peripheral stimuli (Loke and Song, 1991) and are more distracted by peripheral than central distractors (Bavelier et al., 2000, 2001; Proksch and Bavelier, 2002). Unfortunately, in our study we did not control for eye movements and could not guarantee participants' central fixation during peripheral conditions. Future studies should assess the occurrence of eye movements during the presentation of

peripheral visual stimuli as well as differences in eye movements between deaf and hearing individuals.

Temporal precision in the motor-sensory task appears impaired in deaf individuals (i.e. deaf individuals showed higher JNDs than hearing controls), regardless of the eccentricity of the visual stimulus. This temporal impairment may result from the lack of auditory cross-sensory calibration (see Gori, 2015 for a review). In fact, the auditory modality seems to be critical for temporal perception (Morein-Zamir et al., 2003; Recanzone, 2003; Repp and Repp, 2003; Shams et al., 2000) and it dominates other senses during temporal judgment tasks in the developing child (Gori et al., 2012). Conversely, the mechanism of motor-sensory recalibration develops late in humans, given the late maturation of the temporal processing of motor and sensory events (Vercillo et al., 2014). For this reason, we believe that the absence of the auditory information during early childhood might disrupt the development of temporal processing, thus impairing sensory-motor timing. However, the lack of recalibration effect in the central visual field that we found in deaf individuals cannot be explained completely by their poor temporal precision. First, unlike the recalibration effect, temporal JNDs did not change with stimulus location. Secondly, the recalibration effect disappeared after increasing the delay between the motor action and the sensory feedback during the adaptation phase. This latter result makes the widening of the motor-sensory temporal binding window an unlikely cause of the lack of recalibration for centrally presented stimuli in deaf individuals. We believe that the double dissociation we found between hearing and deaf individuals might partially arise from temporal distortions induced by attentional differences between the two populations. As suggested by a previous study, the ability to adjust temporal judgments depending on recent sensory history is subject to top-down attentional modulation (Heron et al., 2010). Specifically, diverting attention toward the temporal structure of asynchronous sensory stimuli maximize the effect of temporal recalibration by increasing the perceived salience of the temporal events. Therefore, the asymmetry in allocating visual attentional resources between deaf and hearing people might partially account for the spatial dependence in the temporal recalibration effect we observed.

An alternative, but not mutually exclusive explanation for these results is that dorsal visual functions might be especially susceptible to auditory deprivation. This idea is supported by observations that deaf individuals show an enhancement of visual functions such as motion processing and peripheral vision (Armstrong et al., 2002; Bosworth and Dobkins, 2002; Brozinsky and Bavelier, 2004) that are primarily processed by the magnocellular pathway (Alain et al., 2001; Livingstone and Hubel, 2009; Parasnis and Samar, 1985; Proksch and Bavelier,

2002). Additionally, previous findings supported the idea that the magnocellular pathway might be involved in the temporal dynamics of visual perception and that those dynamics are modulated by the stimulus eccentricity (Aedo-Jury and Pins, 2008; Johnston et al., 2006; Ross et al., 2001).

Future studies should further investigate the effect of spatial attention on motor-sensory recalibration in deaf and hearing individuals and the contribution of the magnocellular pathway to visual and visuomotor temporal processing.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.neuropsychologia.2017.06.002>.

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