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Spatial modulation of motor-sensory recalibration in early deaf individuals

Tiziana Vercillo*, Fang Jiang

University of Nevada, Reno, United States

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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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* Corresponding author.
E-mail address: tiz.vercillo@gmail.com (T. Vercillo).

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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 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.

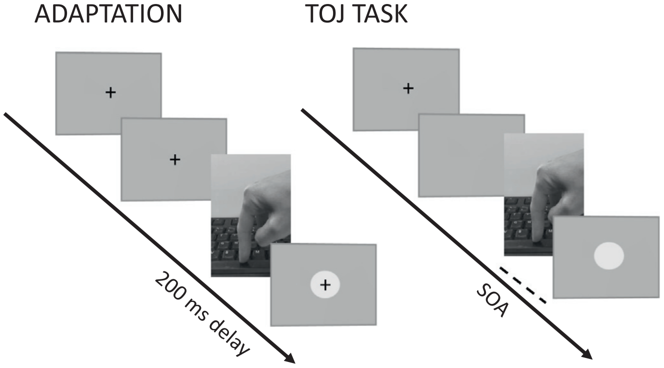

Fig. 1. Methods and procedures. Adaptation (left panel) and TOJ task trials (right panel). In the adaptation trials participants pressed a button and received a visual feedback after 200 or 500 ms. In the TOJ trials participants pressed a button after the fixation cross disappeared and judged whether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

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 be 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).