



Auditory motion in the sighted and blind: Early visual deprivation triggers a large-scale imbalance between auditory and “visual” brain regions

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ABSTRACT

How early blindness reorganizes the brain circuitry that supports auditory motion processing remains controversial. We used fMRI to characterize brain responses to in-depth, laterally moving, and static sounds in early blind and sighted individuals. Whole-brain univariate analyses revealed that the right posterior middle temporal gyrus and superior occipital gyrus selectively responded to both in-depth and laterally moving sounds only in the blind. These regions overlapped with regions selective for visual motion (hMT+/V5 and V3A) that were independently localized in the sighted. In the early blind, the right planum temporale showed enhanced functional connectivity with right occipito-temporal regions during auditory motion processing and a concomitant reduced functional connectivity with parietal and frontal regions. Whole-brain searchlight multivariate analyses demonstrated higher auditory motion decoding in the right posterior middle temporal gyrus in the blind compared to the sighted, while decoding accuracy was enhanced in the auditory cortex bilaterally in the sighted compared to the blind. Analyses targeting individually defined visual area hMT+/V5 however indicated that auditory motion information could be reliably decoded within this area even in the sighted group. Taken together, the present findings demonstrate that early visual deprivation triggers a large-scale imbalance between auditory and “visual” brain regions that typically support the processing of motion information.

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1. Introduction

Area hMT+/V5 is classically considered to support motion processing based on visual inputs only (Watson et al., 1993; Tootell et al., 1995). However, previous studies have shown that this region selectively responds to auditory (Poirier et al., 2006; Bedny et al., 2010; Wolbers et al., 2011; Strnad et al., 2013; Jiang et al., 2014) and tactile motion (Ricciardi et al., 2007) in individuals with early-onset blindness. Whether this non-visual recruitment of hMT+/V5 is specific to the blind due to crossmodal plasticity or could also be observed in sighted individuals remains currently debated. The answer to this question is crucial to unravel the role of developmental vision in shaping the modality tuning of area hMT+/V5 for motion processing. Some studies have shown that

auditory (Warren et al., 2002; Poirier et al., 2005; Alink et al., 2008; Strnad et al., 2013) and tactile (Hagen et al., 2002; Blake et al., 2004; Beauchamp et al., 2007; Ricciardi et al., 2007; Summers et al., 2009; van Kemenade et al., 2014) motion also involves part of hMT+/V5 in sighted individuals. Based on these findings, it was suggested that part of hMT+/V5 may act as a supramodal region for motion computation and develop independently of visual experience (Pascual-Leone and Hamilton, 2001; Ricciardi et al., 2007; Ricciardi and Pietrini, 2011). Other studies however failed to identify a crossmodal involvement of area hMT+/V5 in non-visual motion processing in the sighted (Lewis et al., 2000; Bremmer et al., 2001; Saenz et al., 2008; Bedny et al., 2010; Alink et al., 2011; Jiang et al., 2014, 2015).

Inconsistencies across studies may stem from a variety of parameters such as the sensory modality investigated (audition vs. touch), the specific features of the stimuli, and the experimental paradigm itself (e.g. block vs. event-related design). The choice of analytical steps, such as the use of univariate vs. multivariate analyses and the investigation of whole-brain vs. region-of-interest (ROI) analytic space, may also lead to different conclusions. For example, Bedny et al. (2010) found auditory motion responses in hMT+/V5 in congenitally blind but not in sighted

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subjects when using a univariate approach. However, multivariate pattern analyses conducted on the same dataset revealed that auditory motion could be decoded significantly above chance level in this area in both groups (Strnad et al., 2013).

While the latter study and previous work (e.g. Blake et al., 2004; Wolbers et al., 2011; Jiang et al., 2014) focused on area hMT +/V5 as a region of interest, a whole-brain analytic approach is necessary to ascertain that auditory motion processing specifically maps in this area. The presence of auditory motion information in occipito-temporal regions outside of the typical visual-motion network would challenge the idea of a topological selectivity for auditory motion processing in the occipito-temporal cortex. Indeed, some studies suggested that response preference to auditory motion is widespread across the occipital cortex of blind individuals rather than localized in specific regions (Poirier et al., 2006; Lewald and Getzmann, 2013). Importantly, whole-brain imaging also allows investigating how the crossmodal recruitment of the occipital cortex during auditory motion processing in the early blind affects brain circuits typically dedicated to this input and function *outside* of the occipital cortex. Some evidence points to the presence of plastic changes within the cortices subtending the preserved non-visual modalities in early blind subjects. For instance, blind show enlarged tonotopic maps (Sterr et al., 1998a,b; Elbert et al., 2002) and enhanced voice selective activity (Gougoux et al., 2009) in temporal regions. In contrast, occipital crossmodal recruitment in the blind during auditory, haptic and even language processing can be associated with a *reduced* responsiveness of non-visual areas that typically support these inputs/functions (Cohen et al., 1997; Amedi et al., 2004; Collignon et al., 2009a; Stevens and Weaver, 2009; Jiang et al., 2014; Hölig et al., 2014; Bedny et al., 2015). Hence, whether intramodal plasticity in the cortices that support the preserved non-visual modalities in the early blind emerges as increases or decreases in responsiveness remains debated.

The main goals of the present study were twofold. First, we aimed at clarifying whether crossmodal responses to non-visual motion are specific to the early blind and whether these responses are confined to brain regions that typically support visual motion processing in sighted individuals. Second, we aimed at characterizing how early blindness affects the responsiveness and the connectivity of brain regions outside of the deprived “visual” cortex during auditory motion processing.

For this purpose, we investigated auditory motion selectivity in early blind and sighted subjects using both univariate and multivariate whole-brain analyses. Analyses within individually-defined regions of interest were additionally carried out in the sighted in order to further test the presence of auditory motion information in visual area hMT +/V5. We used 2 types of auditory motion trajectories, in-depth and lateral motion, since there is evidence that distinct neural populations respond to these motion trajectories both in audition (Stumpf et al., 1992; Toronchuk et al., 1992) and vision (radial and translational motion) (Saito et al., 1986; Tanaka and Saito, 1989; Morrone et al., 2000).

2. Materials and methods

2.1. Participants

Sixteen early blind and 15 sighted subjects (matched to the blind group for age, gender, handedness, educational level and musical experience) participated in this study. Blind participants were either totally blind or had only rudimentary sensitivity for brightness differences and no pattern vision. In all cases, blindness was attributed to peripheral deficits with no neurological impairment (Supplementary Table 1). All the procedures were approved by the research ethic and scientific boards of the “Centre for Interdisciplinary Research in Rehabilitation of Greater Montreal (CRIR)” and the “Quebec Bio-Imaging Network (QBIN)”. Experiments were undertaken with the consent of each participant.

Of the 31 participants recruited for the study, 4 participants in total were judged as outliers based on their target detection performance

(hits – false alarms) as it was lower than the average of the subjects in the same group by more than 2 standard deviations. We decided to exclude these participants from the analyses since we could not guarantee that they understood the task and paid sufficient attention to the stimuli. Three participants (1 blind, 2 sighted) were excluded from the analyses in the auditory experiment, and two participants were excluded from the analyses in the visual experiment. A total of 28 participants were therefore included in the analyses in the auditory experiment: 15 early blind participants (5 females, range = 23 to 62 years, mean \pm SD = 44.8 ± 12.6 years) and 13 sighted participants (4 females, range = 22 to 56 years, mean \pm SD = 41.6 ± 10.7 years). A total of 13 sighted participants were included in the analyses in the visual experiment (4 females, range 22 to 56 years, mean \pm SD = 40.6 ± 11 years).

2.2. Task and general experimental design

Participants in both groups were scanned in one auditory run of 390 brain volumes (TR = 2200 ms) and were blindfolded throughout the fMRI acquisition. Sighted participants were additionally scanned in one visual run of 410 brain volumes (TR = 2200 ms) on a separate day. In order to familiarize the participants to the fMRI environment before the fMRI acquisition, participants underwent a training session in a mock scanner. During that session participants practiced the tasks in the bore of the simulator while listening to recorded scanner sounds. In the scanner, auditory stimuli were delivered by means of circumaural, fMRI-compatible headphones (Mr Confon, Magdeburg, Germany). Visual stimuli were projected on a screen at the back of the scanner and visualized through a mirror (127 mm \times 102 mm) that was mounted at a distance of approximately 12 cm from the eyes of the participants.

2.2.1. Auditory experiment

Auditory stimuli consisted of pink noise sounds from 3 different categories: (1) in-depth motion, (2) lateral motion, and (3) stationary sounds (no motion) (Fig. 1A). In line with other neuroimaging studies of auditory motion processing (Griffiths and Green, 1999; Warren et al., 2002; Saenz et al., 2008; Alink et al., 2011; Saldern and Noppeney, 2013), we used the broadband pink noise sounds (44.1 Hz sampling rate) as they match the spectrum of frequencies most commonly heard in the everyday world without referring to a specific object. Additionally, pink noise minimizes the possibility that a putative occipital response in sighted subjects is a consequence of visual imagery. Moreover, pilot experiments in the scanner revealed that pink noises provided a more vivid sensation of motion relative to pure tones. Sounds lasted either 1 s (standard) or 1.8 s (target) in duration. In the in-depth motion condition, sounds (mono) either rose or decreased exponentially in intensity (from 10% to maximal intensity and from maximal intensity to 10% intensity) creating the vivid perception of a sound moving toward or away from the listener. In the lateral motion condition, the same sounds were presented separately to the left and to the right ear (stereo) with intensity increasing in one ear while decreasing simultaneously in the other ear, creating the vivid perception of a sound moving from one ear to the other in the azimuth. All participants reported a strong sensation of motion. In the static condition, 1 s and 1.8 s pink noise sounds (mono) of constant intensity were presented. A 25 ms ascending/descending ramp was applied at the beginning/end of the static sounds. In order to ensure equal global acoustic energy across conditions despite the application of a ramp in the static condition, the static sounds were normalized based on the mean Root Mean Square (RMS) of the sounds from the motion conditions. Examples of the auditory stimuli used in the present study are provided in the Supplementary Material.

A block design was implemented in a single run consisting of 30 consecutive blocks (10 repetitions/category) separated by rest periods of 9 s. The three categories repeated consecutively with no randomization (i.e. lateral–in-depth–static). Each block included 18 consecutive auditory stimuli (no ISI) (Fig. 1A). Stimuli within the motion blocks always

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