

The role of auditory cortex in the spatial ventriloquism aftereffect



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ABSTRACT

Cross-modal recalibration allows the brain to maintain coherent sensory representations of the world. Using functional magnetic resonance imaging (fMRI), the present study aimed at identifying the neural mechanisms underlying recalibration in an audiovisual ventriloquism aftereffect paradigm. Participants performed a unimodal sound localization task, before and after they were exposed to adaptation blocks, in which sounds were paired with spatially disparate visual stimuli offset by 14° to the right. Behavioral results showed a significant rightward shift in sound localization following adaptation, indicating a ventriloquism aftereffect. Regarding fMRI results, left and right planum temporale (IPT/rPT) were found to respond more to contralateral sounds than to central sounds at pretest. Contrasting posttest with pretest blocks revealed significantly enhanced fMRI-signals in space-sensitive IPT after adaptation, matching the behavioral rightward shift in sound localization. Moreover, a region-of-interest analysis in IPT/rPT revealed that the IPT activity correlated positively with the localization shift for right-side sounds, whereas rPT activity correlated negatively with the localization shift for left-side and central sounds. Finally, using functional connectivity analysis, we observed enhanced coupling of the IPT with left and right inferior parietal areas as well as left motor regions following adaptation and a decoupling of IPT/rPT with contralateral auditory cortex, which scaled with participants' degree of adaptation. Together, the fMRI results suggest that cross-modal spatial recalibration is accomplished by an adjustment of unisensory representations in low-level auditory cortex. Such persistent adjustments of low-level sensory representations seem to be mediated by the interplay with higher-level spatial representations in parietal cortex.

1. Introduction

Our senses serve as signal detectors for the brain, in order to obtain adequate estimates of the properties of the physical world. However, these estimates are typically corrupted by noise, leading to perceptual uncertainties (e.g., about the location of an object in space). This issue can be resolved by multisensory integration: By combining multiple signals from different sensory modalities, the signal-to-noise ratio can be increased and thus uncertainty decreased (Alais and Burr, 2004; Atkins et al., 2003; Ernst and Banks, 2002). Nevertheless, the brain needs a certain degree of flexibility to cope with both external changes (e.g., echoes, loudness and luminance changes) and internal changes (e.g., age-related changes) that might affect the correspondence between different sensory representations. Therefore, modality-specific representations of the physical world are constantly kept in alignment through cross-modal

recalibration. This capability has been demonstrated in a number of different species (Bergan et al., 2005; Kopco et al., 2009; Recanzone, 1998; Wallace and Stein, 2007) and at various timescales, ranging from single-trial learning (Wozny and Shams, 2011) over short-term exposure to audiovisual discrepancies for a few minutes (Bruns and Röder, 2015) to adjustments observed after days to weeks of training with altered cross-modal spatial correspondences (Bergan et al., 2005; Zwiers et al., 2003). Together, multisensory integration and cross-modal recalibration enable the brain to navigate through a complex world while flexibly adapting to new conditions.

The behavioral consequences of multisensory integration and cross-modal recalibration of spatial cues have been studied extensively by investigating the ventriloquism effect (VE) and ventriloquism aftereffect (VAE) (for a review, see Chen and Vroomen, 2013). In both effects, the localization of auditory stimuli is biased toward spatially disparate visual

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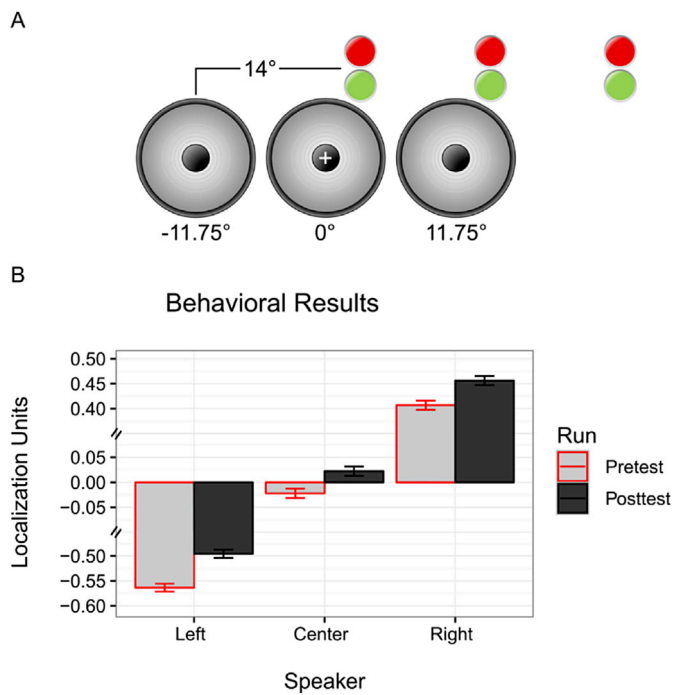


Fig. 1. Experimental setup and behavioral results. A: Sketch of the stimulation array used inside MRI scanner. The three speakers and six LEDs were mounted in a foam pad that was placed on the top of the scanner bore. Speakers were hidden behind a cloth and only the LEDs were visible to the participants. A cross on the cloth marked the fixation point. B: Behavioral results. Negative localization values indicate left-side localization; positive values indicate right-side localization. Error bars depict the standard error of the mean.

stimuli. In the VE, participants' sound localization is attracted toward a *simultaneously* presented visual stimulus (Alais and Burr, 2004; Bertelson and Aschersleben, 1998; Howard and Templeton, 1966; Jack and Thurlow, 1973; Jackson, 1953; Thomas, 1941; Wallace et al., 2004; Welch and Warren, 1980; Witkin et al., 1952). In the VAE, the localization bias is caused by exposing participants to several spatially disparate audiovisual stimuli with a constant audiovisual spatial offset. Following such exposure, participants exhibit a shift in *unimodal* sound localization in the direction that matches the previously experienced offset (Canon, 1971, 1970; Frissen et al., 2005; Held, 1955; Kalil and Freedman, 1967; Kopco et al., 2009; Lewald, 2002; Recanzone, 1998).

Both the VAE and VE indicate that visual stimuli affect the spatial processing of auditory stimuli, yet both presumably depend on mechanisms that can be dissociated in terms of time and their underlying neural processes: Whereas the VE reflects two modalities influencing each other's processing in response to a stimulus (i.e., multisensory interactions), the VAE is an indicator of a learning process, in which unisensory spatial representations are suspected to be changed by cross-modal input (Bruns et al., 2011b; Pages and Groh, 2013).

This conceptual difference is reflected in neurophysiological findings: The VE has been associated with a modulation of event-related potentials (ERP) around 260 ms post-stimulus, which followed the subjective percept of the participants (Bonath et al., 2007; Bruns and Röder, 2010). By contrast, the VAE was related to a modulation of an earlier ERP (N1) in the time window between 70 and 130 ms post-stimulus (Bruns et al., 2011a). These findings suggest distinct processes underlying the VE and VAE. Bruns and colleagues hypothesized that the relatively early ERP modulation associated with the VAE suggests an involvement of low-level auditory cortical processing.

Functional magnetic resonance imaging (fMRI) studies of the VE provided evidence that an asymmetry between the activity in left- and right-hemispheric auditory areas might represent a mechanism by which sound azimuth is coded, with auditory areas being more sensitive to contralateral than ipsilateral sounds (Bonath et al., 2014, 2007; Callan

et al., 2015). Importantly, in the VE situation it has been shown that the spatially disparate visual stimulus influences this asymmetry by attenuating auditory cortex activity in one hemisphere, such that the asymmetry corresponded with the perceived sound location. In particular, Bonath et al. (2007, 2014) found that for central sounds fMRI-signals in the planum temporale (PT) were reduced by a co-occurring peripheral visual stimulus ipsilateral to the side of visual stimulation. With attenuated ipsilateral PT activity, contralateral PT activity may have exerted a relatively stronger influence on the resulting auditory percept, which corresponded with the perceptual shift of the auditory stimulus toward the simultaneously presented visual stimulus. It is currently unknown how these effects in the VE situation are linked to changes of auditory spatial representations underlying the VAE.

In the present study, we aimed at identifying the neural underpinnings of cross-modal recalibration in the VAE in humans using fMRI. Participants had to localize unimodal auditory stimuli before and after an audiovisual adaptation phase with spatially incongruent audiovisual stimuli. It is well-established that localization is shifted in the same direction as the visual stimuli are displaced relative to the auditory stimuli (for reviews, see Chen and Vroomen, 2013; Welch and Warren, 1980). In the present study, visual stimuli were always displaced to the right of the auditory stimuli. Accordingly, we expected a rightward bias in sound localization during the posttest. This bias was hypothesized to be reflected in a stronger asymmetric activity of left- and right-hemispheric auditory areas. Specifically, a rightward shift in spatial hearing should result either in a reduction of activity in right-hemispheric auditory areas, in an enhancement of activity in left-hemispheric auditory areas, or in a mixture of both.

Furthermore, we hypothesized to observe a modulation specifically in low-level cortical auditory areas. Previous studies on the VAE have reported mixed results as to whether the typical shift in sound localization occurs for sound frequencies other than the one used during audiovisual adaptation (Frissen et al., 2005, 2003) or not (Lewald, 2002; Recanzone, 1998). Recently, a study by Bruns and Röder (2015) reconciled these seemingly contradictory findings by showing that recalibration operates

Table 1

Local maxima for the comparisons of peripheral sounds vs. central sounds. Threshold $p \leq 0.001$ (uncorrected), $k \geq 10$; thresholding in accord with previous studies (e.g., Bonath et al., 2007, 2014).

Contrast/Region	Cluster Size	t Value	p Value	MNI Coordinates		
				x	y	z
<i>Left > Central Sounds</i>						
R Planum Temporale	22	3.67	<0.001	46	-30	12
R Middle Temporal Gyrus	34	3.86	<0.0001	44	-70	14
R Insula	12	3.79	<0.0001	46	-6	-4
R Precentral Gyrus	16	3.64	<0.001	30	-6	34
L Postcentral Gyrus	41	4.25	<0.0001	-38	-20	42
R Inferior Occipital Gyrus	25	3.91	<0.0001	38	-74	-4
<i>Right > Central Sounds</i>						
L Planum Temporale	19	3.73	<0.001	-46	-32	6
L Posterior Superior Temporal Sulcus	12	3.77	<0.0001	-50	-52	10
R Superior Temporal Gyrus	24	4.25	<0.0001	46	-30	8
L Supramarginal Gyrus	21	3.85	<0.0001	-64	-46	24
R Inferior Frontal Gyrus	30	4.12	<0.0001	52	40	-2
L Superior Frontal Gyrus	27	3.71	<0.001	-8	12	70
R Anterior Insula	17	3.78	<0.001	24	28	10
R Anterior Insula	18	4.0	<0.0001	32	12	16
R Insula	12	3.65	<0.001	26	-16	24
L Calcarine Sulcus	225	4.04	<0.0001	-18	-70	16
L Lingual Gyrus	38	4.34	<0.0001	-24	-54	-6
L Cerebellum	19	4.0	<0.0001	-16	-40	-30

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