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Emotion modulates activity in the 'what' but not 'where' auditory processing pathway

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ABSTRACT

Auditory cortices can be separated into dissociable processing pathways similar to those observed in the visual domain. Emotional stimuli elicit enhanced neural activation within sensory cortices when compared to neutral stimuli. This effect is particularly notable in the ventral visual stream. Little is known, however, about how emotion interacts with dorsal processing streams, and essentially nothing is known about the impact of emotion on auditory stimulus localization. In the current study, we used fMRI in concert with individualized auditory virtual environments to investigate the effect of emotion during an auditory stimulus localization task. Surprisingly, participants were significantly slower to localize emotional relative to neutral sounds. A separate localizer scan was performed to isolate neural regions sensitive to stimulus location independent of emotion. When applied to the main experimental task, a significant main effect of location, but not emotion, was found in this ROI. A whole-brain analysis of the data revealed that posterior-medial regions of auditory cortex were modulated by sound location; however, additional anterior-lateral areas of auditory cortex demonstrated enhanced neural activity to emotional compared to neutral stimuli. The latter region resembled areas described in dual pathway models of auditory processing as the 'what' processing stream, prompting a follow-up task to generate an identity-sensitive ROI (the 'what' pathway) independent of location and emotion. Within this region, significant main effects of location and emotion were identified, as well as a significant interaction. These results suggest that emotion modulates activity in the 'what,' but not the 'where,' auditory processing pathway.

Introduction

The ability to interact effectively in an environment requires the accurate recognition and localization of surrounding objects and the capacity to prioritize these objects for behavior. One characteristic known to modulate this is the emotional nature of the stimuli (Adolphs, 2008; Lang and Davis, 2006; Pessoa and Ungerleider, 2004; Vuilleumier, 2005). Considerable evidence suggests that emotional visual stimuli gain rapid and often preferential access to the brain's processing resources. At the behavioral level, emotional visual stimuli are detected faster than neutral stimuli (Graves et al., 1981), are more likely to enter into awareness (Amting et al., 2010; Mitchell and Greening, 2012) and can cause significantly greater influence on task-relevant behaviors (Mitchell et al., 2008; Vuilleumier and Driver, 2007). These effects are thought to be conferred by enhanced sensory processing; thus, in the visual domain, emotional stimuli elicit greater activity than similar neutral stimuli within areas of the visual cortex (Morris et al., 1998; Vuilleumier and Driver, 2007). Just like in the visual domain, studies of auditory processing have demonstrated that the analysis of emotional auditory stimuli occurs rapidly (Goydke et al., 2004; Sauter and Eimer, 2009) and is associated with enhanced activity in sensory (i.e., auditory) cortices (Fecteau et al., 2007; Viinikainen et al., 2012). Despite some emerging work concerning the influence of emotion on the representation of auditory objects, essentially nothing is known about how emotion influences auditory stimulus localization.

There is accumulating evidence that auditory processing occurs within two separate cortical streams (Ahveninen et al., 2006; Alain et al., 2001; Barrett and Hall, 2006; Clarke et al., 2002; Lomber and Malhotra, 2008; Mathiak et al., 2007; Rauschecker, 2012; Rauschecker and Tian, 2000) that may share some similarities with the well-established dorsal and ventral processing streams of the visual system (Haxby et al., 1991; Milner and Goodale, 1993). Spatial cues used for localization are processed primarily in posterior-medial regions of the auditory cortex (Arnott et al., 2004; Bushara et al., 1999; Lomber

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et al., 2007) including the posterior superior temporal gyrus (STG) and the transverse temporal gyrus. In contrast, sound identity cues, including pitch and language features, are processed in anterior-lateral regions of auditory cortex along the anterior STG (Altmann et al., 2008; Warren and Griffiths, 2003). However, despite continuous advances toward understanding the neural mechanisms underlying both enhanced representation of emotion within sensory cortices and our representations of auditory space, the impact of emotion during auditory localization remains unknown. Specifically, it remains unclear whether evidence of enhanced activity observed in prior studies to emotional relative to neutral, non-spatialized auditory stimuli (Fecteau et al., 2007; Viinikainen et al., 2012) would also translate into enhanced auditory stimulus localization and enhanced activity in areas of auditory cortex sensitive to object location.

The potential of auditory virtual environments (AVEs) as a method to examine neural pathways associated with auditory stimulus localization has been described in previous studies (Bohil et al., 2011; Fujiki et al., 2002; Langendijk and Bronkhorst, 2000; Wightman and Kistler, 1989a,b). Previous neuroimaging studies investigating auditory localization have created AVEs using generic head-related transfer functions (HRTFs) generated from measurements of mannequins or a prototypical head shape (Ahveninen et al., 2006; Bushara et al., 1999; Krumbholz et al., 2009). These, however, fail to accommodate individual differences in head size and pinnae structure that alters sound as it enters the ear canals, resulting in imperfect perception of spatialized sounds (Middlebrooks et al., 2000; Wenzel et al., 1993). Such variables have been shown to influence reactions to and ratings of emotional auditory stimuli (Vastfjall, 2003). Despite its potential importance, we are not aware of any neuroimaging studies utilizing unique AVEs created from individualized HRTFs.

In the present study, we investigated whether the emotion-related enhancements observed in the visual domain at the behavioral (Amting et al., 2010; Graves et al., 1981) and neural levels (Morris et al., 1998; Vuilleumier and Driver, 2007) would also be found during auditory stimulus localization. We hypothesized that positive and negative auditory cues would receive prioritized processing relative to neutral stimuli. We predicted that this prioritization would be reflected by increased accuracy, decreased reaction time, and increased neural activity within the posterior-medial 'where' pathways of auditory processing during the localization of emotional compared to neutral sounds. However, as will be described below, the data did not fit this prediction, and instead we found slower response times for emotional auditory stimuli compared to neutral ones. Additionally, consistent with previous studies involving non-spatialized emotional auditory cues (Fecteau et al., 2007), we predicted that anterior-lateral areas of auditory cortex (i.e., the putative 'what' processing pathway) would also show enhanced activity for emotional compared to neutral sounds. Furthermore, in light of lesion data suggesting that the what/where pathways are doubly dissociable (Lomber and Malhotra, 2008), we predicted that anterior-lateral regions of auditory cortex would not be modulated by sound location.

To test these predictions, we created AVEs by generating sounds based on each individual's unique HRTFs. While undergoing fMRI, participants located or identified a series of auditory stimuli presented in these virtual environments. The current study consisted of three related tasks. Task 1 was designed as a functional localizer, aimed at independently identifying ROIs specifically related to sound localization while controlling for object identity. Task 2 was conducted in the same scanning session as Task 1. In this task, participants were required to identify the source locations of positive, negative and neutral sounds presented within a virtual auditory environment. This task served two purposes. First, the 'where' ROI derived from the Task 1 localizer was applied to the data in Task 2 and interrogated to determine potential effects of emotion on location-sensitive areas of auditory cortex. Second, Task 2 allowed us to perform an exploratory whole-brain analysis examining the effects of, and interactions between, emotion and location during auditory stimulus localization. Contrary to expectations, the results showed that emotion did not modulate regions of auditory cortex sensitive to location. However, a distinct region of anterior lateral temporal cortex identified in this exploratory study was modulated by emotion. This area strongly resembled regions associated with sound-identity processing in previous studies (i.e., the putative 'what' pathway; Barrett and Hall, 2006; Warren and Griffiths, 2003). To help determine the degree to which this area could be characterized as part of the 'what' auditory pathway, a follow-up localizer was conducted in a subset of participants in a subsequent session. This functional 'what' pathway localizer identified ROIs that were modulated by sound identity while location and emotion were held constant. The resulting ROI was extracted and applied to the data generated from Task 2, allowing us to independently test the effects of emotion on the resulting 'what' pathway.

Methods

Subjects

Eighteen healthy human subjects, (9 male, 9 female) with a mean age of 23.56 (range 19–35, SD 4.51), completed Tasks 1 and 2. All subjects granted informed consent and were in good mental health, as assessed by a Structured Clinical Interview for DSM-IV (*Diagnostic and Statistical Manual of Mental Disorders*, 4th Edition). All subjects had normal hearing, normal or corrected-to-normal vision and were fluent English speakers. Ten of these subjects (5 male, 5 female), with a mean age of 24.3 (range 19–35, SD 5.42), returned to complete Task 3. All participants were reimbursed for their time at the end of the study. All experiments were approved by the Health Science Research Ethics Board at the University of Western Ontario.

Stimuli and apparatus

Stimuli

Twelve sounds were chosen from the *International Affective Digitized Sound* (IADS) stimuli set that were of a neutral, negative or positive affective nature as defined by standardized ratings (Bradley and Lang, 1999). Each stimulus category contained two single-source non-verbal human vocalizations, one multi-source non-verbal human vocalization, and one non-human sound. All sounds were presented with a variable duration of 2000–3000 ms (balanced across stimuli; variable durations were used to facilitate deconvolution of the BOLD signal). Importantly, all stimuli were matched for their onset amplitude and root mean-square amplitude, which ensures that the power and energy were consistent. Positive and negative stimuli were balanced for arousal ratings (mean positive = 6.58, mean negative = 6.92) and valence levels (positive = 7.56, negative = 2.36, absolute neutral = 5). In addition, to create a novel unrecognizable noise for Task 1, the 12 task sounds of Task 2 were merged into a single audio file, segmented into <3 ms fragments, and subsequently scrambled, reconstituted and cropped to a duration of 15,000 ms. This sound maintains the average long-term power spectrum of the stimulus set of Task 2, while remaining unidentifiable.

In order to localize neural regions that were sensitive to stimulus identity, a novel set of nine neutral sounds were chosen from the IADS (mean valence 5.28, SD 0.98) for use in Task 3. These nine sounds were human, animal, or machine in origin (3 of each). An additional three segments of scrambled noise (identical to that used in Task 1) comprised a fourth sound class. All sounds in this set were 5000 ms in duration, and were matched for onset amplitude and root-square mean amplitude.

Auditory virtual environment

Throughout the experiment, all sounds were presented within an auditory virtual environment through Sensimetric MRI-Compatible