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Cortical networks for auditory detection with and without informational masking: Task effects and implications for conscious perception

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ABSTRACT

Ambiguous and masked stimuli have been used to study conscious perception by comparing neural activity during different percepts of identical physical stimuli. One limitation of this approach is that it typically requires a reporting task that may engage neural processes beyond those required for conscious perception. Here, we explored potential fMRI correlates of auditory conscious perception with and without overt report. In experiment 1, regular tone patterns were presented as targets under informational masking, and participants reported their percepts on each trial. In experiment 2, regular tone patterns were presented without masking, while the uninformed participants (i) passively fixated, (ii) performed an orthogonal visual task, and (iii) reported trial-wise the presence of the auditory pattern as in experiment 1 (in fixed order). Under informational masking, target-pattern detection was associated with activity in auditory cortex, superior temporal sulcus, and a distributed fronto-parieto-insular network. Unmasked and task-irrelevant tone patterns elicited activity that overlapped with the network observed under informational masking in auditory cortex, the right superior temporal sulcus, and the ventral precentral sulcus in an ROI analysis. We therefore consider these structures candidate regions for a neural substrate of auditory conscious perception. In contrast, activity in the intraparietal sulcus, insula, and dorsal precentral sulcus were only observed for unmasked tone patterns when they were task relevant. These areas therefore appear more closely related to task performance or top-down attention rather than auditory conscious perception, *per se*.

Introduction

The neural underpinnings of conscious perception are critical for understanding our experience of the world (Block, 2007; Crick and Koch, 1998; Dehaene and Changeux, 2011). An important step towards studying the neural basis of conscious perception has been the use of ambiguous, bistable stimuli (Leopold and Logothetis, 1996), i.e, identical physical stimuli that can be perceived in different ways. Based on the assumption that sensory processes are coupled mainly to physical stimulus properties, neural processes that differ between varying percepts have been deemed strong candidates for neural correlates of conscious perception. This approach revealed a covariation of perception and neural activation patterns in several secondary visual areas (Blake and Logothetis, 2002). In audition, studies have identified a negative-going[1] component of the evoked response in auditory cortex that covaries with the conscious perception of a masked tone pattern, but not with the physical presence of individual tones (Gutschalk et al., 2008; Snyder et al., 2015).

Functional imaging studies have observed activity in a distributed, fronto-parietal network during conscious visual detection (Dehaene and Changeux, 2011); this fronto-parietal network has been associated with a global workspace whose activation is thought to be necessary for conscious perception. To correctly dissociate trials with different percepts during functional neuroimaging, participants are usually required to report their percepts on a trial-by-trial basis. By themselves, such reporting tasks are associated with activation in a general task-related network in fMRI (Fox et al., 2005; Hugdahl et al., 2015) and a P3b

Abbreviations: AC, auditory cortex; IPS, intra-parietal sulcus; iPCS, inferior precentral sulcus; sPCS, superior precentral sulcus; STS, superior temporal sulcus; TPJ, temporo parietal junction; VLPFC, ventro-lateral prefrontal cortex.

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[1] In the nomenclature used here, negative polarity of dipole-source components is equivalent to negativity at the cortical surface. This nomenclature can be used for both, EEG and MEG. In traditional EEG nomenclature, polarity of auditory-evoked potentials is provided for electrode Cz. For generators in auditory cortex, this coincides with the source-component-based nomenclature in most cases.

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potential in human EEG recordings (Hillyard et al., 1971). While these task-related responses very likely indicate conscious processing, they are also expected to comprise neural processes that are not necessarily required for the perception, *per se* (Aru et al., 2012; Pitts et al., 2014). Several workarounds have recently been suggested around this dilemma (Tsuchiya et al., 2015), for example the use of spontaneous eye movements and pupil-dilation responses to reconstruct the timing of perceptual reversals in binocular rivalry (Frassle et al., 2014) in the absence of overt task responses. A number of studies have also suggested involvement of fronto-parietal networks during auditory perception (Eriksson et al., 2007; Giani et al., 2015), but the degree to which these systems are necessarily required for conscious auditory perception remains currently unclear (Dykstra et al., 2017).

Another challenge for understanding the neural basis of conscious perception is its close link with attention (Posner, 1994)[2] [but see (Hsieh et al., 2011; Watanabe et al., 2011; Wyart et al., 2011)]. In audition, volitional orienting of attention enhances neural activity in auditory cortex (Hillyard et al., 1973; Rif et al., 1991; Voisin et al., 2006; Mesgarani and Chang, 2012; Seydell-Greenwald et al., 2014), but also in dorsal areas of frontal and parietal cortex (Huang et al., 2012; Krumbholz et al., 2009; Salmi et al., 2007; Shomstein and Yantis, 2004; Uhlig and Gutschalk, 2017). These areas comprise part of the so-called dorsal attention system (Corbetta et al., 1995, 2000), and are thought to be important for attentional control. Volitional orienting of attention can facilitate conscious perception of acoustic targets in the presence of informational masking (Leek et al., 1991; Richards and Neff, 2004). Alternatively, attention can also be “captured” by salient stimuli. In this case, the ventral attention system – in which the temporo-parietal junction (TPJ) is a key structure (Corbetta et al., 2008) – plays an important role (Alho et al., 2015; Corbetta et al., 2000; Downar et al., 2000; Stevens et al., 2005).

A powerful paradigm to study auditory conscious perception is the detection of a tone pattern in the presence of a random multi-tone masker (Gutschalk et al., 2008), which produces informational masking (Durlach et al., 2003; Kidd et al., 2008). In contrast to energetic masking, which is based on direct spectral competition in the cochlea (Moore, 1995), informational masking can occur in the absence of spectral overlap between target and masker (Fig. 1A), and is highly variable both within and across listeners (Oxenham et al., 2003). When participants report hearing a regular target pattern under informational masking, perceived tones in the pattern evoke a negative-going response (Gutschalk et al., 2008) and enhanced high-gamma activity (Dykstra et al., 2016) in auditory cortex in a latency range from 50 – 250 ms. Enhanced auditory-cortex activity for detected targets under informational masking was also observed in fMRI (Wiegand and Gutschalk, 2012). However, in these studies, a motor response was only given when a target was detected inside the multi-tone masker. While motor-related and sound related activity can be temporally dissociated in MEG and EEG, the contrast of detected minus undetected targets would be expected to reveal motor-related activity in fMRI, limiting the analysis to auditory cortex in our previous fMRI study (Wiegand and Gutschalk, 2012).

Here, we first introduce a modified setup to study auditory detection under informational masking in fMRI with a whole-brain analysis: participants received a visual response cue to ensure similar motor responses for detection, miss, and correct-rejection trials. The paradigm was then used to identify all areas that showed stronger activation for detected versus missed target trials.

A second experiment was performed to explore potential post-perceptual, task-related components of auditory target detection: a similar setup with visual response cue was used, but the auditory stimulus pattern was presented without the multi-tone masker. For this unmasked stimulus, activation was first measured without the auditory task; because

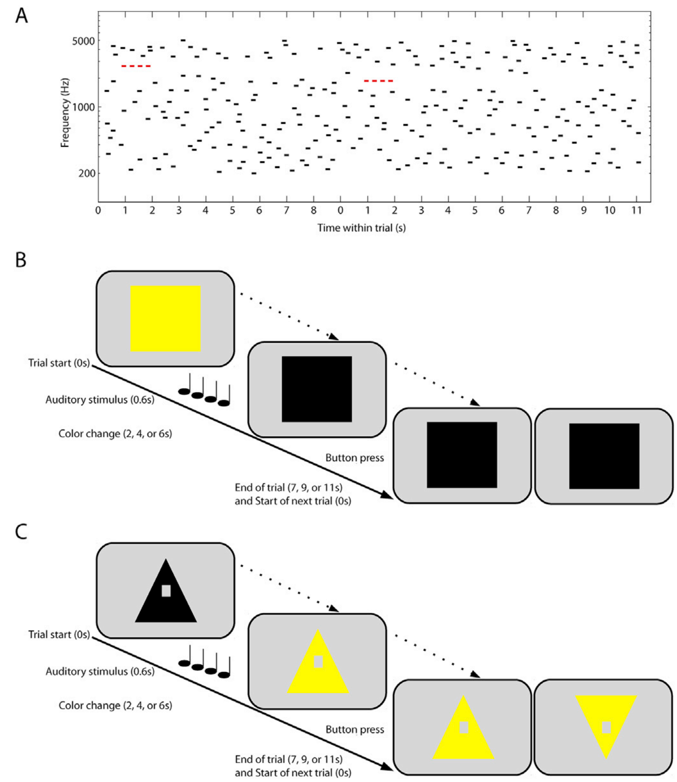

Fig. 1. Schematic of the multitone masker and visual response cue. (A) The schematic shows two subsequent trials of experiment 1A. The random masker tones spanning from 200 to 5 000 Hz are plotted in black. The first trial is 9s, the second 11s long. Both trials comprise a target (red), which consists of four identical isochronous tones, the first of which starts 0.6s after trial onset. The random multi-tone masker continues from one trial to the next, such that there is no audible transition between trials. (B) shows the response cue used in experiment 1. The square changed its color 2, 4, or 6s after trial onset, indicating to participants that they should indicate with a button press whether they heard a target since the last color change or not. The trial then continued and lasted overall 7, 9, or 11s from trial onset. The color of the response cue had the same color at the end of the old and the beginning of the new trial. (C) A triangle was used as response cue in experiment 2, where the auditory stimulus also comprised four isochronous tones, but not masker. Three different task instructions were used: First, participants were instructed to fixate the small square in the middle. Second, participants were instructed to indicate whether the triangle was pointing upwards or downwards upon every color change. The orientation of the triangle was randomly chosen at the beginning of each trial, i.e. the orientation changed at the beginning of half of the stimulus trial, as indicated in the schematic from trial end to the beginning of the next trial. Third, participants were instructed to indicate if an auditory cue was present in the interval between two color changes, like in experiment 1.

the unmasked tone pattern was salient, we expected it to be perceived irrespective of task. Two sets of instructions were used where the unmasked auditory stimuli were not task relevant: once where the presentation was completely passive (fixation), and once where listeners performed an orthogonal, non-demanding visual task. As third instruction, the unmasked stimulus was presented with an auditory detection task, similar to experiment 1. We hypothesized that a potential correlate of conscious auditory perception identified in experiment 1 should also be observed in experiment 2, independent of the task-relevance of the auditory stimulus. Conversely, task-related activity was expected for target-detection trials in the active auditory task, irrespective of the masker's presence.

Materials and method

Participants

In experiment 1, 15 (eight female) participants (aged between 20 and 44 years, mean 24) were included in the final analysis. In experiment 2,

[2] Note that executive functions, which are part of the task-related activity introduced in the previous paragraph, are sometimes subsumed under attention, e.g. in the model by Petersen and Posner (2012).