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Activity in part of the neural correlates of consciousness reflects integration

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ABSTRACT

Integration is commonly viewed as a key process for generating conscious experiences. Accordingly, there should be increased activity within the neural correlates of consciousness when demands on integration increase. We used fMRI and "informational masking" to isolate the neural correlates of consciousness and measured how the associated brain activity changed as a function of required integration. Integration was manipulated by comparing the experience of hearing simple reoccurring tones to hearing harmonic tone triplets. The neural correlates of auditory consciousness included superior temporal gyrus, lateral and medial frontal regions, cerebellum, and also parietal cortex. Critically, only activity in left parietal cortex increased significantly as a function of increasing demands on integration. We conclude that integration can explain part of the neural activity associated with the generation conscious experiences, but that much of associated brain activity apparently reflects other processes.

1. Introduction

A myriad processes constantly occur in our brains, of which only a fraction is mirrored by conscious experiences. However, we tend to think of this fraction as a fundamental feature of the human condition. A basic question is therefore what makes some brain processes consciously experienced while others go unnoticed. A prominent view is that integration is a key process associated with consciousness (e.g., Naghavi & Nyberg, 2005). In relation to the phenomenal experience of perception, the "unity of consciousness" refers to the integration of distinct sensory features into a unified perceptual experience (Searle, 2000), for example seeing a flower rather than a gathering of lines, curves, and color patches, or hearing a word rather than a series of phonemes. Integration related to conscious perception may at the neuronal level be accomplished by interactions among disperse brain regions that together make out a "global workspace" (Baars, 2005; Dehaene, Charles, King, & Marti, 2014), possibly by synchronization of activity across neuronal populations (Melloni et al., 2007) including sensory, frontal, and parietal regions. Also, integration has more formally been suggested fundamental for consciousness in the "information integration theory" (Tononi, 2008; Tononi, Boly, Massimini, & Koch, 2016). The information integration theory does not specify which parts of the brain that are specifically involved in conscious perception, and instead focus on specific characteristics that a physical substrate of consciousness must have. However, thalamocortical interactions that involve at least "sensory" regions are commonly highlighted. While changes in the *state* of consciousness have been related to measures of integration (Boly et al., 2012; Ferrarelli et al., 2010), there are no previous reports on the effects from a direct manipulation of integration in relation to brain activity associated with conscious perception.

Here we aim to test the hypothesis that brain activity specifically related to consciousness reflects integration, by manipulating

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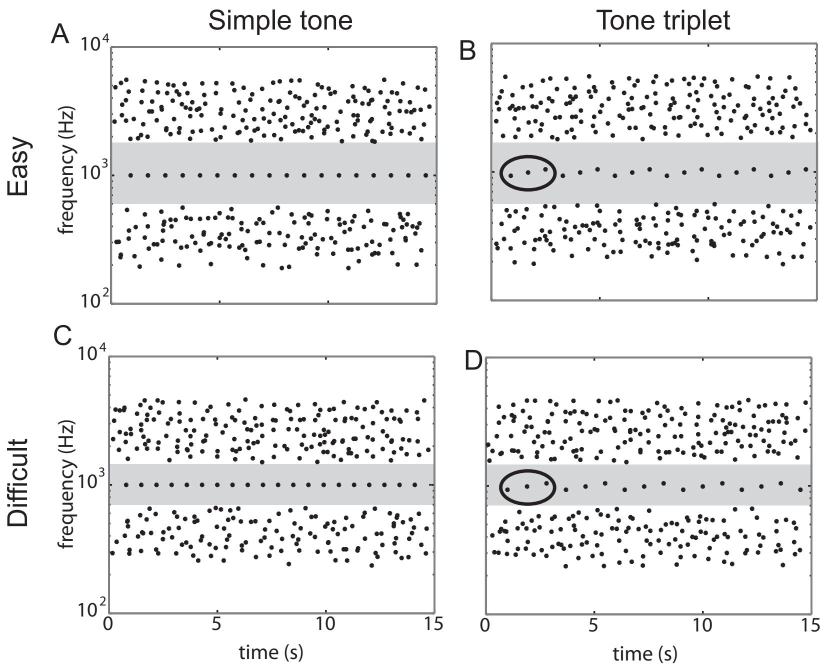

Fig. 1. Graphical representation of the auditory stimuli. A target tone was presented repeatedly throughout each trial, masked with tones in frequencies above and below the target. The discord of sounds made by the masking tones makes target identification difficult, but after some time of focused listening participants can identify the target and tone perception can be relatively clear due to the distance in frequency space between targets and masking tones (grey). There is thus a shift in the conscious experience of the sounds that is unmatched in the stimulus itself, enabling identification of neural activity specifically related to conscious perception. The feature integration required to perceive the target was manipulated by comparing simple reoccurring tones (A, C) with harmonic tone triplets (B, D; circled). Perceptual difficulty was manipulated by reducing the distance in frequency space between the targets and the masking tones (AB vs. CD).

the content of consciousness while measuring brain activity with fMRI. To separate brain activity driven by stimulus parameters and initial sensory processing from that related specifically to conscious perception, we used the phenomenon of auditory "informational masking" (Gutschalk, Micheyl, & Oxenham, 2008; Wiegand & Gutschalk, 2012). Here, a target tone is repeatedly presented with a regular interval and pitch throughout each trial, together with masking tones that have irregular timing and pitch. Further, the target tone is presented within a "protected" frequency band surrounded by masking tones, enabling a relatively clear percept of the target once identified (Fig. 1). The stimuli are therefore first perceived as a cacophony of random tones, but after some time of focused listening the target can be perceived, thereby changing the content of consciousness despite unchanged sensory input. As such, the current experimental strategy for isolating the neural correlates of consciousness is similar to previous research using multi-stable stimuli such as binocular rivalry (Pressnitzer & Hupé, 2006; Sterzer, Kleinschmidt, & Rees, 2009).

Based on previous research, conscious target perception was expected to associate with increased activity in superior temporal and frontal regions (Eriksson, Larsson, Ahlström, & Nyberg, 2007). The specific aim of the current experiment was to find out how activity in such candidate neural correlate of consciousness would be altered as an effect of manipulating the amount of required integration. We therefore compared the experience of hearing simple reoccurring tones to hearing harmonic tone triplets (three-tone "melodies"). Hearing tone triplets requires additional integration across frequency space (pitch) and across a longer time window compared to simple tones. If integration is a key process that drives brain activity during the generation of conscious perception, there should be increased activity within the neural correlates of consciousness as demands on integration increases.

To control for a possible increase in difficulty with higher demands on integration, perceptual difficulty was manipulated orthogonally to the manipulation of integration. Specifically, the frequency distance between targets and masking tones was reduced, thereby making the process of differentiating between signal and noise more difficult (Fig. 1ab vs. cd). Thus, the experimental design was an integration-by-difficulty factorial design where the effects of increasing integration could be identified by the main effect of integration, and confounds from perceptual difficulty could be identified by either the main effect of difficulty or the integration-by-difficulty interaction. Although it may not be possible to uniquely identify the neural correlates of consciousness by comparing target identification with hearing only noise (see for example Aru, Bachmann, Singer, & Melloni, 2011, for critique of such approach), processes not specifically related to conscious perception such as report generation (the button press indicating target identification) is here matched across the different factors (integration, difficulty) and factor levels.