

Testing domain-general theories of perceptual awareness with auditory brain responses

Joel S. Snyder¹, Breanne D. Yerkes¹, and Michael A. Pitts²

¹ Department of Psychology, University of Nevada, Las Vegas, NV, USA

² Department of Psychology, Reed College, Portland, OR, USA

Past research has identified several candidate neural correlates of consciousness (NCCs) during visual perception. Recent research on auditory perception shows promise for establishing the generality of various NCCs across sensory modalities, as well as for revealing differences in how conscious processing unfolds in different sensory systems.

Neural correlates of consciousness

Research aimed at identifying NCCs has benefited in recent years from improved experimental paradigms as well as from important theoretical developments [1,2]. With the human visual system as a model, significant progress has been made in identifying potential NCCs and in distinguishing these from pre-conscious and post-perceptual activity. It is vital to pursue similar research in other sensory modalities to test the domain-generality of mechanisms supporting perceptual awareness.

Recent progress in auditory awareness research

As shown in Figure 1, we focus on auditory event-related potential (ERP) and magnetoencephalography (MEG) studies because they are relatively common and easy to compare with visual studies. fMRI data are also considered when possible.

Analogous to crowding in vision, informational masking is a phenomenon in which participants fail to hear target sounds when presented around the same time as masking sounds, despite the fact that the target and masking sounds do not overlap in frequency. Using MEG, one study showed that, when a metronome-like pattern of target tones is masked, no long-latency response with 100 ms peak latency is evoked, despite the fact that such responses are often thought to occur for any auditory stimulus. However, when the tones were consciously detected, a prolonged long-latency negative-going response was evident. Based on these findings, this response was labeled the awareness-related negativity (ARN) [3]. An earlier response (peaking around 60 ms) was observed regardless of auditory awareness, but did not occur in control conditions when

the target was absent. Importantly, no late positive responses were elicited in this experiment, suggesting that such late responses are not necessary for consciousness, despite the fact that such responses have been implicated as potential NCCs in several visual experiments [1,2].

As in vision, bistable perception can occur for auditory stimuli, allowing the identification of potential NCCs while controlling for physical stimulus differences. Stream segregation of interleaved tones with different stimulus properties is the best-studied bistable auditory perception paradigm [4]. When participants hear two segregated streams versus one integrated stream, increased activity in auditory cortex (AC) and two parietal regions (intraparietal sulcus, precuneus) has been detected with fMRI [5]. This increase in activity for two streams is consistent with the presence of two segregated neural representations, as observed in several animal and human studies of stimulus-driven (rather than percept-driven) neural activity during stream segregation [4]. Another fMRI study showed that activity in AC occurred after a switch from perceiving one stream to two streams of tones, or vice versa [6]. Switch-related activity also occurred in the inferior colliculus, most likely because the two tones differed in terms of inter-aural time difference, another low-level cue that is represented in this brainstem nucleus. Recently, a novel bistable paradigm was created in which perceived pitch motion between a pair of tones reversed or remained stable across successive trials [7]. ERPs revealed a bilateral fronto-central negativity (at around 120 ms), followed by a subsequent late positivity (at 320 ms) associated with changes in perceived pitch motion, despite unchanging sensory input.

Analogous to change-blindness in vision, change-deafness occurs when participants listen to a scene of multiple concurrent sounds and fail to detect when there is an added, deleted, or replaced sound (e.g., when the sound of a dog barking in a noisy city soundscape is replaced by a cat meowing when presented a moment later). As with informational masking, enhanced long-latency sensory responses occur during conscious auditory-change detection, whereas earlier activity in AC occurs regardless of perceptual awareness [8,9]. Enhanced late positive responses are also commonly observed for detected auditory changes (suggesting activation of frontal and parietal networks). However, unlike masking studies, change-deafness paradigms require participants to evaluate each stimulus, and late positive responses may be associated with this evaluation.

Corresponding authors: Snyder, J.S. (joel.snyder@unlv.edu);

Pitts, M.A. (mpitts@reed.edu)

Keywords: neural correlates of consciousness; bistable perception; informational masking; change-deafness; event-related potentials; functional magnetic resonance imaging.

1364-6613/

© 2015 Elsevier Ltd. All rights reserved. <http://dx.doi.org/10.1016/j.tics.2015.04.002>

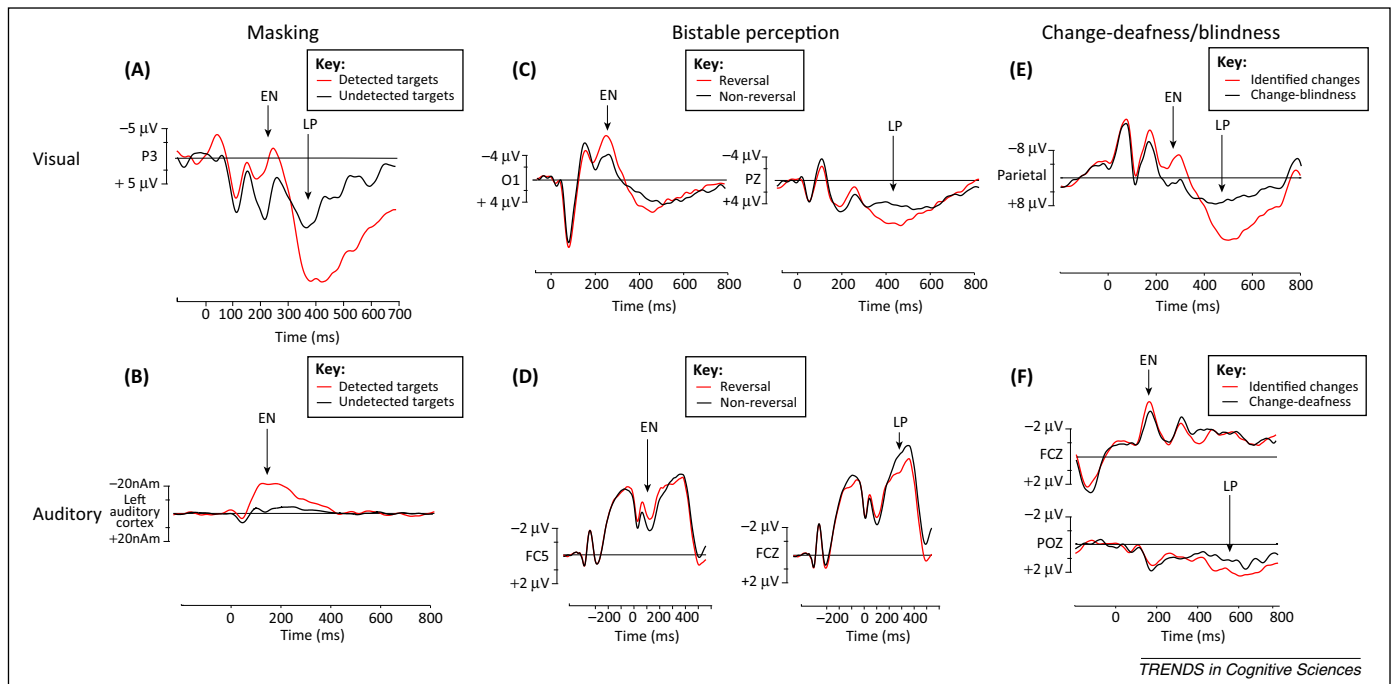


Figure 1. Event-related potential (ERP)/magnetoencephalography (MEG) correlates of visual (top) and auditory (bottom) conscious perception across three common paradigms (columns, left to right: masking, bistable perception, change-blindness/deafness; note that negative is plotted upwards). (A) ERPs from a visual masking study to detected and undetected targets. Adapted from [10] with permission from Wolters Kluwer Health/Lippincott Williams & Wilkins. (B) Grand average source waveforms within the left auditory cortex from an MEG auditory informational masking study showing detected and undetected targets. Adapted from [3] with permission from John Wiley & Sons. (C) ERPs from a visual bistable perception study showing responses to perceptual reversals and non-reversals. Adapted from [11] with permission from Elsevier. (D) ERPs from an auditory bistable perception study showing responses to perceptual reversals and non-reversals. Adapted from [7]. (E) ERPs from a change-blindness study for detected and non-detected (i.e., change-blindness) changes. Adapted from [12] with permission from MIT Press. (F) ERPs from a change-deafness study for detected and non-detected (i.e., change-deafness) changes. Adapted from [8] with permission from Elsevier. Across these various studies, early negativities (EN) are present or enhanced during conscious perception, and are viable candidates for true NCCs. Late positivities (LP) may reflect post-perceptual processes related to performing detection, discrimination, or reporting tasks. Abbreviations: FC5, left fronto-central electrode; FCZ, midline fronto-central electrode; O1, left occipital electrode; P3, left parietal electrode; POZ, midline parieto-occipital electrode; PZ, midline parietal electrode.

Despite this recent progress, a key question that has not been addressed is to what extent these auditory NCCs reflect conscious perception, as opposed to pre-conscious or post-perceptual activity [2]. Long-latency sensory activity in AC around 100 ms (similarly to responses with around 150–300 ms latencies in vision) appears to be a prime candidate for a true NCC because it is consistently found across studies, even under different task and response demands, whereas late positive activity in frontal and parietal areas is more likely to reflect cognitive operations involved in carrying out the discrimination or reporting tasks. Some caution is required, however, because it is well known that the long-latency sensory responses are strongly modulated by attention [4]; it is therefore possible that some of the NCCs found in previous studies reflect subtle differences in auditory attention between detected and undetected conditions instead of perceptual awareness *per se*.

Auditory versus visual NCCs: same or different?

NCCs are frequently observed in sensory and association cortices for both vision and hearing. The similar laminar structure and high degree of integration across the neocortex leaves open the possibility that auditory and visual conscious perceptions rely on similar mechanisms and overlapping circuitry. MEG and ERP studies suggest a very similar sequence of events: intact early sensory responses

regardless of perceptual awareness, followed by long-latency waves (negative potentials in ERP studies) that are enhanced or only present during conscious perception, and finally late positivities that only occur when subjects are tasked with reporting conscious perceptual content. Figure 1 demonstrates some of the similarities between visual and auditory NCCs across three common paradigms.

Although most studies to date suggest a combination of distinct and shared neural signatures of perceptual awareness across sensory modalities, it is important to consider the specific contrasts made in each individual study. Paradigms designed to isolate neural correlates of the contents of consciousness are likely to find different neuroanatomical sources for auditory versus visual NCCs. By contrast, studies that are able to isolate neural mechanisms that bring these contents into awareness, which may be a distinct process, could reveal overlapping neural sources between auditory and visual modalities. For example, if conscious perception results from specific types of interactions between attentional mechanisms and perceptual representations, some of the attentional aspects of this interaction may be domain-general (e.g., dorsal/ventral attention networks), whereas others may be domain-specific (auditory/visual perceptual representations). It will be important to carefully dissect these interactions with targeted manipulations in future studies. Outstanding questions are listed in Box 1.

Box 1. Outstanding questions

- To what extent is the auditory awareness-related negativity related to the visual awareness negativity (see 'EN' effects in Figure 1), and can either of these be isolated from attention-related activity (or other precursors of consciousness)?
- What portions of auditory cortex are activated differentially depending on awareness of stimulus presence/absence, awareness of specific perceptual details, and awareness of changes in perceptual content?
- What is the role of late activity in frontal and parietal circuits (indexed by late positive responses) in auditory and visual awareness, and are the same frontal and parietal regions activated across the two modalities?
- To what extent do auditory and visual cortices interact before, during, and after conscious perception of objects when auditory and visual information about an object arrive simultaneously?
- Are individual differences in conscious perception stable across sensory modalities – for example, the severity of change-blindness/deafness, susceptibility to inattention blindness/deafness, switching-rates for bistable stimuli, or perceptual thresholds for masking?
- In what situations are auditory NCCs more useful than visual NCCs for assessing the integrity of consciousness in clinical populations with disorders of consciousness, and in what ways can auditory NCCs be used to enable communication with people suffering from severe brain damage?

Concluding remarks

Extending work on visual NCCs into the auditory domain shows potential to offer unique insight from both a methodological and theoretical perspective. As experimental paradigms continue to be refined, future studies should attempt to carefully control for attention and task-related confounds, and consider testing the same participants on closely matched auditory and visual

tasks to allow more direct comparisons of NCCs across sensory modalities.

Acknowledgments

J.S.S. was supported by the Army Research Office [W9IINF-I2-I-0256]. We thank Drs Niko Busch, Alexander Gutschalk, Mika Koivisto, and Juergen Kornmeier for sharing their data for display in this paper.

References

- 1 Dehaene, S. and Changeux, J.P. (2011) Experimental and theoretical approaches to conscious processing. *Neuron* 70, 200–227
- 2 Aru, J. et al. (2012) Distilling the neural correlates of consciousness. *Neurosci. Biobehav. Rev.* 36, 737–746
- 3 Königs, L. and Gutschalk, A. (2012) Functional lateralization in auditory cortex under informational masking and in silence. *Eur. J. Neurosci.* 36, 3283–3290
- 4 Snyder, J.S. et al. (2012) Attention, awareness, and the perception of auditory scenes. *Front. Psychol.* 3, 15
- 5 Hill, K.T. et al. (2011) Pattern of BOLD signal in auditory cortex relates acoustic response to perceptual streaming. *BMC Neurosci.* 12, 85
- 6 Schadwinkel, S. and Gutschalk, A. (2011) Transient bold activity locked to perceptual reversals of auditory streaming in human auditory cortex and inferior colliculus. *J. Neurophysiol.* 105, 1977–1983
- 7 Davidson, G.D. and Pitts, M.A. (2014) Auditory event-related potentials associated with perceptual reversals of bistable pitch motion. *Front. Hum. Neurosci.* 8, 572
- 8 Gregg, M.K. and Snyder, J.S. (2012) Enhanced sensory processing accompanies successful detection of change for real-world sounds. *Neuroimage* 62, 113–119
- 9 Puschmann, S. et al. (2013) Electrophysiological correlates of auditory change detection and change deafness in complex auditory scenes. *Neuroimage* 75, 155–164
- 10 Koivisto, M. et al. (2005) Independence of visual awareness from attention at early processing stages. *Neuroreport* 16, 817–821
- 11 Kornmeier, J. and Bach, M. (2005) The Necker cube: an ambiguous figure disambiguated in early visual processing. *Vision Res.* 45, 955–960
- 12 Busch, N.A. et al. (2010) Electrophysiological evidence for different types of change detection and change blindness. *J. Cogn. Neurosci.* 22, 1852–1869

Emotional contagion: its scope and limits

Guillaume Dezacache^{1,2}, Pierre Jacob¹, and Julie Grèzes²

¹ Institut d'Etude de la Cognition, Unité Mixte de Recherche (UMR) 8129, Centre National de la Recherche Scientifique (CNRS) and Institut d'Etude de la Cognition (IEC), Ecole Normale Supérieure and Ecole des Hautes Etudes en Sciences Sociales, Paris, France

² Laboratory of Cognitive Neuroscience, Institut National de la Santé et de la Recherche Médicale (INSERM) Unité 960 and IEC, Ecole Normale Supérieure, Paris, France

The contagion model of emotional propagation has almost become a dogma in cognitive science. We turn here to the evolutionary approach to communicative interactions to probe the limits of the contagion model.

The appeal of the contagion model

According to much recent work in cognitive social neuroscience, the propagation of emotions between individuals is essentially a replicative process variously termed

'contagion', 'resonance', 'sharing', 'mirroring', and 'direct matching' [1]. The currently prevalent contagion model of emotional propagation is a two-step model: first, the perception of another's expressive behavior automatically causes the observer to covertly replicate the agent's behavior. Second, the covert replication of the agent's behavior automatically causes the observer to share the agent's affective or emotional state [1,2]. Interestingly, one may trace the early emergence of this contagion model to Gustave Le Bon's epidemiological approach to crowd psychology [3] (Box 1).

What makes this parsimonious model appealing is that it offers the prospect of a unified account of human social cognition along the following lines. When an agent performs a goal-directed instrumental action, her intention can be construed as the cause of her bodily movements.

Corresponding author: Dezacache, G. (guillaume.dezacache@gmail.com)

Keywords: emotional contagion; contingent response; evolutionarily stable communication.

1364-6613/

© 2015 Elsevier Ltd. All rights reserved. <http://dx.doi.org/10.1016/j.tics.2015.03.011>