



Selective entrainment of brain oscillations drives auditory perceptual organization



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ABSTRACT

Perceptual sound organization supports our ability to make sense of the complex acoustic environment, to understand speech and to enjoy music. However, the neuronal mechanisms underlying the subjective experience of perceiving univocal auditory patterns that can be *listened to*, despite *hearing* all sounds in a scene, are poorly understood. We hereby investigated the manner in which competing sound organizations are simultaneously represented by specific brain activity patterns and the way attention and task demands prime the internal model generating the current percept. Using a selective attention task on ambiguous auditory stimulation coupled with EEG recordings, we found that the phase of low-frequency oscillatory activity dynamically tracks multiple sound organizations concurrently. However, whereas the representation of ignored sound patterns is circumscribed to auditory regions, large-scale oscillatory entrainment in auditory, sensory-motor and executive-control network areas reflects the active perceptual organization, thereby giving rise to the subjective experience of a unitary percept.

1. Introduction

Perception can be thought of as an act of inference (Gregory, 1980; Helmholtz, 1866). Modern neuroscience views the brain as a predictive machine, continuously generating internal models of the causal dynamics of the world in an attempt to interpret its observations (Bar, 2009; Friston, 2005). Although relevant to all sensory systems, this assumption especially applies to audition (Baldeweg, 2006; Garrido et al., 2009; Winkler et al., 2012). Particularly, it applies to sequential organization, which refers to the sorting of interleaved sounds (Dowling, 1973; Bregman, 1990; Sussman et al., 1999; Shamma et al., 2011; Winkler et al., 2009). Meaningful auditory objects rely on binding distributed spectrotemporal patterns into coherent streams (Bregman, 1990; Nelken and Bar-Yosef, 2009; Sussman et al., 1999). Yet, auditory information can sometimes be feasibly explained by more than one internal model. For instance, in a musical piece, a single note from an instrument could belong simultaneously to a melodic line, to a harmonic progression and to a rhythmic pattern featuring several instruments. However, despite

hearing all sounds, we consciously *perceive* univocal organizations that we can flexibly *listen to*. Our subjective experience therefore conforms to the Gestalt principle of exclusive allocation (Kohler, 1947), which states that any sensory element should not be used in more than one description of the natural scene at a time. Whether this principle also applies at the neural level, specifying memory representations of the stimulus input (i.e., whether multiple internal models are held simultaneously or only the current attended one) is still a matter of intense debate (Sussman et al., 2014; Denham et al., 2014; Grossberg et al., 2004).

How the brain flexibly assigns individual events to any of the possible perceptual organizations they could fit into is optimally studied with ambiguous, multistable stimulation, because perception depends on the model currently explaining unchanging sensory input (Sterzer et al., 2009). Behavioral evidence on auditory spontaneous perceptual switches suggests that multiple alternative organizations are held simultaneously and compete to describe the acoustic scene (Denham et al., 2014; Pressnitzer and Hupe, 2006; Sterzer et al., 2009; Sussman et al., 2014). Electrophysiological studies in humans have traditionally embedded

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violations of established regularities within the acoustic streams in order to use change detection auditory evoked potentials, such as the mismatch negativity (MMN) (Näätänen et al., 1978), as an index of sound organization (Sussman et al., 1998, 1999). However, besides yielding conflicting results, with some studies showing simultaneous encoding of alternative organizations (Pannese et al., 2015; Sussman et al., 2014) while others suggesting that only the currently perceived organization is represented (Sussman et al., 2002; Sussman, 2013; Winkler et al., 2006), evidence of this nature is intrinsically indirect and does not inform about the neural mechanisms underlying the representation of sound organization.

Several studies have shown that any existing regularity in the auditory scene is reflected in oscillatory activity tuned to its temporal pattern (Henry et al., 2014; John et al., 2001, 2002; Luo et al., 2006; Luo and Poeppel, 2007; Pannese et al., 2015). This is an interesting observation because synchronized oscillatory activity has been proposed as an effective means for neuronal communication (Fries, 2005). Moreover, since the high-excitability phase of ongoing low-frequency oscillations can be selectively entrained to events occurring in an attended stream (Schroeder and Lakatos, 2009), we speculate that neuronal entrainment could underlie our perceptual ability to flexibly reorganize sequential sounds.

We hereby designed a novel ambiguous sound sequence that allowed the study of active perceptual reorganization while controlling for sensory input. Given the quasi-rhythmic nature of most behaviorally relevant acoustic information (Patel, 2008), rhythmic attention (Jones and Boltz, 1989; Large and Jones, 1999), and its neurophysiological counterpart oscillatory entrainment (Herrmann and Henry, 2014; Schroeder and Lakatos, 2009) would likely play a key role (Pannese et al., 2015). Nozaradan et al. (2011) demonstrated that oscillatory entrainment underlies meter imagery, the voluntary organization of musical beats. However, the imagined meter was imposed on a sound sequence with acoustic energy only at the main beat rate. This leaves open the question of whether oscillatory entrainment actually helps to disambiguate a rhythmic structure that has multiple potential meters. With energy at more than one possible meter, task demands may act to enhance the attended meter while suppressing the unattended one, rather than driving the overall meter of the sequence.

To target the dynamics of large-scale neuronal slow oscillatory activity, we combined spectral analyses with source localization of EEG data, seeking to explore the distinction between the neurophysiological nature of simultaneously encoded representations of the auditory scene, and the selected internal model underlying the perceived auditory object.

2. Materials and methods

2.1. Participants

Fourteen healthy volunteers (mean age: 28.9 years; age range: 24–38 years; 8 males; 2 left-handed) with no self-reported history of neurological, psychiatric, or hearing impairment and with normal or corrected-to-normal visual acuity participated in the experiment. All participants passed a hearing screening including pure tones of 500, 1000, 2000, and 4000 Hz at 20 dB HL prior to the recording session. One participant reported being an active amateur musician without formal training. Data from two participants were excluded due to poor task performance. All volunteers gave written informed consent in accordance with the guidelines of the Internal Review Board of the Albert Einstein College of Medicine (New York City, NY, USA) before their participation and after the procedures were explained to them. The study conformed to the Code of Ethics of the World Medical Association (Declaration of Helsinki). Data is fully available upon request.

2.2. Auditory stimuli

Sixty-four different pure sinusoidal tones (35000 Hz sampling rate)

were generated with Matlab (R2008a; Mathworks) and delivered binaurally via insert earphones by the Stim interface system (NeuroScan Labs, Sterling, VA). The tones featured 16 different frequencies, ranging from 440 Hz (A4) to 1046.5 Hz (C6) in steps of one semitone, two different values of duration (40 and 120 ms) and two different intensities (70 and 85 dB SPL), with rise and fall times of 5 ms (Hanning window).

2.3. Sound sequence

Auditory stimuli were arranged in separate sequences (see Fig. 1A), each containing 12 repetitions of a four-tone melodic ascending-descending pitch pattern including three different tones (i.e., f1-f2-f3-f2). The frequency separation between adjacent tones was set to one semitone to facilitate sound integration into melodic patterns (Bregman, 1990). Stimulus Onset Asynchrony (SOA) and inter-pattern interval were set to 200 ms. In order to minimize effects of neuronal adaptation across sequences, each sequence randomly presented a different set of three tone frequencies from the pool of 16, with the constraint that any frequency featured in a sequence could not appear in the subsequent one. Because all sequences would have 48 stimuli, in order to avoid the participants' expectancy of sequence length (which could influence task performance - see *Delayed response task*), we varied the number of tones in a sequence by randomly shortening or lengthening it by half a pattern (± 2 tones). Tone duration alternated between short (40 ms) and long (120 ms) every four tones (800 ms), coinciding with the onset of the melodic pattern. A sequence started with a melodic pattern of short or long tones at random, with a 50% probability. Tone intensity varied in a three-tone pattern (600 ms) consisting of 1 loud tone (85 dB SPL) followed by 2 soft tones (70 dB SPL). The intensity of the first tone in the sequence was always a loud one. This arrangement of tone features resulted in a perceptually ambiguous sound sequence with a rhythm of 5 Hz (tone presentation), a rhythm of 1.25 Hz (corresponding to the duration/melodic pattern) and a rhythm of 1.67 Hz (corresponding to the intensity pattern), as illustrated by the sequence spectrum at Fig. 1D (see also [sound1.mp3](#)).

2.4. Delayed response task

In order to bias and stabilize the perceptual organization of the sequence, and to minimize muscle contamination during the EEG recording, participants were asked to perform a delayed response task associated with each of the two possible percepts. Therefore, hit rate measures, but not reaction times, could be analyzed. To ensure sound organization according to the duration/melodic pattern, participants were asked to attend to tone duration and detect whether a group of five consecutive tones of same length, appearing randomly between stimulus 36th and 48th (towards the end of the sequence) featured short or long duration. To ensure sound organization according to the intensity pattern, participants were asked to silently count the louder tones and report how many appeared in the sequence (either 14 or 15; from these to the end of the sequence all tones were soft in intensity). Importantly, the sound sequence was the same during the first 7.2 s regardless of the task. Two response buttons in a joystick were enabled at the end of each sequence and participants could respond until the next trial started. The order of the response buttons (left/right) was fixed during the experimental conditions and counterbalanced across participants. Participants used the left and the right thumbs to press the left and right buttons, respectively.

2.5. Procedure

Prior to recording, volunteers participated in a practice session in which they performed the duration pattern task in a sequence without loudness changes and the intensity pattern task in a sequence without duration changes. Once the tasks were clear, they practiced on an experimental (ambiguous) sequence until performing accurately (>75%

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