



Research paper

Stream segregation in the anesthetized auditory cortex

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ABSTRACT

Auditory stream segregation describes the way that sounds are perceptually segregated into groups or streams on the basis of perceptual attributes such as pitch or spectral content. For sequences of pure tones, segregation depends on the tones' proximity in frequency and time. In the auditory cortex (and elsewhere) responses to sequences of tones are dependent on stimulus conditions in a similar way to the perception of these stimuli. However, although highly dependent on stimulus conditions, perception is also clearly influenced by factors unrelated to the stimulus, such as attention. Exactly how 'bottom-up' sensory processes and non-sensory 'top-down' influences interact is still not clear.

Here, we recorded responses to alternating tones (ABAB ...) of varying frequency difference (FD) and rate of presentation (PR) in the auditory cortex of anesthetized guinea-pigs. These data complement previous studies, in that top-down processing resulting from conscious perception should be absent or at least considerably attenuated.

Under anesthesia, the responses of cortical neurons to the tone sequences adapted rapidly, in a manner sensitive to both the FD and PR of the sequences. While the responses to tones at frequencies more distant from neuron best frequencies (BFs) decreased as the FD increased, the responses to tones near to BF increased, consistent with a release from adaptation, or forward suppression. Increases in PR resulted in reductions in responses to all tones, but the reduction was greater for tones further from BF. Although asymptotically adapted responses to tones showed behavior that was qualitatively consistent with perceptual stream segregation, responses reached asymptote within 2 s, and responses to all tones were very weak at high PRs (>12 tones per second).

A signal-detection model, driven by the cortical population response, made decisions that were dependent on both FD and PR in ways consistent with perceptual stream segregation. This included showing a range of conditions over which decisions could be made either in favor of perceptual integration or segregation, depending on the model 'decision criterion'. However, the rate of 'build-up' was more rapid than seen perceptually, and at high PR responses to tones were sometimes so weak as to be undetectable by the model.

Under anesthesia, adaptation occurs rapidly, and at high PRs tones are generally poorly represented, which compromises the interpretation of the experiment. However, within these limitations, these results complement experiments in awake animals and humans. They generally support the hypothesis that 'bottom-up' sensory processing plays a major role in perceptual organization, and that processes underlying stream segregation are active in the absence of attention.

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Abbreviations: BF, best frequency; SU, single unit; MU, multi-unit; VS, vector strength; PSTH, post-stimulus time histogram; FD, frequency difference; PR, presentation rate

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1. Introduction

One of the most impressive outcomes of processing in the auditory system is the separation of elements in the complex acoustic waveforms at each ear and their recombination (grouping) into relevant perceptual objects (see Bregman, 1990 for a comprehensive account). This 'auditory scene analysis' can be split into a 'primitive', hard-wired stage and a 'schema-based' stage which involves modulation by experience, prior stimuli and attention (for

reviews see Carlyon, 2004; Snyder and Alain, 2007; Winkler et al., 2009; Shamma and Micheyl, 2010). However, the interplay between primitive (bottom-up) and schema-based (top-down) processing is still a matter of debate (Macken et al., 2003; Thompson et al., 2011; Snyder et al., 2012; Spielmann et al., 2014).

Many studies of auditory scene analysis focus on stream segregation: the way that a temporal sequence of sounds is grouped or split perceptually. This has been most thoroughly investigated for pure tones, where the resulting perceptual organization depends on the proximity of the tones in frequency and time (van Noorden, 1977). These perceptual effects are reflected both in responses to tone sequences in central auditory neurons in animals (Fishman et al., 2001; Kanwal et al., 2003; Bee and Klump, 2004, 2005; Micheyl et al., 2005; Pressnitzer et al., 2008; Elhilali et al., 2009; Bee et al., 2010; Christison-Lagay et al., 2015) and non-invasive measures in humans (such as far-field electrophysiological responses to individual tones: Snyder et al., 2006).

Neurophysiological studies have revealed that tones in perceptually separate streams are, qualitatively at least, represented by different populations of neurons. Recordings from auditory cortex of monkeys (Fishman et al., 2004), bats (Kanwal et al., 2003), birds (the avian analogue Field L: Bee and Klump, 2004; Itatani and Klump, 2014), ferrets (Elhilali et al., 2009), and from the auditory brainstem of guinea pigs (Pressnitzer et al., 2008) all show that tones with small frequency differences (FDs) stimulate overlapping populations of neurons whilst tones with large FDs tend to stimulate different populations. This is at least in part due to frequency selectivity established in the cochlea (Rose and Moore, 2000). However, the degree of overlap between stimulated populations also decreases with increasing presentation rate (PR), similar to the perceptual dependence (e.g. Fishman et al., 2004).

The second important perceptual effect is the 'build-up' of stream segregation. A tone sequence is always perceived as a single stream initially; the perception of segregated streams only builds up over several seconds, with the rate of build-up also dependent on the FD and PR (Bregman, 1978; Anstis and Saida, 1985). Neural responses decrease over time and this 'adaptation' has been posited as a neurophysiological correlate of build-up (Micheyl et al., 2005). In this paper, we use adaptation to refer to the general decrease in neural response with repeated tone presentation, and we use 'suppression' to refer to the decrease in the response to a tone that is preceded by another (relative to when that tone is presented alone). In neither case do we imply an underlying mechanism. The neurophysiological build-up of streaming has been characterized in single units in the auditory cortex of awake macaque (Micheyl et al., 2005), in multi-units in field L of the awake starling (Bee et al., 2010) and also at lower levels of the auditory system of the anesthetized guinea pig, in single units of the ventral cochlear nucleus (Pressnitzer et al., 2008).

The build-up of stream segregation and the dependence on FD and PR are often held to result from 'primitive' processing (Macken et al., 2003). However, 'schema-based' processes such as attention (van Noorden, 1977; Bregman, 1990) and spontaneous perceptual changes (flipping between two different perceptions of the same stimulus: Pressnitzer and Hupe, 2006) HuHupoe clearly influence stream segregation. Similarly, non-invasive imaging studies demonstrate both bottom-up (Snyder et al., 2006; Sussman et al., 2007) and top-down effects (Hillyard et al., 1973; Alain and Woods, 1994; Gutschalk et al., 2005; Cusack, 2005; Snyder et al., 2006; Bidet-Caulet et al., 2007; Hill et al., 2011; Lakatos et al., 2013).

Previous neurophysiological studies of auditory streaming in the cortex were conducted in awake animals, but, with one exception (Micheyl et al., 2005) the animals were listening passively and attention was not controlled. Here, to identify those elements of streaming that are based only upon primitive (bottom-up)

processing, we characterize streaming in neural responses in the auditory cortex of anesthetized animals, where there are no effects of attention. The current study is partly at the single unit level and hence complements the previous studies in cortex which reported the combined responses of several neurons at a time using either multi-unit (Fishman et al., 2001, 2004; Bee et al., 2010) or current source density analysis of local field potentials (Fishman et al., 2001, 2004). It also provides a basis for comparison with other studies of cortical adaptation and suppression in anesthetized animals (e.g. Ulanovsky et al., 2004; Scholes et al., 2011; Taaseh et al., 2011).

2. Methods

2.1. Subjects and surgical procedures

Experiments were performed on 12 pigmented guinea pigs of both sexes weighing 370–737 g (mean 565 g). All animals were anesthetized with an intra-peritoneal injection of urethane (4.5 ml/kg in a 20% solution), supplemented with intra-muscular injections of 0.2 ml Hypnorm (Fentanyl citrate 0.315 mg/ml, fluanisone 10 mg/ml) whenever a forepaw withdrawal reflex could be elicited. A pre-medication of 0.06 mg/kg Atropine Sulphate was administered subcutaneously to suppress bronchial secretions. Each animal was tracheotomised, artificially respired and core temperature was maintained at 38 °C by means of a heating blanket. The animals were placed in a stereotaxic frame with hollow plastic speculae replacing the ear bars, inside a sound-attenuating room. To equalize pressure across the tympanic membrane, the bulla on each side was vented with a polyethylene tube (22 cm long, 0.5 mm diameter). The membrane overlying the foramen magnum was opened to release the pressure of the cerebrospinal fluid. A craniotomy with a diameter of around 5 mm was performed to expose the primary auditory cortex, the dura was removed and the brain was covered with a layer of 1.5% Agar. A linear multi-electrode array, consisting of four to eight glass-coated sharp tungsten micro-electrodes was advanced together and directly into auditory cortex using a piezoelectric motor (Burleigh Inchworm IW-700/710). All experiments were conducted under license from the Home Office in the UK.

2.2. Acoustic stimuli and electrophysiological recording

Auditory stimuli were delivered diotically through sealed acoustic systems, consisting of modified Radio Shack 40–1377 tweeters coupled to damped probe tubes that fitted into the speculae. The maximum output level of the system was calibrated a few mm from the eardrum using a 1 mm probe tube microphone (Bruel & Kjaer 4134). This was to ensure that sound levels were consistent across experiments (± 3 dB). All stimuli were generated by an array processor (TDT AP2, Alachua, FL, USA) and output at a sample rate of 100 kHz. Stimulus control was from a PC using Brainware (developed by J. Schnupp, University of Oxford). Responses from the electrodes were acquired using a Medusa Headstage and Tucker Davis RX7, sampled at 25 kHz with 16-bit resolution, and digitally filtered (300 Hz–3 kHz) and amplified ($\sim \times 40$ k). Spike waveforms and spike times were recorded to disk by Brainware. They were further analyzed off-line with Plexon (Dallas, TX) spike-sorting software to isolate action potentials from separate single units (SU) and multi-unit (MU) clusters.

2.3. Stimuli

We presented sequences of interleaved ABAB tones (where A and B are different frequencies), as used previously to investigate the effect of varying FD and PR (Fishman et al., 2004). Tones were

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