Behind the scenes of auditory perception

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'Auditory scenes' often contain contributions from multiple acoustic sources. These are usually heard as separate auditory 'streams', which can be selectively followed over time. How and where these auditory streams are formed in the auditory system is one of the most fascinating questions facing auditory scientists today. Findings published within the past two years indicate that both cortical and subcortical processes contribute to the formation of auditory streams, and they raise important questions concerning the roles of primary and secondary areas of auditory cortex in this phenomenon. In addition, these findings underline the importance of taking into account the relative timing of neural responses, and the influence of selective attention, in the search for neural correlates of the perception of auditory streams.

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Introduction

We are usually surrounded by multiple sound sources. The sound waves produced by these sources mingle before reaching our ears, creating complex vibration patterns on our eardrums. An essential function of the auditory system is to analyze these patterns to recover the sound sources that generated them (Figure 1a). This is known as the 'auditory scene analysis' problem [1] or, more colloquially, as the 'cocktail party' problem [2]. Understanding how the auditory system solves this problem is one of the most fascinating tasks facing auditory scientists today. During the past decade, studies devoted to exploring how, and where, auditory scenes are analyzed in the brain have multiplied, using techniques ranging from single-unit recordings to electroencephalography (EEG), magnetoencephalography (MEG), and functional magnetic resonance imaging (fMRI). Although the results of some of these studies were reviewed in earlier publications [3–12], during the past two years, several new findings have emerged.

Some of these findings qualify the conclusions of earlier studies, and raise important questions for future research.

The aim of this article is twofold: first, to provide a brief overview of the current state of knowledge concerning the neural basis of auditory scene analysis, for readers who are not familiar with this research; second, to summarize the three (in our view) most significant questions that have emerged from findings published on this topic within the past two years. Being brief, this review is also, necessarily, selective. It focuses on an important aspect of auditory scene analysis, which the auditory-perception and auditory-neuroscience literatures commonly refer to as 'auditory streaming' (Box 1).

Do auditory streams emerge below, in, or beyond the auditory cortex?

The auditory system is a multi-storey building (Figure 1b). As sensory information ascends from the cochlea to the primary auditory cortex, it passes through several nuclei. Neurons at each level exhibit complex response properties, which reflect sophisticated signal-processing operations. An important task for auditory researchers is to clarify the role of these different processing stages in auditory scene analysis. Most of the studies that have been performed during the past decade concerning the neural basis of auditory streaming have focused on the auditory cortex. In particular, several studies have been devoted to identifying single-unit or multi-unit correlates of auditory streaming in the primary auditory cortex (A1) of mammals [13–16]—or in the corresponding field in the avian forebrain, the field L [17–19]. The results of these studies have revealed striking relationships between neural responses to sequences of alternating tones in A1 (or field L) and psychophysical measures of auditory streaming obtained using similar stimuli in humans. These findings have led to the view that auditory streams are formed in the primary auditory cortex, or perhaps *below* it. The latter possibility is supported by the results of a study, which demonstrates that neural-response properties in the cochlear nucleus (the very first central auditory nucleus) can account for several features of the perceptual organization of sequences of alternating tones [20••]. This finding raises important questions; in particular, what is the *actual* contribution of the primary auditory cortex to the formation of auditory streams? Are there conditions under which the perceptual organization of sound sequences is reflected in neural responses *in*, but not *below*, the primary auditory cortex? Do the neural-response patterns that have been putatively identified as neural correlates of auditory streaming in these studies actually co-vary with the animal's perception

Figure 1
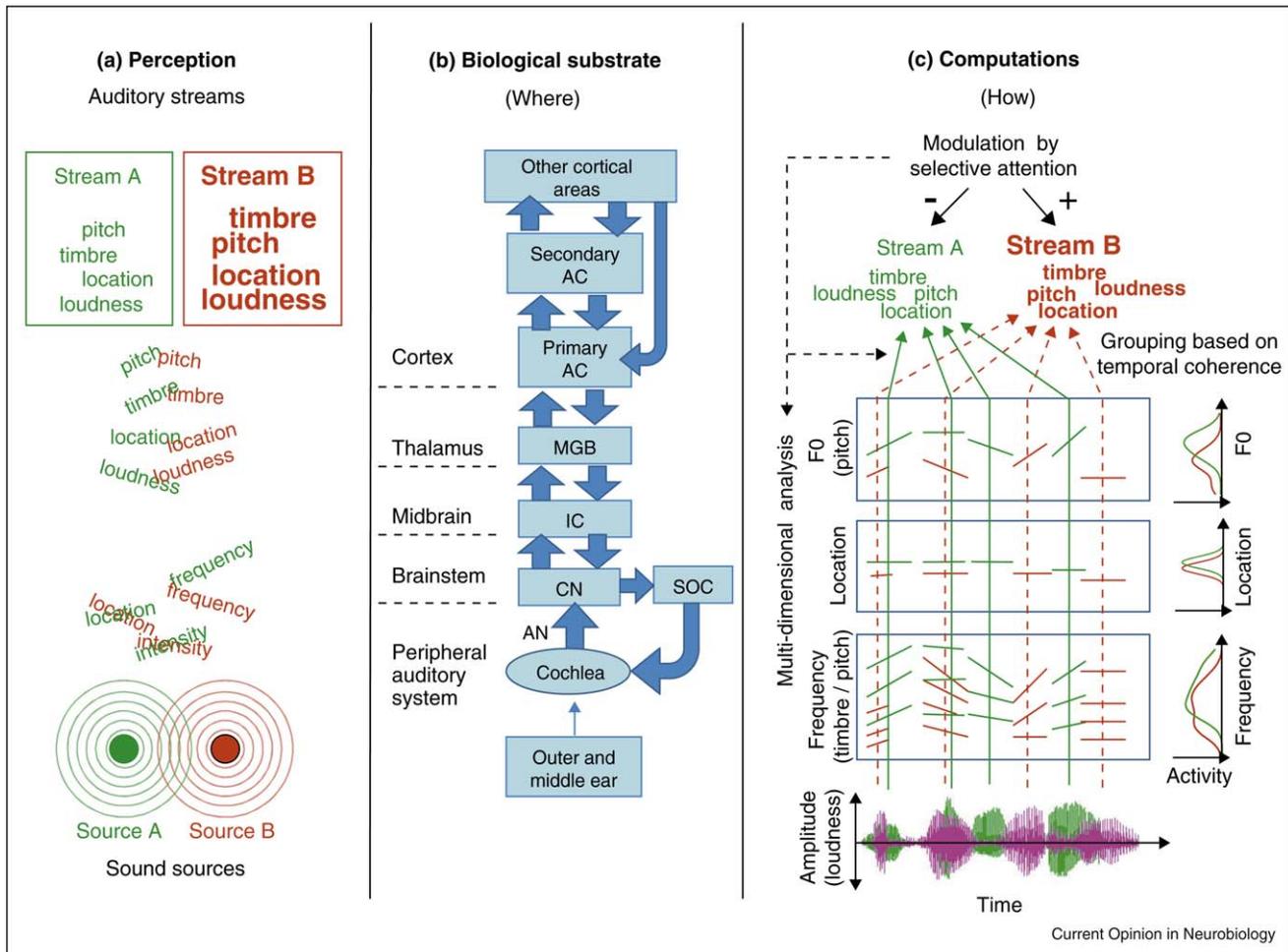
The psychophysical, biological, and computational facets of the 'auditory scene analysis' problem. **(a)** From bottom to top: Acoustic waves coming from different sound sources mingle in the propagating medium. The physical characteristics (intensity, frequency, spatial location) of the sounds produced by these sources become entangled before entering the listener's ear. However, listeners rarely experience natural or artificial acoustic scenes as an inextricable jumble of sounds. Instead, they hear separate auditory 'streams', each having its own perceptual attributes (loudness, pitch, timbre, and perceived location). They can attend selectively to one of these streams and to its attributes (shown here in red). **(b)** The mammalian auditory system is a multi-storey building. From bottom to top: outer and middle ear, cochlea, and auditory nerve (AN); cochlear nucleus (CN) and superior olivary complex (SOC) in the brainstem; inferior colliculus (IC) in the midbrain; medial geniculate body in the thalamus; primary and secondary auditory cortex (AC). The challenge, for auditory scientists, is to clarify how neural responses at each of these multiple processing stages relate (or not) to the listener's perception, and at which stage the conscious percept of an auditory stream emerges. The task is further complicated by the presence of ascending and descending projections, which provide opportunity for both bottom-up and top-down influences at all stages, including the cochlea and the secondary AC. Moreover, cortical areas that are not traditionally considered part of the auditory system may additionally contribute. **(c)** A computational auditory scene-analysis model based loosely on physiological findings. From bottom to top: input waveforms (amplitude of vibration as a function of time) are transformed into representations involving other dimensions, such as frequency (a determinant of pitch and timbre), fundamental frequency (F0, a determinant of pitch), or location (left–right). Temporally coherent 'events' in these representations are grouped *within* each dimension, as well as *across* different dimensions. This results in auditory streams with associated attributes. Stream formation also depends on how well the events are separated along the dimensions. For instance, non-synchronous events may still be grouped into a common stream if they are close in frequency or fundamental frequency. Finally, attention is directed selectively toward one of the streams. This enhances the representation(s) of that stream, and suppresses the representations of concurrent streams. The dashed lines and associated interrogation marks indicate potential influences of selective attention on the analysis of sound features, and on the stream-formation process itself.

of the stimulus (as inferred using behavioral tasks) *during* the neural recordings?

In parallel to these single-unit and multi-unit studies in animals, several studies have investigated cortical correlates of auditory streaming in humans using EEG [21–26,27•], MEG [28–30], or fMRI [30–33,34••]. The advantage of working in humans is that percepts can be probed simply by asking the listener what he/she perceives while brain activity is being measured. Perhaps the most significant outcome of these studies was the demonstration of co-variations between cortical responses and

Box 1 What is 'auditory streaming'?

An essential aspect of the analysis of auditory scenes relates to the perceptual organization of sounds into 'streams'—commonly referred to as 'auditory streaming'. Broadly speaking, a 'stream' is a sound, or group of sounds, which is perceived by the listener as a coherent entity. It can be selectively attended to, amid other sounds. The word 'stream' emphasizes the fact that sounds are often embedded in temporal sequences. Speech and music provide examples of this. Streams usually correspond to sound sources in the listener's environment. In some cases, however, sounds from multiple sources are heard as a single stream. Whether different sounds are heard as a single stream, or as separate streams, depends partly on stimulus characteristics, partly on the listener's intentions, that is, whether the listener is actively trying to hear out certain sounds. In general, two sounds (A and B) that have approximately the same pitch, timbre, and location are heard as a single stream when played in a sequence (e.g., ABAB...). By contrast, sounds that differ markedly in pitch, timbre, or location usually form separate streams.

Although 'auditory streaming' is sometimes used to mean specifically: 'the perceptual organization of *sequential* sounds', sounds usually consist of many spectral components, which often span a wide frequency range (from several Hz to several kHz). Thus, when forming auditory streams, the auditory system must group sounds across time, and in addition, group simultaneous frequency components that arose from a common source—while keeping these components separate from those produced by other sources. Synchrony provides a useful cue for solving this problem. Spectral components that start at approximately the same time (within a few tens of ms) are usually grouped together in perception, while frequency components that start at different times tend to be heard as separate.

perceptual judgments of *in the absence of corresponding changes in the physical stimulus* (e.g., [26,27[•],29,32,34[••]]). This was achieved by using perceptually ambiguous sound sequences, the perception of which switched randomly between 'one stream' and 'two streams' over time. Interestingly, in the EEG and MEG studies [26,27[•],29], these co-variations involved long-latency responses (such as the N1 or $N1_m$), which are thought to be generated in *secondary* areas of auditory cortex. Using a perceptual-camouflaging paradigm in which listeners had to detect a stream of (target) tones embedded in a stochastic background, a recent MEG study found that long-latency responses to the target tones were only evoked on trials on which the corresponding stream had been detected by the listener [35[••]]. By contrast, steady-state responses, which were presumably generated in *primary* auditory cortex, were evoked by the target tones regardless of whether or not the listener detected the target stream. On the basis of these EEG and MEG findings, it is tempting to speculate that neural activity in the *secondary* auditory cortex is more closely related to the listeners' actual perception of an auditory stream than primary auditory-cortex activity. However, further study is needed before a strong conclusion can be reached on this point.

The fMRI data are not as clear-cut. Several studies have found differences in blood oxygen level-dependent

(BOLD) signals in regions corresponding to the primary and/or secondary auditory cortex depending on factors known to influence auditory streaming [30,31,33]. However, until recently, the only fMRI study of auditory streaming in which potential stimulus confounds had been eliminated (by using physical constant but perceptually ambiguous stimuli) had failed to find significant co-variations between listeners' percepts and BOLD signals in auditory cortex [32]. This state of affairs recently changed, as an fMRI study, which also used perceptually ambiguous sequences, found significant differences in the relative timings of activations in the auditory cortex and the medial geniculate body (MGB) during perceptual reversals [34[••]]. Although further work is needed to clarify the implications of this recent finding, one interpretation of this result is that the perception of sound sequences such as those used in studies of auditory streaming emerges from interactions between the auditory cortex and the thalamus.

The possibility that cortical areas beyond the auditory cortex contribute to the perception of auditory streams is suggested by fMRI data. In particular, one study found significantly greater activation in the intraparietal sulcus (IPS) when listeners heard a perceptually ambiguous sequence of tones as two streams than when the same listeners heard the same sequence as a single stream [32]. The IPS has been implicated in visual binding. However, it remains unclear whether the change in IPS activation that was observed in this study was a cause, or a consequence, of the perceptual change from one to two streams. Whether, and how, neural activity in cortical regions located outside of auditory cortex influence the formation of auditory streams are still open questions.

How are auditory streams formed in the brain? The role of temporal coherence

Auditory streaming has traditionally been studied using sequences of pure tones at two frequencies (A and B), which are played in alternation (forming a repeating AB or ABA pattern)—an audio demo can be found at: http://www.tc.umn.edu/~cmicheyl/demos.html. The probability that the A and B tones are heard as separate streams usually increases with their frequency separation, the pace of tone presentation, and – provided that the sequence is continuously attended to by the listener – the time elapsed since the onset of the stimulus sequence. It has been suggested that these perceptual effects are mediated by three important response properties of auditory neurons: frequency selectivity, forward suppression, and adaptation [13–18]. The net effect of these properties is that the A and B tones activate increasingly distinct neural populations in A1 as the frequency separation, presentation rate, and stimulation time increase. According to this view, sounds form separate streams when they activate distinct (or weakly overlapping) populations in central auditory neurons; by contrast, sounds that activate the same (or largely overlapping) neural populations form

a single stream. This idea can be generalized to explain stream segregation based on other sound attributes than frequency. For instance, segregation based on differences in spectral envelope (timbre), periodicity (pitch), or modulation rate (pitch or roughness) can be explained by considering populations of neurons selective to these attributes [19,30].

Recent findings indicate that spatial separation between responsive neural populations in A1 is not a *sufficient* condition for stream segregation, however. This was revealed by altering the classic ABAB stimulus, in such a way that the A and B tones were *synchronous* instead of alternating. Under such conditions, the tones were heard as a single stream, even when they were sufficiently far apart in frequency to activate well-separated populations of neurons in A1 [36••]. Thus, it appears that, for sounds to be separated into streams, the tones must not only activate different neural populations; in addition, the populations must be activated at different times. Conversely, well-separated neural populations in A1 can support a single stream percept, if they are activated in a temporally coherent fashion. This is especially important because many naturally occurring sounds, such as speech, contain multiple spectral components spread over wide frequency range; the temporal coherence of these components promotes their grouping into a common stream even when they are widely separated in frequency (see the schematic illustration of this idea in Figure 1c).

The role of temporal coherence in perceptual grouping need not be limited to frequency-selective neural populations. The grouping of temporally coherent responses across neural populations that encode different auditory attributes (e.g., pitch and spatial location) can explain how the auditory system successfully associates multiple attributes with the correct stream—so that the pitches of sounds arising from different locations are not confused by the listener (Figure 1c). This idea may be thought of as an instantiation of the 'binding hypothesis' in audition. Recent computational models based on the principle of grouping-by-temporal-coherence can mimic the perceptual organization of a wide variety of sounds [36••,37•]. However, further study is needed to clarify how this principle of stream formation based on temporal coherence is implemented in the central auditory system.

How does attention influence auditory stream formation at the neural level?

The influence of attention on the formation of auditory streams has inspired several studies during the past decade. EEG studies have identified neural indices of stream segregation, such as the mismatch negativity (MMN), which are *modulated by* attention, but can be detected in averaged responses even when the listeners are engaged in a task that draws their attention away from the evoking sounds [21,38–40]. The 'object related nega-

tivity' (ORN), a neural index of the perceived segregation of concurrent sounds, can also be recorded when the participant's attention is not focused on the auditory stimulus [22–24,41]. These findings suggest that, under many circumstances, incoming sounds can be parsed 'automatically' by the auditory system, based on stimulus properties (such as temporal coherence); attention may only come into play *after* streams have been formed, as one of the streams is being selected for further listening.

On the contrary, psychophysical data (and introspection) indicate that selective attention can influence stream formation. For instance, listening actively for high-pitch tones in a sound sequence that contains both low-pitch and high-pitch tones can promote the perception of this sequence as two separate streams instead of a single stream. The neural basis of this effect remains unclear. Several studies within the past 20 years (e.g., [42]), including recent ones [43,44•], have found that cortical responses to sounds that form part of a selectively attended stream are enhanced compared to responses to unattended sounds. An important goal for future studies is to determine whether this modulation of neural responses depending on selective attention affects neural representations of already formed streams, or whether it influences the neural stream-formation process itself.

Conclusions

Over the past decade, a rapidly increasing number of studies have started to explore *where* and *how* auditory streams are formed in the brain. Neural correlates of auditory streaming have been identified in, below, and even beyond the auditory cortex—in cortical regions not traditionally associated with auditory processing. This suggests that the formation of auditory streams involves a broadly distributed neural network. An important goal for future research will be to clarify the roles of primary and secondary areas of auditory cortex in this phenomenon. This may require the use of micro-stimulation and selective-deactivation (e.g., cooling) techniques combined with behavioral measures. Awaiting such studies, experiments in which behavioral measures are combined with simultaneous single-unit recordings may represent the next most important step toward a clearer understanding of the neural basis of auditory streaming.

The grouping of temporally coherent responses across neurons tuned to different frequencies or different stimulus attributes appears as an important aspect of how the auditory system forms auditory streams and, at the same time, solves the 'binding' problem. However, further research is needed to determine if, how, and where this principle of temporal coherence is implemented in the central auditory system.

Finally, the extent to which neural representations of auditory streams in (and below) the auditory cortex are

influenced by selective attention deserves further investigation. The abundance of descending (efferent) connections in the auditory system provides ample opportunity for 'top-down' influences, and makes it quite possible that effects of selective attention affect early stages of the neural analysis of auditory scenes. Teasing apart 'bottom-up' and 'top-down' influences on neural responses to sound sequences at different levels of processing within the auditory system promises to be an exciting challenge.

Acknowledgements

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it is embedded.