Effects of prior stimulus and prior perception on neural correlates of auditory stream segregation

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Abstract

We examined whether effects of prior experience are mediated by distinct brain processes from those processing current stimulus features. We recorded event-related potentials (ERPs) during an auditory stream segregation task that presented an adaptation sequence with a small, intermediate, or large frequency separation between low and high tones (Δf), followed by a test sequence with intermediate Δf. Perception of two streams during the test was facilitated by small prior Δf and by prior perception of two streams and was accompanied by more positive ERPs. The scalp topography of these perception-related changes in ERPs was different from that observed for ERP modulations due to increasing the current Δf. These results reveal complex interactions between stimulus-driven activity and temporal-context-based processes and suggest a complex set of brain areas involved in modulating perception based on current and previous experience.

Descriptors: Auditory scene analysis, Auditory cortex, Context, Sensory memory, Event-related potentials, Scalp topography

Auditory scene analysis involves the grouping of sounds originating from different physical sources into distinct auditory representations (for reviews, see Bregman, 1990; Carlyon, 2004; Darwin, 1997; Moore & Gockel, 2002; Snyder & Alain, 2007b). A well-studied laboratory task meant to model real-world object formation entails the presentation of low (A) and high (B) tones and a pause (-) in a galloping pattern (Van Noorden, 1975). Typically, participants are more likely to hear the tones as a single object or "stream" (ABA-ABA- . . .) when the frequency difference between A and B tones (Δf) is small; when Δf is large, participants are more likely to perceive two streams or "streaming" (A-A-A-A-, B- - -B- - -). At intermediate Δf, there is a "buildup" period of several seconds after which participants' perception switches from one stream to two streams (Anstis & Saida, 1985; Bregman, 1978). After buildup, participants experience bistable alternations between perceiving one or two streams similar to bistability in visual perception (Pressnitzer & Hupé, 2006).

The "peripheral channeling" theory of streaming proposes that segregation arises from spatially distinct activations in tonotopic maps of the cochlea and auditory nerve and is supported by computational and psychophysical evidence (Beauvois & Meddis, 1996; Hartmann & Johnson, 1991). Although it is clear from this evidence that segregation based on pure-tone frequency is very likely to begin in the periphery, this theoretical account cannot explain phenomena such as perceptual segregation based on centrally computed cues (Vliegen & Oxenham, 1999), effects of attention (Carlyon, Cusack, Foxton, & Robertson, 2001; Cusack, Deeks, Aikman, & Carlyon, 2004) and bistability (Pressnitzer & Hupé, 2006). Therefore, it remains an open and important question of intense investigation how the brain segregates and groups complex patterns of sounds into distinct auditory streams based on activity at multiple stages of the auditory system (Denham & Winkler, 2006; Micheyl et al., 2007; Moore & Gockel, 2002; Snyder & Alain, 2007b).

A powerful strategy to probe the nature of perceptual representations is by comparing different types of adaptation, with the goal of isolating functionally distinct processes. Previous studies of streaming buildup have used this strategy, in particular revealing that stream formation relies on representations that adapt with time constants of several seconds (Beauvois & Meddis, 1997; Bregman, 1978) and are easily disrupted by changes in stimulus properties such as frequency, intensity, and location (Anstis & Saida, 1985; Roberts, Glasberg, & Moore, 2008; Rogers & Breg-

man, 1993, 1998) or shifts in attention (Carlyon et al., 2001; Cusack et al., 2004). Recently, studies in humans and nonhuman animals have studied the neurophysiological correlates of adaptation underlying buildup in both brain stem (Pressnitzer, Sayles, Micheyl, & Winter, 2008) and cortical areas (Micheyl, Tian, Carlyon, & Rauschecker, 2005; Snyder, Alain, & Picton, 2006; Sussman & Steinschneider, 2006), suggesting the existence of distributed representations during stream segregation.

Besides buildup, other effects of prior stimulation may occur in streaming and provide additional insights into the mechanisms of auditory stream formation. We recently measured the psychophysical effects of prior stimulus and prior perceptual state during auditory stream segregation (Snyder, Carter, Hannon, & Alain, 2009; Snyder, Carter, Lee, Hannon, & Alain, 2008). The greater the Δf during adaptation, the less likely a subsequent test pattern was heard as two segregated streams, an effect opposite in direction to the classic finding that greater Δf causes more perception of two streams for the current sequence. Unlike with buildup (Anstis & Saida, 1985), this effect of context was not severely disrupted by changing the frequency of the tones between the context and test sequences (Snyder et al., 2009), suggesting that any adaptation underlying the novel context effect occurred in brain areas with relatively wide frequency tuning. One possible explanation for the effect of the prior stimulus is that neurons sensitive to large Δf levels adapt such that, during the subsequent test sequence, neurons sensitive to small Δf respond disproportionately more and therefore cause more perception of one stream. Similarly contrastive effects of prior stimuli occur in vision, in particular when the adaptation stimulus has a relatively long duration and a high contrast and when the interval between the adaptation and test stimuli is relatively short (Brascamp, Knapen, Kanai, van Ee, & van den Berg, 2007; Kanai & Verstraten, 2005).

The effect of prior Δf was not simply due to an effect of perception during adaptation because when identical bistable sequences were presented during both adaptation and test (i.e., both with intermediate Δf), the perception of two streams during the adaptation sequence actually increased the likelihood that two streams would again be experienced during the test sequence. This is similar to findings of perceptual stabilization (also called facilitation or priming) in vision (e.g., Brascamp et al., 2007; Kanai & Verstraten, 2005; Leopold, Wilke, Maier, & Logothetis, 2002). Effects of prior stimulus and prior perception in streaming were specific to adaptation within the auditory modality because presenting a visual task that is analogous to streaming during adaptation did not have any effect on perception during the auditory test (Snyder et al., 2009). It is likely that these novel effects of recent auditory experience co-occur with other effects such as buildup and the influence of current Δf.

The purpose of the current study is to identify neural correlates of the novel effects of prior stimulus and prior perception on auditory stream segregation. Recent research has identified neural modulations in human auditory cortex reflecting the encoding of stimulus features (e.g., current Δf) that lead to perceptual segregation (Gutschalk et al., 2005; Gutschalk, Oxenham, Micheyl, Wilson, & Melcher, 2007; Snyder et al., 2006; Wilson, Melcher, Micheyl, Gutschalk, & Oxenham, 2007). Using event-related brain potentials (ERPs), Snyder et al. (2006) found enhanced amplitude of the P2 wave (positive deflection at about 200 ms after sound onset) as a result of larger Δf that was localized to auditory cortex. Based on this ERP finding and the psychophysical result that larger prior Δf leads to less

subsequent perception of two streams (Snyder et al., 2008, 2009), we expected that presenting a large Δf as an adaptation sequence would result in smaller ERPs during presentation of a test sequence. Similarly we expected that perception of two streams during the adaptation sequence would result in enhanced ERPs during the test sequence. A further question we addressed is whether effects of the prior stimulus and prior perception arise from brain areas that are also involved in processing the current stimulus. To address this question, we compared the scalp topographies of the modulations due to prior Δf and prior perception with ERPs reflecting encoding of current Δf.

Methods

Participants

Twenty normal-hearing (<30 dB HL from 250 to 8000 Hz) adults (10 men and 10 women, age range $= 18$–32 years, mean age $= 22.5$ years) from the University of Nevada, Las Vegas community participated after giving written informed consent. The first author participated.

Materials and Procedure

Auditory stimuli were generated off-line in Matlab (The Math-Works, Inc., Natick, MA) and consisted of pure tones (50 ms in duration, including 10 ms rise/fall times). The tones were presented binaurally through ER3A headphones (Etymotic Research, Inc., Elk Grove Village, IL) at 70 dB SPL. The time between adjacent A and B tone onsets within each ABA- cycle was 120 ms, as was the silent duration between ABA triplets. Stimuli were presented and behavioral responses were collected by a custom program written in Presentation (Neurobehavioral Systems, Inc., Albany, CA), running on a Pentium 4 computer with a SB X-Fi sound card (Creative Technology, Ltd.). Behavioral responses were collected using an RB-830 button box (Cedrus Corporation, San Pedro, CA).

Each trial consisted of a 6.72-s (14 ABA- repetitions) *adaptation sequence*, a 1.44-s *silent period*, and a 6.72-s *test sequence* (Figure 1). The intertrial interval was 3 s. The Δf for the test period was 6 semitones with the following set of A and B tone frequencies: A $= 300$ Hz, B $= 424$ Hz. This Δf of 6 semitones was chosen because it usually leads to a bistable percept in which it is possible to hear one or two streams. There were three different adaptation sequences: (a) A $= 300$ Hz, B $= 357$ Hz; (b) A $= 300$ Hz, B $= 424$ Hz; and (c) A $= 300$ Hz, B $= 600$ Hz, corresponding to Δfs of 3, 6, and 12 semitones. Five blocks were presented, each containing 30 trials (10 of each trial type). Thus, each trial type was presented 50 times to each participant. Four practice trials were presented prior to beginning the experiment.

Participants were seated in a comfortable chair in a single-walled sound-attenuated room (Industrial Acoustics Corp., Bronx, NY) and were asked to maintain fixation on a white cross on a black background in the center of a computer screen throughout the experiment. Participants were asked to listen to the stimuli during electrophysiological recording and to avoid moving their eyes, head, or other body parts while the stimuli were being presented. At the end of each sequence, participants indicated by pressing one of two buttons whether they perceived one stream for the entire sequence or two streams at any point during the sequence. Participants were not explicitly told about the two types of sequences, and they were encouraged to let their
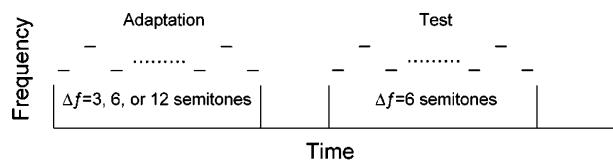
Figure 1. Stimuli presented in trials during ERP recording. The adaptation period of the trial consisted of a repeating ABA pattern with Δf of 3, 6, or 12 semitones between the A and B tones. The test period of the trial consisted of an ABA pattern with Δf of 6 semitones. There was a 1.44-s interval between the adaptation and test and a 3.0-s interval between trials.

perception take a natural time course and not to bias their perception in favor of one stream or two streams.

Electrophysiological Recording and Analysis

Electroencephalographic (EEG) signals were digitized continuously (512-Hz sampling rate and a 104-Hz bandwidth) using a Biosemi ActiveTwo system (http://www.biosemi.com). The EEG was recorded from an array of 72 electrodes, with a Common Mode Sense (CMS) active electrode and Driven Right Leg (DRL) passive electrode serving as ground (see http://www.biosemi.com/faq/cms&drl.htm), placed at 64 points based on the 10/20 system in a Biosemi electrode cap and 8 additional points below the hair line (both mastoids, both pre-auricular points, outer canthus of each eye, and inferior orbit of each eye) and recorded onto a PC desktop computer for off-line analysis. Before EEG recording, conducting gel was applied to the skin at each electrode site with the cap on, and sintered Ag-AgCl pin-type electrodes were fit into place at each site in the cap. Sintered Ag-AgCl flat-type electrodes were attached with adhesive to sites below the hair line. No abrading of the skin was performed. Voltage offsets were below 40 mV prior to recording, and the resting EEG was checked for any problematic electrodes prior to and throughout the recording session.

All off-line ERP analyses were performed using Brain Electrical Source Analysis software (BESA; MEGIS Software GmbH, Gräfelfing, Germany), except for baseline correction and amplitude measurements, which were performed by custom scripts in Matlab (The MathWorks, Inc., Natick, MA). Electrodes that were noted during the recording as being noisy throughout the experiment were interpolated prior to analysis. Ocular artifacts (blinks, saccades, and smooth movements) were corrected automatically with a Principal Component Analysis based method. Epochs contaminated by artifacts (amplitude $> 150\,\mu V$, gradient $> 75\,\mu V$, low signal $< 0.10\,\mu V$) were automatically rejected before averaging. EEG epochs were averaged separately across all non-artifact trials for each of the three stimulus conditions, for the adaptation and test sequences, and for each electrode site, and re-referenced to the average of all electrodes not adjacent to the eyes. Epochs were digitally bandpass filtered to attenuate frequencies below 0.5 Hz (6 dB/octave attenuation, forward) and above 30 Hz (24 dB/octave attenuation, symmetrical).

To examine effects of prior Δf on the onset response at the beginning of the test sequence, epochs were segmented with a 480-ms pre-trigger baseline period and a 960-ms post-trigger active period and baseline corrected by subtracting the mean of the -30 to 0-ms portion of the baseline from each point in the epoch. For this analysis, the amplitude criterion was not used for artifact rejection because of the small number of trials and the long duration of the epochs.

To examine effects of adaptation Δf on the remainder of the sequence, trial epochs were segmented with a 480-ms pre-trigger baseline period and a 480-ms post-trigger active period (corresponding to one cycle of the ABA- pattern). The first ABA-pattern of each sequence was not analyzed because of the large onset response that was analyzed separately. The last ABA-pattern of each trial was also not analyzed because participants were getting ready to make a manual response, which may have contaminated the ERP data with muscle-related activity or movement-related activity. To examine effects of Δf, ERPs were baseline corrected by subtracting the mean of the 90 to 120-ms portion of the epoch (30 ms preceding B tone) from each point in the epoch. The baseline interval for this analysis and the following analysis were chosen empirically. The response for the Δf effect appears to be time-locked to the B tone. Choosing a different baseline for this effect did not change the difference wave qualitatively.

To examine effects of perception during adaptation on Δf-related activity, EEG epochs were processed as described above except that only epochs with an adaptation Δf of 6 semitones were used and these epochs were divided according to perception reported during the adaptation sequence. We reaveraged the data for this condition during adaptation for 16 participants who had at least 100 nonartifact epochs for both percepts in the adaptation and test periods, resulting in four ERPs for each participant. ERPs were baseline corrected by subtracting the mean of the 30 to 0-ms portion (30 ms preceding first A tone) from each point in the epoch. The response for the perception effect occurred starting prior to the B tone, so it was sensible to baseline at the beginning of the ABA- pattern.

ERP mean amplitudes were calculated in time ranges showing maximal differences in the grand averaged waveforms between conditions of interest at electrodes showing the maximal difference. Mean amplitudes were averaged across electrode sites for each participant and submitted to repeated measures analyses of variance (ANOVAs).

Results

Behavioral Data

For each participant and for each of the three different trial types, we calculated the proportion of trials that participants reported hearing two streams for the adaptation and test sequences, separately. The values were entered into one-way repeated measures ANOVAs to test for differences in perception of streaming during the adaptation and test periods depending on the Δf of the adaptation sequence (3, 6, or 12 semitones). The degrees of freedom were adjusted with the Greenhouse–Geisser ε and all reported probability estimates were based on the reduced degrees of freedom. This adjustment was applied to all ANOVAs. To assess the impact of prior perception on streaming during the test, we compared the likelihood of reporting streaming at test when the 6-semitone Δf adaptation sequence was heard as either one or two streams. These values were entered into a one-way repeated measures ANOVA to test for differences in perception of streaming during the adaptation and test periods depending on perception during the adaptation sequence.

Figure 2a shows the proportion of trials heard as two streams for the adaptation and the test sequences. As expected, the perception of two streams during the adaptation sequence increased significantly as current Δf increased, $F(1,19) = 96.33$, $p < .001$.
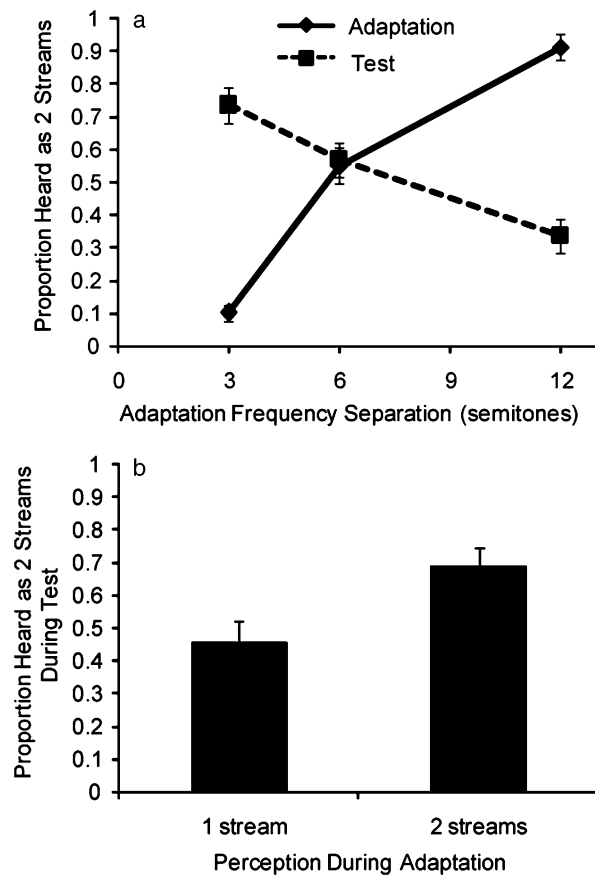
Figure 2. Behavioral results. a: Effects of Δf on perception during the adaptation and during the test sequence. b: Effect of perception during the adaptation on perception during the test for trials with a 6-semitone Δf adaptation.

More importantly, perception of two streams during the test sequence decreased significantly as prior Δf (i.e., Δf during adaptation) increased (Figure 2a), $F(1,19) = 32.36$, $p < .001$, replicating previous psychophysical findings (Snyder et al., 2008, 2009). Finally, reports of hearing two streams during the test sequence were greater when participants also heard two streams during the prior sequence (Figure 2b), $F(1,19) = 14.99$, $p < .005$, also replicating the previous findings.

Electrophysiological Data

As shown in Figure 3 (top left panel), increased Δf during the adaptation sequence resulted in increased positivity in response to the B tone (265–335 ms), $F(2,38) = 10.47$, $p < .001$. The effects of Δf on neural activity is best illustrated in the difference wave between ERPs elicited during the 3 and 12 semitones adaptation sequences (Figure 3, top right panel). The scalp topography of the difference was quite stable, with a maximum at fronto-central channels that reversed in polarity at mastoid sites (Figure 3, bottom panels), consistent with generator(s) located in the superior temporal plane near Heschl's gyrus. The Δf-related increase likely reflects the activation of additional neural populations in tonotopically organized regions of auditory cortex when the A and B tones are distant in frequency, as suggested by studies in nonhuman animals (for reviews, see Micheyl et al., 2007; Snyder & Alain, 2007b). A negative modulation was also apparent prior to the positive modulation, likely to be a mod-

ulation of the N1 wave, but was smaller and not statistically reliable, $F(2,38) = 1.91$, $p < .10$.

The key aspect of this study is the examination of ERPs during the test sequence as a function of prior auditory experience. Two different analyses were performed. In one analysis we examined the impact of the prior stimulus (Δf during adaptation) on the ERPs elicited during the test sequence. In the second analysis, we sorted the ERPs recorded during the test sequence as a function of participants' prior perception (perception during adaptation).

The ERPs elicited at the onset of the test sequence consisted of P1, N1, and P2 waves (at 80, 130, and 200 ms, respectively), which were maximal at six fronto-central electrodes (i.e., FCz/1/2, Cz/1/2). As shown in Figure 4, the P1 wave (80–90 ms) elicited by the beginning of the test decreased in amplitude as the prior Δf in the adaption sequence increased, $F(2,38) = 3.57$, $p < .001$. This effect appeared specific to the P1 wave, as the amplitudes of the N1 and P2 deflections elicited by the onset of the test sequence were little affected by the prior context.

Consistent with our hypothesis, Figure 5 (top panels) shows that presenting an adaptation sequence with a large Δf resulted in a decreased positivity during the remainder of the test sequence (i.e., after the onset of the test sequence), following the B tone. This positivity overlapped in time with the positive modulation due to increased Δf during adaptation (see Figure 3). The early portion of the positivity exhibited a maximum response at left frontal scalp regions (F3/5, FC3/5) with smaller amplitude over the right frontal area (F4/6, FC4/6). During the early positivity (230–275 ms), there was a main effect of hemisphere, $F(1,19) = 13.29$, $p < .005$, and an interaction between hemisphere and prior Δf, $F(2,38) = 4.15$, $p < .05$. This interaction was due to a larger effect of prior Δf in the left than the right hemisphere. The late portion of the ERP during the test sequence (315–345 ms) also exhibited larger increases at left frontal sites (F1/3, FC1/3) compared to right frontal electrodes (F2/4, FC2/4), $F(2,38) = 4.00$, $p < .05$. As shown in Figure 5 (bottom panels), the positive modulations at left fronto-central electrodes reversed polarity at left inferior parietal electrodes.

Figure 6 shows ERP modulations during the test as a function of perception during the adaptation when the tones composing the sequences were separated by 6 semitones. A positive modulation was observed during the test sequence that peaked at fronto-central electrodes (quantified at 110–140 ms) after participants perceived two streams during adaptation, $F(1,15) = 14.12$, $p < .005$. This modulation was not time-locked to the B tone, as with the modulations due to current and prior Δf, but instead began evolving at the beginning of the ABA- pattern. A distinct prior-perception-related positive modulation occurred during the test at left centro-parietal electrodes (CPz/1, Pz/1; quantified at 190–280 ms), $F(1,15) = 16.73$, $p < .001$. Figure 6 (bottom panels) shows that the positive modulations at fronto-central electrodes reversed polarity at mastoid electrodes. The fact that the prior-perception-related modulations were time-locked to the beginning of the ABA pattern suggests a neural process that biases perception in a sustained fashion during stimulus presentation. In contrast, the prior-stimulus-related modulation, which was time-locked to the B tone, may specifically reflect a decreased neural segregation of representations for the A and B tones when the adaptation stimulus had a large Δf.

To assess whether the effects of prior experience we observed were from the same neural generators as the effect of the current stimulus, we measured scalp patterns of voltage distribution in time ranges used in the ANOVAs above (see Figure 7). ERP
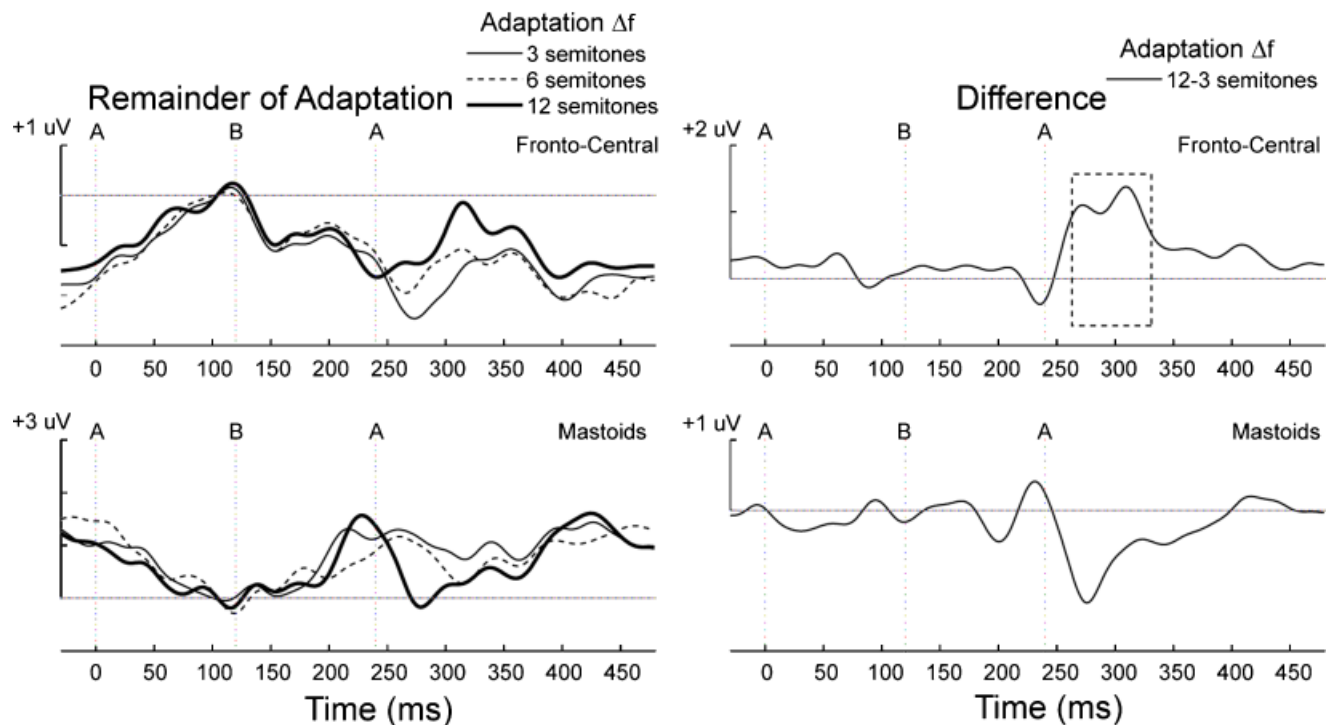
Figure 3. Effect of Δ*f* on ERPs during the remainder (not onset) of adaptation. Following the B tone, larger Δ*f* resulted in an increased positivity at fronto-central electrodes (top left) that reversed polarity at the mastoids (bottom left). Subtracting the 3-semitone condition from the 12-semitone condition revealed a positive difference wave at fronto-central electrodes that reversed polarity at mastoids (right panels). Vertical lines with labels indicate tone onsets in the ABA pattern. Dotted box on fronto-central difference wave shows time window for statistical analysis.

topographies of difference waves were quantitatively compared to each other across conditions by first normalizing amplitudes in time ranges showing maximal difference in grand averaged waveforms to values from 0 to 1 across all 72 electrodes for each participant (McCarthy & Wood, 1985). The topographies were then compared to each other using repeated measures ANOVAs, with condition and electrode (72) as factors.

We compared voltage patterns reflecting the effect of current Δ*f* (265–335 ms), both early and late effects of prior Δ*f* (230–345 ms), and the late effect of prior perception (190–280 ms). A different pattern of scalp distribution across the 72 electrodes was

observed between the difference wave reflecting current Δ*f* and prior Δ*f*, as reflected by a significant interaction between difference wave (current vs. prior) and electrode, $F(1,71) = 5.62$, $p < .001$. A significant interaction was also observed when we compared the difference waves reflecting current Δ*f* and prior perception $F(1,71) = 2.46$, $p < .05$. The topographies for prior Δ*f* and prior perception were not reliably different from each other, although this could be due to both modulations being quite small and resulting in a less powerful statistical test. Further information could be potentially gained from source localization of these modulations. Source localization of current Δ*f* modulations was consistent with previous findings, showing sources in the superior temporal plane (Gutschalk et al., 2005, 2007; Snyder & Alain, 2007a; Snyder et al., 2006). However, the small size of modulations related to prior Δ*f* and prior perception prevented the discovery of stable source locations.

Discussion

The current results demonstrated novel effects of a prior adapting stimulus and effects of prior perception on subsequent neural processing during an auditory stream segregation task. Scalp topographic analysis showed that these prior-stimulus-related and prior-perception-related neural modulations were distinct from neural modulations due to processing the current Δ*f*. Previous research has shown that activity from human primary and secondary auditory cortex is enhanced for large Δ*f* during streaming (Gutschalk et al., 2005; Snyder et al., 2006; Wilson et al., 2007). The current results therefore suggest the presence of brain regions, other than the auditory cortical areas that encode
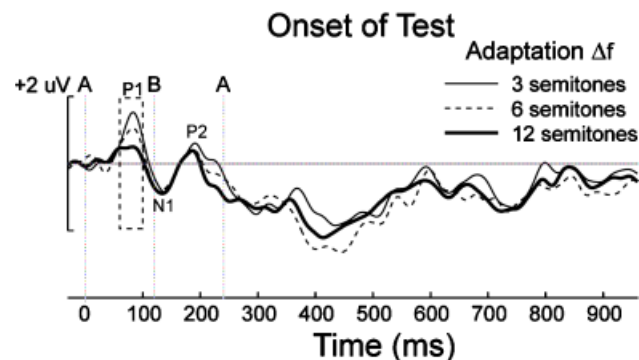
Figure 4. Effect of prior Δ*f* on ERPs at the onset of the test. Smaller Δ*f* resulted in a larger P1 response to the first tone of the test at fronto-central electrodes (mean across FCz/1/2, Cz/1/2). Vertical lines with labels indicate tone onsets in the ABA pattern. Dotted box shows time window for statistical analysis.
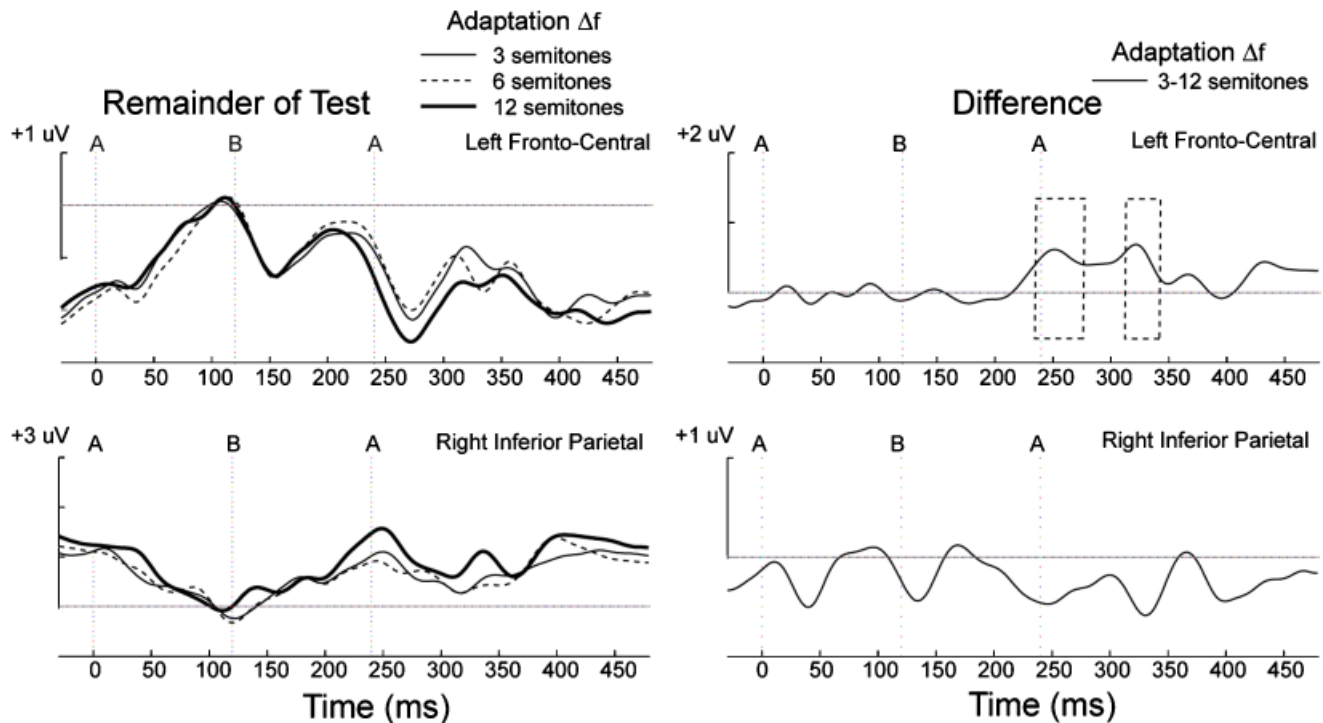
Figure 5. Effect of prior Δf on ERPs during the remainder (not onset) of test. Following the B tone, smaller Δf resulted in an increased positivity at left fronto-central electrodes (mean across FC1/3; F/1/3; top left panel) that reversed in polarity at right inferior parietal electrodes (mean across P8, P10, P08; bottom left panel). Subtracting the 12-semitone condition from the 3-semitone condition revealed a positive difference wave at fronto-central electrodes that reversed polarity at mastoids (right panels). Vertical lines with labels indicate tone onsets in the ABA pattern. Dotted box on left fronto-central difference wave shows time windows for statistical analysis.

current Δf, that are responsible for modulating perception based on prior auditory experience. Specifically, we propose that even for stream segregation based on pure-tone frequency, a complex set of processes in multiple brain regions is required to explain perception (Snyder & Alain, 2007b).

However, it is unlikely that completely different sets of brain areas are involved in coding prior auditory experience compared to the current stimulus. Specifically, despite the different topographies for modulations due to current Δf and prior Δf, the fact that neural modulations during the P1 (to the first A tone of the test pattern) and during the P2 (to the B tone of subsequent ABA-patterns) suggests that some of the neural processes affected by prior Δf are in common with those coding the current Δf (Gutschalk et al., 2005; Snyder et al., 2006). Further research using functional brain imaging measurements and source localization of ERPs could more directly show the extent of overlap in cortical areas modulated by prior auditory experience and current stimuli.

It is illuminating to compare the current results with another contextual influence during stream segregation. As already mentioned, streaming is not instantaneous, but rather occurs several seconds after the onset of the sequence (Anstis & Saida, 1985; Bregman, 1978). This buildup phenomenon coincides with changes in neural activity in primary auditory cortex (Micheyl et al., 2005; also see Snyder et al., 2006), as well as in the cochlear nucleus (Pressnitzer et al., 2008), areas that are involved in encoding the current stimulus (i.e., current Δf). Given the neural correlates of buildup in the cochlear nucleus, it is possible that buildup ultimately arises from adaptation in the auditory nerve (i.e., the periphery) and is further transformed in other subcortical and cortical brain areas. In contrast to the case of buildup, the current ERP evidence suggests that brain networks giving rise

to effects of prior experience are distinct from those giving rise to segregation based on the current stimulus. However, it is likely that despite the topographical differences, some brain regions in common are activated by current Δf and prior Δf, especially given the similar time course of activity observed for ERP modulations due to current Δf and prior Δf.

Although the precise neurophysiological mechanisms for effects of prior stimulus and prior percept are not clear, a clue is provided by the fact that a small prior Δf resulted in enhanced P1 response to the first tone of the test sequence. The neuromagnetic P1 has been shown to be sensitive to Δf and Δf_0 (difference in fundamental frequency for complex tones) during streaming and was localized to auditory cortex (Gutschalk et al., 2005, 2007). Therefore, increased P1 during the test following adaptation with small Δf could reflect increased responsiveness of the auditory cortex to tone onsets specifically when tones in a prior sequence had other tones that were nearby in frequency (i.e., small Δf). Further research using ERPs or other neurophysiological recording methods should investigate whether this represents a rebound in responsiveness of neurons following strong adaptation or some other process. It should also be determined what effect prior perception has on responses at the onset of the test, which was not possible here due to inadequate numbers of trials.

The results of this study point out that the importance of understanding how prior stimuli are encoded in auditory brain areas. Much is known about memory for prior sensory stimuli in various modalities (for a review, see Pasternak & Greenlee, 2005). However, most of this research comes from studies of discrimination of sequentially presented stimuli, in which participants are explicitly instructed to remember the first stimulus in order to compare it with a second stimulus. In both the visual and
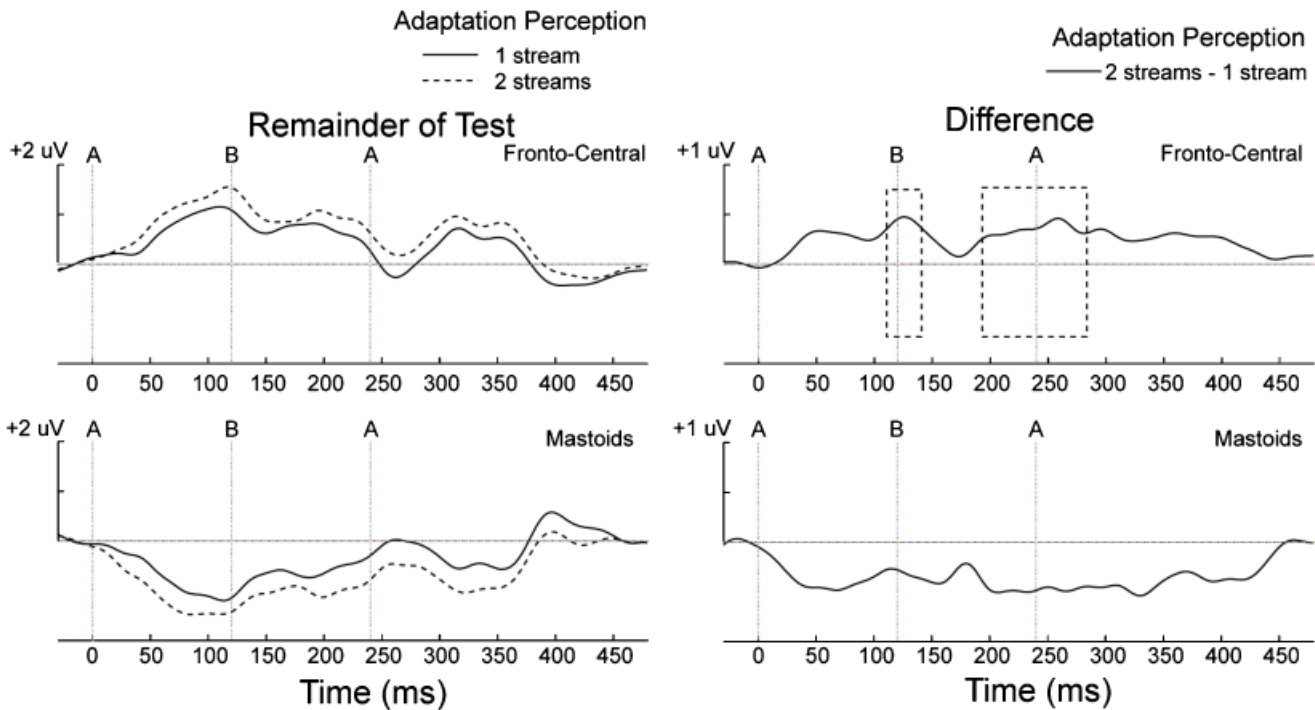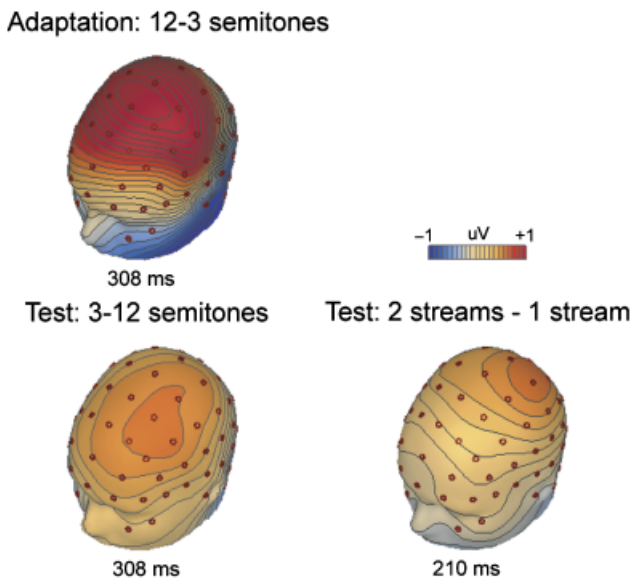
Figure 6. Effect of perception during adaptation on ERPs during test. Perceiving two streams during the adaptation resulted in an increased positivity at fronto-central electrodes (top left panel) that reversed in polarity at mastoids (bottom left panel). Subtracting the two-streams wave from the one-stream wave revealed a positive difference wave at fronto-central electrodes that reversed polarity at mastoids (right panels). Vertical lines with labels indicate tone onsets in the ABA pattern. Dotted box on fronto-central difference wave shows time window for statistical analysis.

auditory domain, various stimulus features can be stored in memory for several seconds in order to compare them with a subsequent stimulus. Thus, one important question is whether memory for stimulus details is encoded automatically even when there is no task demand to do so, as in the current study and in studies of perceptual stabilization (Pearson & Brascamp, 2008).

Figure 7. Topographies of difference waves for effect of Δf on adaptation sequence (top left), effect of prior Δf on test sequence (bottom left), and effect of perception during adaptation sequence on test sequence (bottom right). Isopotential contours reflect 0.1 µV/step.

In the auditory domain there is strong evidence for such automatic encoding in auditory cortex, based on the mismatch negativity ERP in humans (Näätänen & Winkler, 1999) and microelectrode recordings in animals (Ulanovsky, Las, Farkas, & Nelken, 2004; Ulanovsky, Las, & Nelken, 2003). Importantly, even higher order features such as melodic patterns can be encoded automatically in human auditory cortex (Alain, Achim, & Woods, 1999; Nordby, Roth, & Pfefferbaum, 1988; Schröger, 1994; Trainor, McDonald, & Alain, 2002; also see Demany & Ramos, 2005), which might be required for prior Δf to influence subsequent perception.

Very little prior research has provided evidence concerning whether prior stimuli or prior percepts modulate perception of subsequent stimuli through activity in the same or different brain areas as those responsible for encoding the current stimulus. In a study of auditory stream segregation using functional magnetic resonance imaging (fMRI), greater activity was present in the intraparietal sulcus when participants perceived two streams compared to when they perceived one stream (Cusack, 2005). It is possible that perception-related activity in this brain area could persist for several seconds and play a role in biasing perception of subsequent stimuli to be perceived as two streams. Future research using fMRI should therefore more directly pinpoint the precise brain areas that are modulated as a result of prior auditory stimuli and prior auditory perception during processing of a subsequent stimulus.

In summary, the results of this study provide evidence that recent experience of auditory stimuli or perceptual states can influence the formation of auditory streams through mechanisms that are at least partially independent from those responsible for coding the current auditory stimuli. Future research should therefore aim to show what specific brain regions are modulated

by prior experience. The current study also clearly shows that a full description of auditory stream formation will require a thorough understanding of how the representations of prior and current experience are combined to determine an individual's auditory perception.

REFERENCES

Alain, C., Achim, A., & Woods, D. L. (1999). Separate memory-related processing for auditory frequency and patterns. *Psychophysiology*, *36*, 737–744.

Anstis, S., & Saida, S. (1985). Adaptation to auditory streaming of frequency-modulated tones. *Journal of Experimental Psychology: Human Perception and Performance*, *11*, 257–271.

Beauvois, M. W., & Meddis, R. (1996). Computer simulation of auditory stream segregation in alternating-tone sequences. *Journal of the Acoustical Society of America*, *99*, 2270–2280.

Beauvois, M. W., & Meddis, R. (1997). Time decay of auditory stream biasing. *Perception & Psychophysics*, *59*, 81–86.

Brascamp, J. W., Knapen, T. H., Kanai, R., van Ee, R., & van den Berg, A. V. (2007). Flash suppression and flash facilitation in binocular rivalry. *Journal of Vision*, *7*, 1–12.

Bregman, A. S. (1978). Auditory streaming is cumulative. *Journal of Experimental Psychology: Human Perception and Performance*, *4*, 380–387.

Bregman, A. S. (1990). *Auditory scene analysis: The perceptual organization of sound*. Cambridge, MA: MIT Press.

Carlyon, R. P. (2004). How the brain separates sounds. *Trends in Cognitive Sciences*, *8*, 465–471.

Carlyon, R. P., Cusack, R., Foxton, J. M., & Robertson, I. H. (2001). Effects of attention and unilateral neglect on auditory stream segregation. *Journal of Experimental Psychology: Human Perception and Performance*, *27*, 115–127.

Cusack, R. (2005). The intraparietal sulcus and perceptual organization. *Journal of Cognitive Neuroscience*, *17*, 641–651.

Cusack, R., Deeks, J., Aikman, G., & Carlyon, R. P. (2004). Effects of location, frequency region, and time course of selective attention on auditory scene analysis. *Journal of Experimental Psychology: Human Perception and Performance*, *30*, 643–656.

Darwin, C. J. (1997). Auditory grouping. *Trends in Cognitive Sciences*, *1*, 327–333.

Demany, L., & Ramos, C. (2005). On the binding of successive sounds: Perceiving shifts in nonperceived pitches. *Journal of the Acoustical Society of America*, *117*, 833–841.

Denham, S. L., & Winkler, I. (2006). The role of predictive models in the formation of auditory streams. *Journal of Physiology (Paris)*, *100*, 154–170.

Gutschalk, A., Micheyl, C., Melcher, J. R., Rupp, A., Scherg, M., & Oxenham, A. J. (2005). Neuromagnetic correlates of streaming in human auditory cortex. *Journal of Neuroscience*, *25*, 5382–5388.

Gutschalk, A., Oxenham, A. J., Micheyl, C., Wilson, E. C., & Melcher, J. R. (2007). Human cortical activity during streaming without spectral cues suggests a general neural substrate for auditory stream segregation. *Journal of Neurosciece*, *27*, 13074–13081.

Hartmann, W. M., & Johnson, D. (1991). Stream segregation and peripheral channeling. *Music Perception*, *9*, 155–184.

Kanai, R., & Verstraten, F. A. (2005). Perceptual manifestations of fast neural plasticity: Motion priming, rapid motion aftereffect and perceptual sensitization. *Vision Research*, *45*, 3109–3116.

Leopold, D. A., Wilke, M., Maier, A., & Logothetis, N. K. (2002). Stable perception of visually ambiguous patterns. *Nature Neuroscience*, *5*, 605–609.

McCarthy, G., & Wood, C. C. (1985). Scalp distributions of event-related potentials: An ambiguity associated with analysis of variance models. *Electroencephalography and Clinical Neurophysiology*, *62*, 203–208.

Micheyl, C., Carlyon, R. P., Gutschalk, A., Melcher, J. R., Oxenham, A. J., Rauschecker, J. P., et al. (2007). The role of auditory cortex in the formation of auditory streams. *Hearing Research*, *229*, 116–131.

Micheyl, C., Tian, B., Carlyon, R. P., & Rauschecker, J. P. (2005). Perceptual organization of tone sequences in the auditory cortex of awake macaques. *Neuron*, *48*, 139–148.

Moore, B. C. J., & Gockel, H. (2002). Factors influencing sequential stream segregation. *Acta Acustica United with Acustica*, *88*, 320–333.

Näätänen, R., & Winkler, I. (1999). The concept of auditory stimulus representation in cognitive neuroscience. *Psychological Bulletin*, *125*, 826–859.

Nordby, H., Roth, W. T., & Pfefferbaum, A. (1988). Event-related potentials to breaks in sequences of alternating pitches or interstimulus intervals. *Psychophysiology*, *25*, 262–268.

Pasternak, T., & Greenlee, M. W. (2005). Working memory in primate sensory systems. *Nature Reviews Neuroscience*, *6*, 97–107.

Pearson, J., & Brascamp, J. (2008). Sensory memory for ambiguous vision. *Trends in Cognitive Sciences*, *12*, 334–341.

Pressnitzer, D., & Hupé, J. M. (2006). Temporal dynamics of auditory and visual bistability reveal common principles of perceptual organization. *Current Biology*, *16*, 1351–1357.

Pressnitzer, D., Sayles, M., Micheyl, C., & Winter, I. M. (2008). Perceptual organization of sound begins in the auditory periphery. *Current Biology*, *18*, 1124–1128.

Roberts, B., Glasberg, B. R., & Moore, B. C. (2008). Effects of the build-up and resetting of auditory stream segregation on temporal discrimination. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 992–1006.

Rogers, W. L., & Bregman, A. S. (1993). An experimental evaluation of three theories of auditory stream segregation. *Perception & Psychophysics*, *53*, 179–189.

Rogers, W. L., & Bregman, A. S. (1998). Cumulation of the tendency to segregate auditory streams: Resetting by changes in location and loudness. *Perception & Psychophysics*, *60*, 1216–1227.

Schröger, E. (1994). An event-related potential study of sensory representations of unfamiliar tonal patterns. *Psychophysiology*, *31*, 175–181.

Snyder, J. S., & Alain, C. (2007a). Sequential auditory scene analysis is preserved in normal aging adults. *Cerebral Cortex*, *17*, 501–512.

Snyder, J. S., & Alain, C. (2007b). Toward a neurophysiological theory of auditory stream segregation. *Psychological Bulletin*, *133*, 780–799.

Snyder, J. S., Alain, C., & Picton, T. W. (2006). Effects of attention on neuroelectric correlates of auditory stream segregation. *Journal of Cognitive Neuroscience*, *18*, 1–13.

Snyder, J. S., Carter, O. L., Hannon, E. E., & Alain, C. (2009). Adaptation reveals multiple levels of representation in auditory stream segregation. *Journal of Experimental Psychology: Human Perception and Performance* (in press).

Snyder, J. S., Carter, O. L., Lee, S.-K., Hannon, E. E., & Alain, C. (2008). Effects of context on auditory stream segregation. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 1007–1016.

Sussman, E., & Steinschneider, M. (2006). Neurophysiological evidence for context-dependent encoding of sensory input in human auditory cortex. *Brain Research*, *1075*, 165–174.

Trainor, L. J., McDonald, K. L., & Alain, C. (2002). Automatic and controlled processing of melodic contour and interval information measured by electrical brain activity. *Journal of Cognitive Neuroscience*, *14*, 430–442.

Ulanovsky, N., Las, L., Farkas, D., & Nelken, I. (2004). Multiple time scales of adaptation in auditory cortex neurons. *Journal of Neuroscience*, *24*, 10440–10453.

Ulanovsky, N., Las, L., & Nelken, I. (2003). Processing of low-probability sounds by cortical neurons. *Nature Neuroscience*, *6*, 391–398.

Van Noorden, L. P. A. S. (1975). *Temporal coherence in the perception of tone sequences*. Unpublished doctoral dissertation. Eindhoven: Eindhoven University of Technology.

Vliegen, J., & Oxenham, A. J. (1999). Sequential stream segregation in the absence of spectral cues. *Journal of the Acoustical Society of America*, *105*, 339–346.

Wilson, E. C., Melcher, J. R., Micheyl, C., Gutschalk, A., & Oxenham, A. J. (2007). Cortical fMRI activation to sequences of tones alternating in frequency: Relationship to perceived rate and streaming. *Journal of Neurophysiology*, *97*, 2230–2238.