

Probability dependence and functional separation of the object-related and mismatch negativity event-related potential components

Alexandra Bendixen^{a,b,*}, Simon J. Jones^c, Georg Klump^c, István Winkler^{a,d}

^a Institute for Psychology, Hungarian Academy of Sciences, Szondi utca 83-85, H-1068 Budapest, Hungary

^b Institute for Psychology I, University of Leipzig, Germany

^c Institute for Biology and Environmental Sciences, Carl von Ossietzky University of Oldenburg, Germany

^d Institute of Psychology, University of Szeged, Hungary

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ABSTRACT

The separation of concurrently presented sounds into distinct auditory objects is accompanied by the elicitation of the object-related negativity (ORN) component of the event-related potential (ERP). In the present study, participants were exposed to tone sequences containing not only concurrent (harmonicity), but also sequential cues (similarity to previous stimuli in the series) for auditory object formation. Although ORN was consistently elicited by two-object relative to one-object sounds, it was modulated by the presentation rate. With increasing probability of sound segregation, ORN amplitude decreased, and its scalp topography shifted from a bilateral towards a unilateral (left-hemispheric) activation pattern. Probability dependence of the ORN matches previous behavioral data. The differential sensitivity of the left- and right-hemispheric response to this manipulation may explain why an ORN probability effect was not obtained in previous electrophysiological studies. The specific functional role of ORN for concurrent sound perception was confirmed by dissociating it from the mismatch negativity (MMN) component as a correlate of processing sequential cues. ORN probability dependence is argued to be functionally relevant for the interaction of concurrent and sequential mechanisms of auditory scene analysis.

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Introduction

The auditory system is constantly confronted with a mixture of sounds originating from different sources. The decomposition of this mixture rests on two main types of acoustic cues (Bregman, 1990; Carlyon, 2004; Haykin and Chen, 2005; Snyder and Alain, 2007). One cue type is instantaneously available: Acoustic signals are likely to come from the same source if they share features such as location, onset, or harmonic relation. A purely *concurrent* strategy of decomposition is, however, not sufficient. For example, two sound sources moving towards each other will emit signals from the same location at the crossing point. Therefore, the auditory system searches for acoustic signals that behave in a consistent manner over time (e.g., gradual change in location). “Good continuations” most likely reflect the same source that was previously encountered. This second strategy is based on a comparison of current signals with previous input and is thus called *sequential* sound segregation. Thus concurrent and sequential strategies of sound segregation are employed together to provide a veridical decomposition of the auditory scene (Bregman,

1990). The present study was designed to investigate interactions between sequential and concurrent strategies of sound segregation using electrophysiological indices.

The object-related negativity (ORN) component of the event-related potential (ERP) accompanies concurrent sound segregation (Alain et al., 2001, 2002). ORN is usually observed between 140 and 180 ms from stimulus onset; it has a frontocentral maximum and inverts polarity at the mastoids (Alain et al., 2001; Alain and McDonald, 2007). The presence and amplitude of ORN are correlated with participants’ report on perceiving two distinct sound sources rather than just one source (Alain and McDonald, 2007; Alain et al., 2003; McDonald and Alain, 2005). The concurrent cues to which ORN is sensitive include harmonicity (Alain et al., 2001, 2002), location (McDonald and Alain, 2005), and dichotic pitch (Hautus and Johnson, 2005; Johnson et al., 2003). ORN has been successfully applied as an electrophysiological tool in developmental studies of sound segregation (Alain and McDonald, 2007; Alain et al., 2003) and speech perception (Alain et al., 2005; Snyder and Alain, 2005).

Behavioral studies have demonstrated an interaction between sequential and concurrent cues on sound organization (e.g., Ciocca and Darwin, 1999; Darwin et al., 1995; Lee and Shinn-Cunningham, 2008; Steiger and Bregman, 1982). Yet the ORN component was previously shown to be unaffected by the global probability of

* Corresponding author. Fax: +36 1 239 6727.

E-mail address: bendixen@cogpsyphy.hu (A. Bendixen).

different types of sounds within the sequence (Alain et al., 2001; Hautus and Johnson, 2005), which is an important sequential cue of sound organization. On the other hand, there is evidence for an influence of the local sequential context (the micro-sequence immediately preceding a given sound) on the event-related brain activity overlapping the ORN (Dyson and Alain, 2008a,b; Dyson et al., 2005). The present experiment was designed to test this issue in more detail. As in the majority of previous ORN studies (Alain et al., 2001, 2002, 2003; Alain and McDonald, 2007), the concurrent cue for sound segregation was chosen to be the mistuning of one harmonic of a complex tone. ORN elicitation by this mistuned partial was probed under different conditions of global sequential probability (90%, 50%, and 10%). The design additionally allowed for the identification of the mismatch negativity (MMN) component of the ERP, which is sensitive to violations of sequential expectations (Näätänen et al., 1978; Schröger, 2005; Winkler, 2007). MMN is elicited between 100 and 250 ms following the onset of a deviation from a sequential regularity (Schröger, 2005; Winkler, 2007). Similarly to that of the ORN, the MMN topography is frontocentral with polarity inversion at the mastoids. However, MMN and ORN have been shown to be distinct ERP components (Alain and Izenberg, 2003). An additional aspect of the present design was to specify this distinction.

Methods

Participants

Twelve healthy volunteers (all right-handed, seven male) participated in the experiment. Two female participants had to be excluded from the analysis due to low signal-to-noise ratio (less than 70% remaining trials after artifact rejection). Mean age of the remaining 10 participants was 21.1 years. All participants had auditory thresholds not higher than 20 dB SPL in the frequency range of 250 to 4000 Hz and no threshold difference exceeding 10 dB between the two ears (assessed with a Mediroll, SA-5 audiometer). None of the participants were taking any medication affecting the central nervous system. Prior to the beginning of the experiment, written informed consent was obtained from each participant according to the Declaration of Helsinki after experimental procedures and aims were explained to them. The study was approved by the Ethical Committee of the Institute for Psychology, Hungarian Academy of Sciences.

Apparatus and Stimuli

Participants were seated in an acoustically shielded chamber at the Institute for Psychology, Hungarian Academy of Sciences. A computer screen was placed in front of them at a distance of 1 m. Complex tones with an intensity of about 35 dB sensation level (above hearing threshold, adjusted individually for each participant) were presented binaurally via headphones and were regularly repeated every 1300 ms. Complex tones were created by combining 12 pure sinusoidal tones: 200 Hz and its 2nd to 12th harmonics (i.e., up to 2400 Hz). All pure tones were of equal amplitude and started in sine phase. Tone duration was 400 ms (including 10- ms rise and 10- ms fall times). The second harmonic was either in tune (400 Hz, subsequently denoted as *tuned* stimulus) or mistuned by 16% upwards (464 Hz, *mistuned* stimulus).

In three conditions, the probability of occurrence of the two types of stimuli was manipulated. In the *predominantly tuned* condition, 90% of the stimuli were tuned and 10% were mistuned. In the *predominantly mistuned* condition, these percentages were reversed (10% tuned, 90% mistuned). In the *balanced* condition, tuned and mistuned stimuli were presented with 50% probability each. Stimulus order was pseudo-randomized individually for each participant, with the restriction of at least four tones of the frequent type being delivered

between two successive infrequent stimuli in the unbalanced (predominantly tuned / mistuned) conditions. In the balanced condition, the number of successive stimulus repetitions was limited to four, and the number of successive stimulus changes was limited to eight. This was done in order to prevent the extraction of sequential regularities of repetition and alternation, respectively.

Procedure

Participants watched a silent, subtitled movie and were instructed to ignore the tones. Stimuli were presented in blocks of 300 stimuli each, with 2 blocks for the balanced condition and 5 blocks for each of the unbalanced conditions. The order of stimulus blocks was randomized individually for each participant. Total duration of the experiment amounted to 78 min.

Data recording and analysis

EEG was continuously recorded with Ag/AgCl electrodes placed at 59 scalp locations according to the 10% extension of the international 10–20 system (Chatrian et al., 1985; Jasper, 1958), excluding Fp1, Fp2, P9, P10, and Iz. Additional electrodes were placed halfway between FPz and the Nasion (serving as on-line reference), at the tip of the nose, and at the left and right mastoid sites. Eye movements were monitored by bipolar recordings from electrodes placed above and below the left eye (VEOG) and lateral to the outer canthi of both eyes (HEOG). EEG and EOG signals were amplified (0 to 200 Hz) by NuAmps amplifiers (Neuroscan Inc.). Electrical signals were sampled at a 500-Hz rate. Data were off-line re-referenced to the nose and filtered using a 0.1- to 30-Hz band pass filter.

For each trial, an epoch of 800-ms duration including a 100-ms pre-stimulus baseline was extracted from the continuous EEG record. Epochs with an amplitude change exceeding 100 μ V on any channel were rejected from further analysis, which led to retaining 81.4% of the stimuli on average. Epochs for the two stimulus types (tuned, mistuned) were separately averaged for the three conditions (predominantly tuned, predominantly mistuned, balanced). In the unbalanced condition, each frequent tone that immediately followed an infrequent tone was excluded from the averaging because these sounds elicit a small mismatch response as compared to the rest of the frequent sounds (Nousak et al., 1996; Sams et al., 1984). The resulting six stimulus categories are denoted as *tuned-90* (tuned stimulus in the predominantly tuned condition), *tuned-50* (tuned stimulus in the balanced condition), *tuned-10* (tuned stimulus in the predominantly mistuned condition), *mistuned-90*, *mistuned-50*, and *mistuned-10* (defined in an analogous manner).

Several types of difference waveforms were calculated to identify the ORN and MMN components. For ORN, ERPs elicited by tuned stimuli were subtracted from those elicited by mistuned stimuli of the corresponding probability, resulting in three waveforms ($ORN-90 = mistuned-90 - tuned-90$, $ORN-50 = mistuned-50 - tuned-50$, $ORN-10 = mistuned-10 - tuned-10$). For MMN, ERPs elicited by frequent stimuli were subtracted from those elicited by physically identical infrequent stimuli, resulting in two waveforms ($MMN-tuned = tuned-10 - tuned-90$; $MMN-mistuned = mistuned-10 - mistuned-90$).

Average ERP amplitudes were measured in the intervals of 125 to 165 ms (ORN) and 180 to 220 (MMN). Measurements were taken at both mastoids and at a frontocentral electrode cluster including F1, Fz, F2, FC1, FCz, and FC2. Following visual inspection, P3a was additionally measured in the ORN difference waveforms from 380 to 420 ms. Component amplitudes were tested against zero using one-sample, two-tailed *t*-tests. Only the frontal amplitudes were included in further analyses. Repeated-measures analyses of variance (ANOVAs) on the frontal amplitudes showed no significant influence of the electrode location within the frontocentral cluster (6 levels: F1, Fz, F2, FC1, FCz, FC2) nor interaction with any of the other factors;

consequently, amplitude data were averaged across these electrodes, and the electrode factor was omitted from all amplitude analyses. ORN amplitudes were compared across probability levels using a repeated-measures ANOVA with the factor Probability (3 levels: 90%, 50%, 10%). MMN amplitudes for tuned and mistuned stimuli were compared in a repeated-measures ANOVA with the factor Harmonicity (2 levels: tuned, mistuned). Both these comparisons were repeated for the latency range of the other component (i.e., activity in the MMN latency range for ORN-90, ORN-50, and ORN-10; and conversely activity in the ORN latency range for MMN-tuned and MMN-mistuned) in ANOVAs of the same structure for testing the effect on the original component.

For studying the scalp topographies in the ORN, MMN, and P3a latency ranges, ERP voltage distributions were transformed into scalp current density (SCD) distributions. The SCD analysis provides a reference-independent measure of the scalp distribution that sharpens the voltage distribution as volume-conducted signals from distant regions of the head are eliminated (Srinivasan, 2005). Therefore, the SCD distribution is primarily determined by electrical activity within a short distance of each electrode (i.e., superficial cortical tissue; Srinivasan, 2005), thus allowing one to assess local contributions to the observed ERP response. The present SCD analyses followed the spherical spline surface Laplacian algorithm of Perrin et al. (1989, 1990). The radial current at a given location on the surface (Laplacian) was computed as the second spatial derivative of the interpolated voltage distribution (Perrin et al., 1989, 1990). The maximum degree of the Legendre polynomials was chosen to be 50, and the order of splines (m) was set to 4. A smoothing parameter of 10^{-4} was applied.

SCD topographies were analyzed in four electrode clusters: left frontal (F3, F5, FC3, FC5), left central (C3, C5, CP3, CP5), right frontal (F4, F6, FC4, FC6), and right central (C4, C6, CP4, CP6). The SCD value used for each electrode cluster was the mean taken across the electrode locations in that cluster. ORN topographies were compared across probability levels in a repeated-measures ANOVA with the factors Probability (3 levels: 90%, 50%, 10%), Laterality (2 levels: left, right), and Frontality (2 levels: frontal, central). MMN topographies were compared between tuned and mistuned stimuli in a repeated-measures ANOVA with the factors Harmonicity (2 levels: tuned, mistuned), Laterality (2 levels: left, right), and Frontality (2 levels: frontal, central). Differences between ORN and MMN topographies were tested by comparing the topography of the mean of the ORN across the three probability levels with the mean of the MMN across tuned and mistuned stimuli. A repeated-measures ANOVA with the factors Component (2 levels: ORN, MMN), Laterality (2 levels: left, right), and Frontality (2 levels: frontal, central) was conducted.

Significant ANOVA effects are reported with the partial η^2 effect size measure. Post-hoc tests for statistical analyses were carried out with the Bonferroni correction of the confidence level for multiple comparisons. The assumption of sphericity was not violated in any of the ANOVAs.

Results

ORN

ERPs associated with the processing of sound harmonicity at different probability levels are depicted in Fig. 1. Significant ORN was elicited at the frontocentral electrode cluster for all probability levels [90%: $t(9) = -3.3712$, $p < .01$; 50%: $t(9) = -3.2495$, $p < .05$; 10%: $t(9) = -4.2462$, $p < .01$]. Polarity inversion at the mastoid electrodes was observed in the 90% condition [$t(9) = 3.3413$, $p < .01$], but neither in the 50% condition [$t(9) = 0.277$, $p = .788$] nor in the 10% condition [$t(9) = 0.0363$, $p = .972$]. Frontocentral ORN amplitudes were significantly modulated by probability level

[$F(2,18) = 5.066$, $p < .05$, $\eta^2 = 0.360$]. Post-hoc tests revealed that ORN amplitudes were significantly larger at 10% probability ($-1.5 \mu\text{V}$) than at 90% probability ($-0.4 \mu\text{V}$), $p < .05$, with 50% probability ranging in between ($-1.1 \mu\text{V}$) and not significantly different from either of the other probability levels (both p values $> .05$). The amplitude increase with decreasing probability was confirmed by a linear trend test, $F(1,9) = 10.691$, $p < .01$, $\eta^2 = 0.543$.

In addition to the amplitude increase, ORN topography changed across probability levels from a predominantly left-hemispheric activation pattern for 90% probability to bilateral activation patterns with a right-hemispheric preponderance for the 50% and 10% probability levels (Fig. 1). This was confirmed by an interaction of Probability and Laterality in the ANOVA on the SCD amplitudes [$F(2,18) = 4.550$, $p < .05$, $\eta^2 = 0.336$]. An additional main effect of Probability [$F(2,18) = 7.256$, $p < .01$, $\eta^2 = 0.446$] again confirmed the stronger activation with lower probabilities [linear trend test, $F(1,9) = 9.575$, $p < .05$, $\eta^2 = 0.515$]. No other main effect or interaction was significant (all p values $> .10$).

ORN was followed by a positive potential around 400 ms in the 10% probability condition [$t(9) = 2.6098$, $p < .05$], but neither in the 50% condition [$t(9) = 1.1786$, $p = .269$] nor in the 90% condition [$t(9) = -0.3948$, $p = .702$]. The SCD topography of this positive deflection (Fig. 1) was consistent with that of the P3a component (Linden, 2005; Polich, 2007) and more anterior than that of the P400 component that has been reported to follow the ORN in active conditions (Alain et al., 2001, 2002; Hautus and Johnson, 2005).

MMN

ERPs elicited by physically identical sounds differing in sequential probability are depicted in Fig. 2. Significant MMN was elicited at frontocentral electrodes by infrequent relative to frequent stimuli, whether these stimuli were tuned [$t(9) = -6.6588$, $p < .001$] or mistuned [$t(9) = -8.4034$, $p < .001$]. Polarity inversion at the mastoids was observed in both conditions [tuned: $t(9) = 6.5942$, $p < .001$; mistuned: $t(9) = 3.6097$, $p < .01$]. Frontocentral MMN amplitudes did not differ depending on the harmonicity of the sounds [$F(1,9) = 0.145$, $p = .712$]. Likewise, no difference was observed in SCD topographies between the MMN for tuned and mistuned stimuli, as Harmonicity showed no significant effect or interaction with any of the other factors in the ANOVA (all p values $> .10$). The only significant effect was one of Frontality [$F(1,9) = 17.846$, $p < .01$, $\eta^2 = 0.665$], caused by larger amplitudes for the frontal than for the central electrode clusters.

Comparing ORN and MMN

Activity in the MMN latency range was not significantly different from zero for the ORN-90, ORN-50, and ORN-10 difference waveforms (all p values $> .06$), nor was it modulated by probability level [$F(2,18) = 2.1054$, $p = .151$]. Conversely, activity in the ORN latency range was significant for mistuned [$t(9) = -5.2087$, $p < .001$] but not tuned stimuli [$t(9) = -2.5107$, $p = .06$], resulting in a significant effect of the factor Harmonicity in the ANOVA [$F(1,9) = 10.691$, $p < .01$, $\eta^2 = 0.543$]. This difference can be attributed to the effect of sequential probability on the ORN, since the MMN-mistuned difference wave results from a subtraction of 10% mistuned and 90% mistuned stimuli, with the former ones being accompanied by a larger ORN component than the latter.

The ANOVA for comparison of mean SCD topographies for ORN and MMN showed a significant interaction of Component and Frontality [$F(1,9) = 17.668$, $p < .01$, $\eta^2 = 0.663$] due to larger frontal than central amplitudes for MMN, but not for ORN. Additional main effects were observed for Component [$F(1,9) = 41.942$, $p < .001$, $\eta^2 = 0.823$] due to larger overall amplitudes for MMN than ORN, and for Frontality [$F(1,9) = 15.986$, $p < .01$, $\eta^2 = 0.640$] due to larger

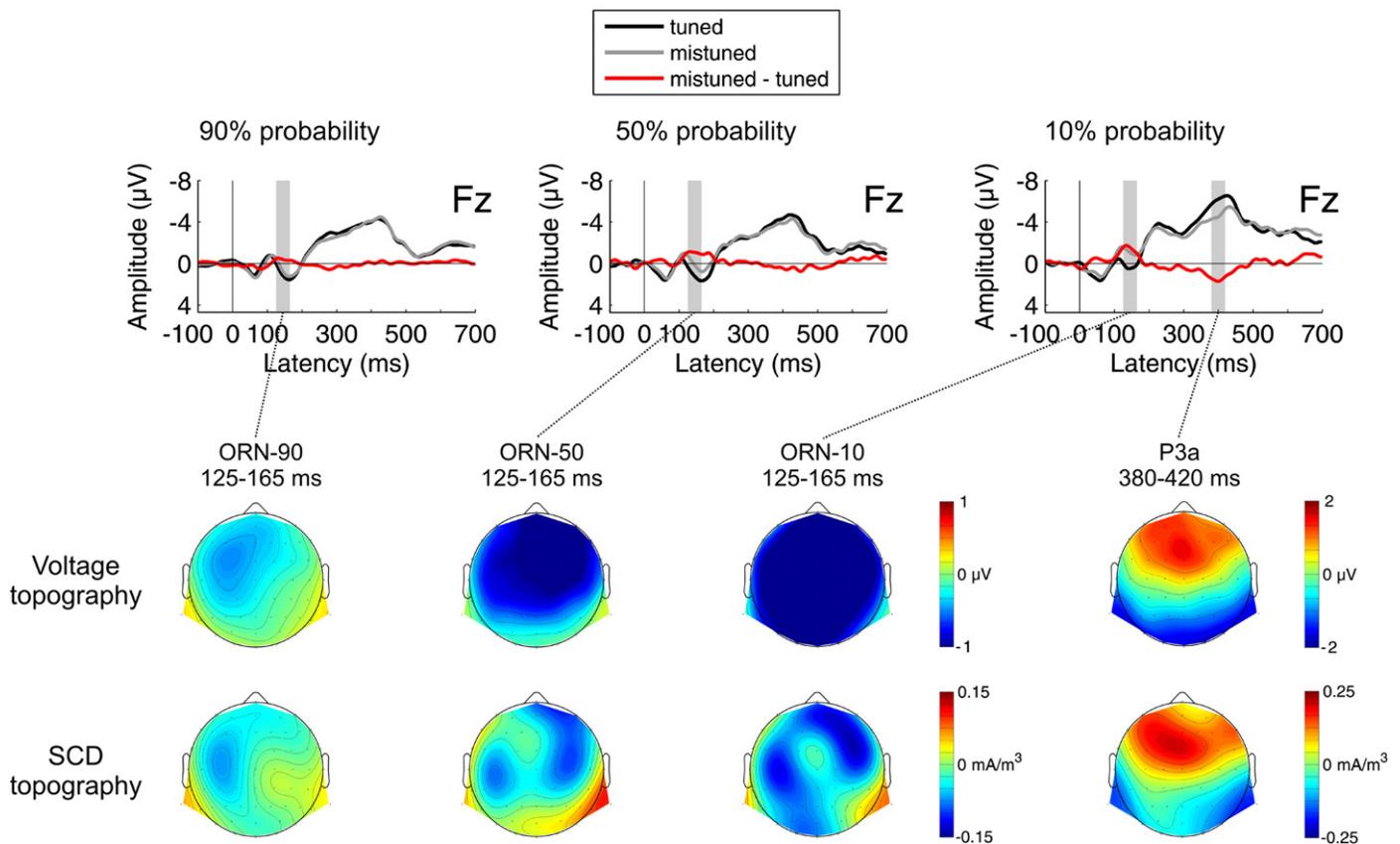


Fig. 1. Electrophysiological markers of processing a concurrent auditory cue (harmonicity). Top: Group-average ($N = 10$) frontal (Fz) ERPs elicited by tuned stimuli (black line), mistuned stimuli (gray line), and the mistuned-minus-tuned difference waveform (red line) for sequential probabilities of 90% (left panel), 50% (middle panel) and 10% (right panel). The zero time point marks tone onset. Bottom: Voltage topographies (in μV ; middle row) and SCD topographies (in mA/m^3 ; bottom row) of the ERP difference waveform in the ORN latency range for each of the probability levels and in the P3a latency range at 10% probability. Note the different scales for the ORN and P3a topographies.

frontal than central amplitudes (qualified by the interaction with Component). No other main or interaction effect reached significance (all p values $>.15$).

Discussion

The present data provide electrophysiological evidence for an influence of the history of stimulation on concurrent sound segregation. The ORN component elicited by mistuned ('two-source') relative to tuned ('single-source') sounds was modulated in amplitude and topography by the sequential probability of these stimuli. When the majority of sounds in a sequence were mistuned (i.e., biased towards perceiving them as coming from two different sources), the ORN activation pattern was stronger in the left than in the right hemisphere, and the overall ORN amplitude was relatively low. Decreasing the probability of mistuned sounds led to additional right-hemispheric activation and to an increase in the overall ORN amplitude. These findings are consistent with an interaction of sequential and concurrent cues for sound segregation (Bregman, 1990; Ciocca and Darwin, 1999; Darwin et al., 1995; Lee and Shinn-Cunningham, 2008; Steiger and Bregman, 1982) and thus further qualify the ORN component as an electrophysiological indicator of concurrent sound segregation.

In a previous study with a comparable design (Alain et al., 2001), ORN was shown to be unaffected by whether the majority of tones (70%) were tuned or mistuned. In contrast, in the same study behavioral reports on sound organization were influenced by the sequential probability of tuned and mistuned stimuli (two-source percepts were less likely when mistuning was more probable in the sequence). The lack of electrophysiological effects in the study of Alain

et al. may be attributed to the less extreme probability manipulation (70% vs. 30% as compared to 90% vs. 10% in the present study). However, Hautus and Johnson (2005) observed an ORN of undiminished amplitude in homogenous blocks (i.e., 100% probability) of 'one-source' versus 'two-source' sounds compared to a mixed (50% probability) condition, which makes it unlikely that probability alone is responsible for the difference in results.

One possibility is that the difference between the result obtained in the current study and in the study of Alain et al. (2001) is due to the fact that two different base frequencies were employed by Alain et al. (resulting in four different stimuli, two of them tuned, two mistuned). This design may have prevented the maintenance of stable sequential associations. In contrast, in the predominantly mistuned condition of the present study, the auditory system probably detected that the repeating harmonic tone and its mistuned partial commenced synchronously and arrived from the same location with a probability of 90%. These cues allowed the formation of strong sequential associations between the sounds, from which the system could have inferred that all acoustic signals came from the same source in spite of their imperfect harmonic relation. Interpreting the sequence as a single stream of sound could have reduced the ORN response by eliminating the two-stream related processes.

Alternatively, it is also possible that a part of the ORN response specifically represents a process initiating the formation of a new stream. Assuming that the mistuned stimuli occurring with a probability of 90% were always processed as coming from two separate sources, then a stable representation of the two streams could have been maintained throughout the whole stimulus block based on sequential associations between the identical mistuned sounds. In this case, the mistuned sounds did not initiate the

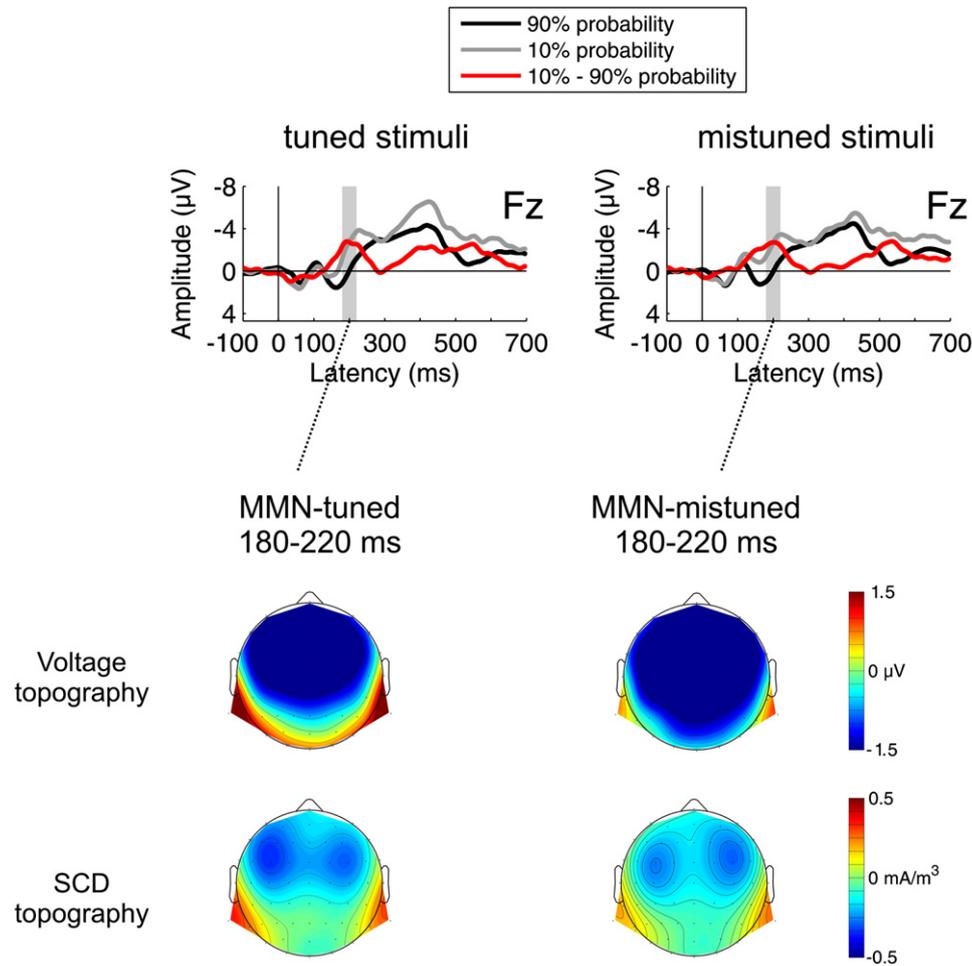


Fig. 2. Electrophysiological markers of processing a sequential auditory cue (probability). Top: Group-average ($N = 10$) frontal (Fz) ERPs elicited by frequent stimuli (black line), infrequent stimuli (gray line), and the infrequent-minus-frequent difference waveform (red line) for tuned stimuli (left panel) and mistuned stimuli (right panel). The zero time point marks tone onset. Bottom: Voltage topographies (in μV ; middle row) and SCD topographies (in mA/m^3 ; bottom row) of the ERP difference wave in the MMN latency ranges for tuned and mistuned stimuli.

formation of a representation for two streams on each presentation (because these representations already existed). In contrast, in the 10% mistuned and the 50% conditions, mistuned sounds would initiate the formation of a new stream on each presentation because they occur relatively infrequently, thus allowing the simpler source configuration promoted by the tuned sounds to become the dominant sound organization most of the time. Although the above two interpretations are mutually exclusive, both imply that a true interaction between sequential and concurrent cues for sound segregation was driving the sensitivity of ORN to stimulus probability. As both interpretations are post-hoc, they should be evaluated in future studies, which include on-line perceptual measures to allow for deciding between the two alternatives.

It remains to be considered why Hautus and Johnson (2005) did not find a probability effect on the ORN with a block-wise presentation of 100% stimuli of the same type. This discrepancy might be reconciled by the present data suggesting the existence of two separate ORN generators with differential sensitivity to stimulus probability. Unlike most previous ORN studies (e.g., Alain and McDonald, 2007; Hiraumi et al., 2005), Hautus and Johnson (2005) reported a left-hemispheric ORN lateralization (possibly due to the specific nature of their stimuli, cf. discussion in Johnson et al., 2003). Since the probability effect observed in the present study mainly concerned the right-hemispheric ORN response, this may explain why a similar effect was not present in the data of Hautus and Johnson (2005).

One might relate the present right-hemispheric activation to the superior spectral resolution in right auditory cortex (e.g., Hyde et al., 2008; Zatorre et al., 2002) while associating the left-hemispheric activation with stream segregation (e.g., Deike et al., 2004). However, it is important to consider that the left-hemispheric ORN response was activated independently of the right-hemispheric one in the 90% condition. The left-hemispheric activity can thus not represent the consequence of a right-hemispheric detection of pitch discrepancy. This consideration suggests that the functions of both ORN generators are more general than detection of mistuning alone (see also the similar conclusions of Hautus and Johnson, 2005; Snyder and Alain, 2005). In view of the limited spatial resolution of the EEG signal, future studies should verify the suggested generator structure of ORN and determine the functions of a putative left- and right-hemispheric ORN generator in concurrent auditory scene analysis.

Another new and interesting observation of the present study is the fact that the P3a component was elicited by infrequently (10%) occurring mistuned sounds as compared to infrequently occurring tuned sounds. Since P3a is associated with involuntary attention switching (Escera, Alho, Schröger, and Winkler, 2000; Friedman et al., 2001), this implies that the unexpected occurrence of a new auditory source elicits stronger attentional orienting than the unexpected absence of a previously encountered source (for a similar conclusion, see Dyson and Alain, 2008a). This asymmetry may reflect another highly functional property of the auditory system, since a new source

might be more biologically relevant (e.g., signaling danger) than the disappearance of an old source.

Although the present results (unlike previous observations) show a dependency of ORN and of its attentional consequences on the frequency of presentation, it is important to note that a significant ORN component was elicited even by 90% mistuned stimuli. Moreover, ORN was clearly different from MMN in latency, topography, amplitude, and conditions of elicitation. The present data thus support the general conclusion of previous studies (Alain et al., 2001; Alain and Izenberg, 2003; Hautus and Johnson, 2005) that the ORN component is not a 'rareness detector,' but truly associated with concurrent sound segregation. This might also shed new light on previous studies in which additional negativities elicited by mistuning partials of complex tones were interpreted as enhanced MMN rather than a combination of MMN and ORN (Tervaniemi et al., 1997, 2000a, b); please note that these studies were conducted prior to the discovery of ORN.

In summary, the present results characterize the ORN component as an electrophysiological correlate of concurrent sound segregation that is, in line with previous behavioral findings, sensitive to sequential cues of sound decomposition. The data additionally suggest the existence of at least two ORN generators with distinct characteristics. Furthermore, the stimulus protocol proved suitable for disentangling the MMN and ORN components of the ERP along several dimensions, which is promising for future studies targeting the underlying neurophysiology of sequential and concurrent sound segregation.

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