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4 **Event-related potential correlates of sound organization: early sensory and late cognitive**
5 **effects**
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4 **Abstract**
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7 We tested whether incoming sounds are processed differently depending on how the preceding
8 sound sequence has been interpreted by the brain. Sequences of a regularly repeating three-tone
9 pattern, the perceived organization of which spontaneously switched back and forth between two
10 alternative interpretations, were delivered to listeners. Occasionally, a regular tone was
11 exchanged for a slightly or moderately lower one (deviants). The electroencephalogram (EEG)
12 was recorded while listeners continuously marked their perception of the sound sequence. We
13 found that for both the regular and the deviant tones, the early exogenous P1 and N1 amplitudes
14 varied together with the perceived sound organization. Percept-dependent effects on the late
15 endogenous N2 and P3a amplitudes were only found for deviant tones. These results suggest that
16 the perceived sound organization affects sound processing both by modulating what information
17 is extracted from incoming sounds as well as by influencing how deviant sound events are
18 evaluated for further processing.
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33 **Keywords:** perceptual bistability; event-related brain potentials (ERP); oddball paradigm; early
34 vs. late processes
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Introduction

Ambiguous stimulus configurations allow more than one interpretation of the same physical input and they often result in perceptual bi-/multistability (Blake & Logothetis, 2002; Leopold & Logothetis, 1999; Pressnitzer & Hupé, 2006). For example, Necker's cube can be perceived in two different ways. When the cube is slowly rotated, the direction of the perceived rotation depends on the currently dominant perceptual alternative (Purves & Andrews, 1997). This as well as similar observations in the auditory modality (Bregman, 1990; Gutschalk et al., 2005; Schadwinkel & Gutschalk, 2011; Sussman, Ritter, & Vaughan, 1999; Winkler, Takegata, & Sussman, 2005) suggest that the current percept modulates the processing of incoming sensory information. Context-dependent processing of information is an important facet of human cognition as it, for example, allows us to identify objects quickly and with minimal processing (Bar, 2007). One important question for research is to determine the stage at which percept-dependent effects take place (Brancucci & Tommasi, 2011). Results of some studies (Gutschalk, et al., 2005; Müller, Widmann, & Schröger, 2005) suggested that the information extracted from incoming stimuli (feature analysis) can be affected by the currently held perceptual organization (early effects). In contrast, other results (Winkler, et al., 2005) suggested that only the evaluation of the extracted information is modulated by the perceptual organization (for a recent review of early vs. late effects in the visual domain, see Railo, Koivisto, & Revonsuo, 2011). The current study employed event-related brain potentials (ERP) to clarify this issue and to test whether the previously observed early percept-dependent ERP differences represent sensory- or task-related processes.

The high temporal resolution of ERPs allows one to establish the timing of effects on perceptual processes, while determining the affected component(s) helps to identify the corresponding functions. Short-latency sensory ERP responses of sound processing (also called exogenous components), such as P1 and N1, are usually associated with the processing of the physical stimulus properties; these components are strongly modulated by attentional processes (Näätänen & Picton, 1987; Picton, 2010; Snyder, Alain, & Picton, 2006). Longer-latency ERP responses such as N2 and P3a (endogenous components) are known to reflect higher-order cognitive processes (Picton, 2010) including conscious perception of sensory events (Leppert, Goodin, &

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4 Aminoff, 2003). Specifically, the N2 component has been linked with stimulus classification
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6 (Ritter & Ruchkin, 1992; Ritter, Simson, Vaughan, & Friedman, 1979), whereas subcomponents
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8 of the P3a have been associated with attention switching (Escera, Alho, Schröger, & Winkler,
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10 2000; Friedman, Cycowicz, & Gaeta, 2001; Polich, 2007; Schröger, 1996) or a contextual
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12 evaluation of novelty (Horváth, Winkler, & Bendixen, 2008).
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14 We investigated the ERP correlates of the consciously experienced auditory percept by utilizing
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16 a bistable auditory stimulus configuration, the auditory streaming paradigm (van Noorden,
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18 1975). In this paradigm, a repeating three-tone pattern is presented to listeners: *ABA*, where *A*
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20 and *B* differ in some feature, such as pitch, and the tone triplets are separated by a silent interval
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22 equaling the sum of the common tone duration and the inter-stimulus interval. Depending on the
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24 amount of feature separation between *A* and *B* and the presentation rate, listeners tend to perceive
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26 the sounds as a single coherent sequence (termed the *integrated percept*) or as two sound streams
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28 (termed the *segregated percept*), one consisting only of the *A*, the other of only the *B* tones
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30 (Bregman, 1990; van Noorden, 1975). For longer (> 1 minute) sequences of this type, perception
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32 switches back and forth between the two sound organizations (Anstis & Saida, 1985; Bendixen,
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34 Denham, Gyimesi, & Winkler, 2010; Denham & Winkler, 2006; Hill, Bishop, Yadav, & Miller,
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36 2011; Pressnitzer & Hupé, 2006; Roberts, Glasberg, & Moore, 2002).
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38 Using the auditory streaming paradigm, three previous studies investigated percept-dependent
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40 changes in sound processing. The results of these studies are not consistent regarding the stage of
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42 the processing influenced by perceptual organization. Gutschalk and colleagues' (2005) results
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44 showed percept-dependent modulation of the auditory magnetic P1 and N1 responses (Picton,
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46 2010), suggesting that perceptual organization affects early sensory processes. In contrast, in
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48 Winkler et al.'s study (2005) short-latency responses were affected only by the parameters of the
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50 stimulus configuration, whereas a later, negative component peaking ca. 175 ms from stimulus
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52 onset varied together with the listener's perception. Although both studies used the auditory
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54 streaming paradigm with stimulus parameters promoting the perception of the integrated and
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56 segregated organizations with approximately equal probabilities, two differences between the
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58 procedures and the strategy of data analysis may have resulted in the contrasting findings. First,
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60 in Gutschalk et al.'s study (2005; Experiment 2), listeners were instructed to focus their attention
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62 differently when experiencing the two possible percepts: whereas listeners were only instructed
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4 to report the perception of the integrated percept, they were to focus either on the high or on the
5 low stream, when experiencing the segregated percept. In contrast, Winkler et al.'s (2005)
6 participants were only required to continuously indicate the experienced sound organization.
7 This procedural difference may have resulted in differences in the allocation of attention in the
8 two studies, and attention is known to modulate the P1 and N1 ERP components (Näätänen &
9 Picton, 1987; Picton, 2010; Snyder, et al., 2006). Therefore, it is not clear whether the early
10 effects observed by Gutschalk et al. (2005) represent direct modulations of sensory processes or
11 whether they were mediated by task-related top-down processes. Second, Winkler et al.'s (2005)
12 data analysis focused on responses to occasional omissions of the middle (*B*) tone of the *ABA*
13 triplets. Thus, unlike Gutschalk et al.'s (2005) results, which describe the processing of the
14 regular sounds, Winkler et al.'s (2005) results characterize deviance detection as a function of
15 the perceived sound organization with no exogenous responses triggered by the deviant events
16 (i.e., the deviant events were caused by the omission of an expected sound). Müller et al. (2005)
17 also showed that the N1 amplitude was influenced by whether participants heard the sound
18 sequences as segregated or integrated. However, these authors manipulated sound organization
19 by presenting the tones at different delivery rates and did not check how participants actually
20 perceived the sound sequence, as they were instructed to ignore the sounds. Therefore, the results
21 of this study cannot be directly compared with those of Gutschalk et al.'s (2005) and Winkler et
22 al.'s (2005) and due to the lack of attention control, possible attentional effects cannot be ruled
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41 In the current study, we measured the ERP correlates of perceived sound organization in
42 sequences composed according to the auditory streaming paradigm while listeners were
43 instructed to continuously indicate the perceived sound organization. The *A* and *B* tones differed
44 in frequency (pitch), and their regular presentation was infrequently violated by exchanging the
45 second *A* tone of the triplet for a tone which was either slightly (termed *small deviants*) or
46 moderately (termed *moderate deviants*) lower in frequency than the standard *A* tones.
47 Participants were instructed to continuously mark their perception during the tone sequences,
48 with no additional instructions in terms of the allocation of attention.
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57 We expected early effects of perceptual organization on auditory processing to be reflected by
58 percept-dependent modulations of the exogenous ERP components (such as P1 or N1), whereas
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4 late effects should appear as modulations of endogenous components such as the N2 and/or P3a.
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6 With respect to the controversy between the two above reviewed studies (Gutschalk, et al., 2005;
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8 Winkler, et al., 2005), if the differences in finding early vs. late percept-dependent ERP effects
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10 stemmed from measuring responses for regular vs. irregular sounds, we should then expect to
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12 find in the current experiment that perceptual organization influences the P1 and N1 components
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14 elicited by the regular tones and the N2 elicited by the deviant tones. If, however the contrasting
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16 results were due to differences in the allocation of attention in the two studies, then similarly to
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18 Winkler et al. (2005) we should find only late percept-dependent effects, as the instructions in
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20 the current study were similar to the ones used in that study.

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22 Finally, based on Helson's adaptation level theory (Helson, 1964) one could expect an
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24 interaction between the effects of perceptual organization and the amount of deviation. This is
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26 because while perceiving the integrated organization, the range of frequencies is wider within the
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28 group of tones belonging to the same perceptual unit than when one perceives separate
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30 homogeneous streams. Therefore, in the segregated case, smaller amounts of deviation could
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32 become more salient. In contrast, larger deviations could induce equal salience under the two
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34 perceptual organizations. Thus on this hypothesis, we should observe an interaction between the
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36 perceptual organization and the amount of deviation.

37 38 39 **Methods**

40 41 42 *Participants*

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46 Twenty-four young healthy volunteers took part in the experiment (19-26 years of age, average:
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48 21.5, 13 female). All of them had normal hearing as their hearing threshold did not exceed 25 dB
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50 HL or 10 dB difference between the ears in the 250 to 8000 Hz frequency range. None of the
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52 participants took any medications affecting the central nervous system. Written informed consent
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54 was obtained from the participants after the experimental procedures were explained to them.
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56 The study was approved by the Ethical Committee of the Institute for Psychology of the
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58 Hungarian Academy of Sciences. Participants received modest financial compensation.

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4 *Stimuli and conditions*
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8 Participants were presented with continuous sequences of *ABA_* cycles where *A* and *B* stand for
9 pure tones differing only in frequency and ‘_’ stands for a silent gap equaling the common tone
10 duration of 75 ms (including 10 ms linear onset and 10 ms linear offset ramps). Individual tones
11 were delivered with a uniform 150 ms onset-to-onset interval. Sound intensity was set 40 dB
12 above the participant’s individual hearing threshold established for the same *ABA_* sequence as
13 was used in the experiment. The frequency of the *A* tones was 400 Hz and *B* tones (504 Hz) were
14 four semitones (ST) higher than the *A* tones. Deviant tones always appeared in the position of the
15 second *A* tone in the *ABA_* cycle (Figure 1). *Small deviants* were 0.5 ST, *moderate deviants* were
16 1.5 ST lower than the regular (standard) *A* tones. These parameters were selected on the basis of
17 a behavioral pilot experiment. The goal of this pilot was to find parameters with which the
18 integrated and segregated percepts are reported in approximately equal percentage of the time.
19 The amount of deviation was set so that even the moderate deviants did not cause a perceptual
20 reset (Cusack, Deeks, Aikman, & Carlyon, 2004). This was tested by comparing the percept
21 proportions between sequences with only standard *ABA_* triplets with those obtained for
22 sequences including deviant tones. Neither in the pilot nor in the main experiment did we find a
23 significant difference in the percept proportions between sequences with and without deviants
24 (see below; results of the pilot experiment are not reported as they were qualitatively identical
25 with those of the main experiment). Thus the introduction of the deviants did not significantly
26 change the dominance percentage of the integrated and segregated percepts compared with the
27 same tone sequence having only standard tones. Each deviant appeared with 5% probability.
28 Deviants were pseudo-randomly intermixed in the sequence with the criterion that successive
29 deviants were separated by at least two standard *ABA_* cycles and that no deviant tones were
30 introduced within the first 30 s of the sequences. Overall, 15 stimulus blocks were delivered,
31 each lasting for 5.5 minutes and consisting of 550 *ABA_* cycles. One stimulus block, delivered at
32 a random position within the experimental session, did not contain deviants and was used for
33 control purposes. The remaining stimulus blocks included 55 deviant tones, each (small and
34 moderate deviants, together).
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Experimental design

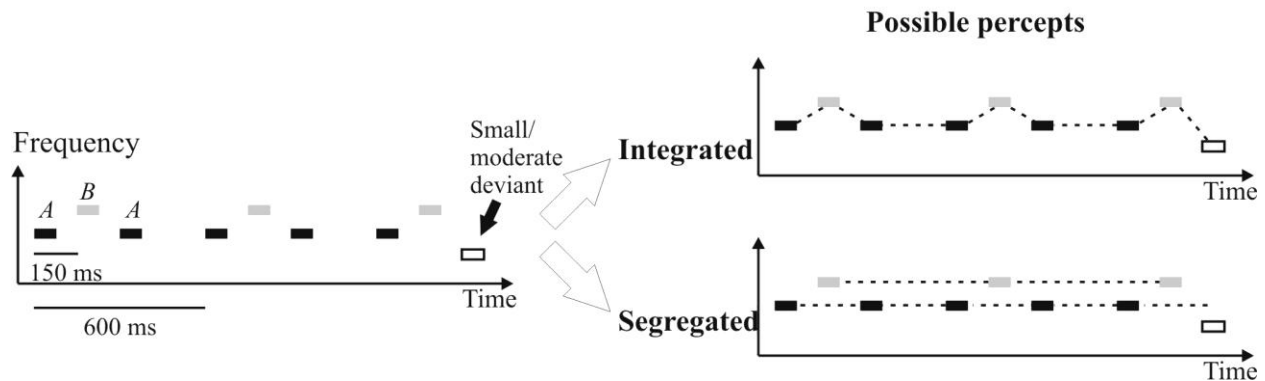


Figure 1. Experimental design. The left panel shows the structure of the sequences including the deviant tones. The black and grey rectangles represent the different tones (A and B). The right panel shows the possible perceptual organizations.

Procedure

Participants were seated in a comfortable chair in a sound-attenuated experimental chamber located at the Institute of Cognitive Neuroscience and Psychology, Research Centre for Natural Sciences, Hungarian Academy of Sciences. Sound sequences were presented binaurally with Sennheiser HD 600 headphones. Participants were instructed to listen to the sequence and continuously mark their perception using two response keys, holding one in each hand. They were asked to release both response keys when they did not hear any regularly repeating sound pattern (termed the *neither percept*). One of the keys was designated to indicate hearing either a repeating A and/or a repeating B tone, with the A tones being connected only with A and B tones only with B tones (e.g. A_A_A... and/or B__B__B...; termed the *segregated percept*). The other response key was to be depressed when a regularly repeating pattern including both A and B tones was heard (e.g., ABA_ABA_...; termed the *integrated percept*). Finally, both keys were to be depressed concurrently when the participant heard a repeating pattern in which the A and the B tones were linked together (e.g., AB__AB...) and, at the same time, another repeating pattern made up of identical tones (e.g., A__A__A...; termed the *both percept*). The state of the response keys was sampled at 250 Hz. In instructing the participants, the experimenter emphasized to always report the currently perceived sound organization and switch between the response keys as soon as their perception changed. The arrangement of the two response keys

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4 was balanced across participants to eliminate the effects of handedness. Participants were
5 instructed to fixate on a cross shown in the middle of a computer screen located ca. 1 m in front
6 of their head, and to keep their eyes open during the stimulus blocks. The experimenter
7 explained the instructions to the participant with the help of auditory and visual illustrations and
8 then made sure that the instructions were understood by presenting short tone sequences which
9 strongly promoted either integration or segregation and asking the participant to press the
10 corresponding response key(s). Depending on the participant, the instruction period lasted for 15-
11 20 minutes. In the main experiment, participants were allowed to relax for about two minutes
12 between stimulus blocks with longer breaks inserted whenever needed. On average, the
13 experimental session lasted for 240 minutes, including pauses, training, as well as electrode
14 application and removal.
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26 *EEG recording*

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30 The electroencephalogram (EEG) was recorded with Ag/AgCl electrodes and Synamps
31 amplifiers (Neuroscan Inc.) at the Fp1, Fp2, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3,
32 Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, O1, Oz, O2 scalp locations (10-20 system)
33 as well as at the left and right mastoids (LM and RM). The common reference electrode was
34 attached to the tip of the nose and the ground electrode to the forehead. The electrooculogram
35 (EOG) was recorded between two electrodes attached above and below the left eye (vertical
36 EOG) and between two electrodes placed lateral to the left and right outer canthi (horizontal
37 EOG). The sampling rate was 1000 Hz and signals were on-line filtered with a 40 Hz low-pass
38 filter.
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48 *Data analysis*

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52 From the continuous record, perceptual phases were extracted. A perceptual phase is a
53 continuous time interval during which the same combination of response keys was depressed
54 indicating that the same sound organization was perceived during the interval (which was
55 preceded and followed by a different percept). Thus the sequence of the sampled response key
56 combinations was analyzed in terms of a sequence of perceptual phases, each having two
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4 parameters: type of percept (segregated, integrated, both, or neither) and duration of percept.
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6 Only the integrated and segregated perceptual phases were analyzed statistically, because the
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8 overall probability of the other two percepts (“both” and “neither”) was marginal (< 6.7%
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10 together on average).

11 12 13 Behavioral data

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17 Because participants may have been inaccurate in synchronizing their button press and release
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19 movements with their percept (e.g., when switching from marking segregated to marking
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21 integrated), perceptual phases shorter than 300 ms were removed from the analysis (cf. Moreno-
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23 Bote, Shpiro, Rinzel, & Rubin, 2010). The proportion of the percepts was calculated as the
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25 percentage of time spent in one or another percept. The percept proportions measured in the
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27 control stimulus block were compared by dependent Student’s *t* test with those averaged from
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29 the 14 stimulus blocks with deviants to check the effects of the presence of deviants on the
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31 perception of the stimulus sequences.

32 33 ERP data

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37 EEG was down-sampled to 250 Hz and off-line filtered with a Kaiser passband filter between 0.1
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39 and 20 Hz. Epochs of different time windows were formed (see below) and averaged for
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41 standard and deviant ERPs after rejecting those epochs in which the signal range throughout the
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43 epoch was below 0.1 μV or above 100 μV at any channel. Five participants out of the twenty-
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45 four had fewer than 75 artifact-free deviant-stimulus ERP responses either in the integrated or
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47 the segregated percept. Data from these participants were excluded from the analysis. Epochs
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49 from the first 30 s of each stimulus block were also excluded from the analysis to reduce the
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51 effect of the first percept on the results. The first percept has been reported to have substantially
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53 different characteristics compared with those of the remaining percepts in the stimulus blocks
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55 (Denham, Gyimesi, Stefanics, & Winkler, 2010, in press). Integrated-minus-segregated ERP
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57 difference waveforms were calculated.

58 59 Responses to the standard tones

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4 From the continuous EEG record, epochs of 825 ms duration were extracted for the standard tone
5 triplets, starting 75 ms before the onset of the first A tone (*A1*). The baseline was set to the 75-ms
6 interval preceding *A1*. Local maxima were identified on the central (Cz) group-average ERP
7 waveforms. Both *A1*, *B*, and the following A (*A2*) elicited a positive-going peak at about 75 ms
8 from tone onset followed by two successive negative-going peaks at about 110 and 200 ms.
9 These waveforms were identified as the P1, N1, and N2 components, respectively (Figure 2, left
10 panel). Note that with a fixed short SOA, the late ERP components elicited by the previous tone
11 and the early components elicited by the next one cannot be fully separated. This issue may have
12 affected the measurement of the early components elicited by *B* and *A2*, and the late components
13 elicited by *A1* and *B*. Amplitudes were measured at F3, Fz, F4, C3, Cz, C4, P3, Pz and P4. Time
14 windows for analyzing the ERP responses to *A1* tones were set at 69-99, 101-131, and 181-211
15 ms from *A1* onset. Time windows for analyzing the ERP responses to *B* tones were set to 217-
16 247, 257-287 and 329-359 ms from the *A1* onset (67-97, 107-137 and 179-209 ms from the onset
17 of *B*). Time windows for analyzing the ERP responses elicited by the *A2* tones were set at 365-
18 395, 405-435, and 497-527 ms from the onset of *A1* (65-95, 105-135, and 197-227 ms with
19 respect to the onset of *A2*). N1 and N2 amplitudes were measured in two ways: 1) relative to the
20 pre-pattern (i.e., pre-*A1*) baseline and 2) relative to the mean amplitude of the preceding P1
21 component. The latter was done in order to test whether these components were separately
22 modulated or together by a slow shift covering the latency range of all three ERP components.
23 For this measurement, the P1 mean amplitude (as defined above) was subtracted from the N1 and
24 N2 amplitudes (again, as defined above). Amplitude measurements were analyzed separately for
25 each tone (*A1*, *B*, and *A2*), component (P1, N1, and N2), and measurement (relative to the
26 pre-pattern baseline and to P1) by repeated-measures analyses of variance (ANOVAs) with the
27 following factors: Percept (integrated, segregated) \times Laterality (left, middle, right) \times Anterior-
28 posterior (frontal, central, parietal).
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51 Responses to the deviant tones

52 For the deviant tones, epochs of 575 ms duration, commencing 75 ms before the onset of the *A2*
53 tone, were collected. The baseline was set to the 75-ms interval before the *A2* onset. Local
54 maxima were identified in the grand average ERP waveforms at the Cz electrode: Deviants also
55 elicited a positive and two successive negative waveforms, peaking at about 75, 110 (segregated
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4 small deviant, only) and 200 ms from stimulus onset, which were identified as P1, N1 and N2,
5 respectively. For the *moderate deviants* only, these were followed by a positive waveform which
6 peaked at about 340 ms from the A2 onset and was identified as a P3a component (Figure 3, top
7 panels). For statistical analyses, amplitudes were measured from 30-ms intervals, set at P1 and
8 N1 peaks (60-90, based on the peak measured for the segregated small deviant, and 95-125 ms,
9 respectively) and at the local maxima of the central (Cz) *integrated-minus-segregated* difference
10 waveform within the latency ranges of N2 (197-227 ms for *small* and 180-210 ms for *moderate*
11 *deviants*). Because *small deviants* did not elicit a discernible P3a, it was only measured for
12 *moderate deviants* in the time window of 335-365 ms. P1, N1, and N2 amplitudes were entered
13 into separate repeated-measures ANOVAs with factors of Percept (integrated, segregated) ×
14 Deviant-type (small, moderate) × Laterality (left, middle, right) × Anterior–posterior (frontal,
15 central, parietal). Because the morphology of the ERPs elicited by *small* and *moderate deviants*
16 were visibly different in the P3a range, separate ANOVAs of Percept (integrated, segregated) ×
17 Laterality (left, middle, right) × Anterior–posterior (frontal, central, parietal) were conducted for
18 them.

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33 Statistical analyses were conducted with the STATISTICA software. All significant effects are
34 reported together with the partial η^2 effect size measure. Greenhouse–Geisser correction was
35 applied where appropriate and the ϵ correction factors are reported. *Post hoc* tests were
36 performed using Tukey HSD.

41 42 **Results**

43 44 45 *Behavioral measures*

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48 On average the integrated percept was experienced in 48.15% of the stimulation time
49 (S.D. = 10.7%) in the experimental and in 52.84% (S.D. = 14.6%) in the control stimulus blocks.
50 The average proportion of the segregated percept was 44.99% (S.D. = 12.2%) and 42.76%
51 (S.D. = 14.9%) in the experimental and control stimulus blocks, respectively. The deviants did
52 not cause significant changes in the proportions of the two percepts (integrated percept:
53 $t(18) = 1.31$; $p = .80$, segregated percept $t(18) = -0.67$; $p = .51$).

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4 *ERP measures*

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6 *Responses to the standard tones*

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8 Table 1. summarizes the significant amplitude effects found for the standard tones. Because our
9 study was aimed at finding ERP correlates of perceptual organization, only main effects and
10 interactions involving the Percept factor are referred in the text. Significant main effects of
11 *Percept* were found for the P1 and N1 components elicited by the *A1* tones with the segregated
12 responses being positively displaced compared to the integrated ones during the latency range of
13 both components. For the N1 component, also significant interactions were found between
14 *Anterior-posterior* and *Percept* and between *Laterality* and *Percept*. The scalp distribution of the
15 N1 component was more parietally distributed for the integrated than for the segregated percept
16 (less positive; Figure 2, right panel). This was verified by post-hoc tests showing larger
17 amplitude differences between the integrated and segregated N1 components over parietal than
18 central or frontal electrode sites (Tukey HSD with $df=36$: all p values $<.05$), and on the left side
19 and the midline than over the right electrode sites (Tukey HSD with $df=36$: all p values $<.05$).
20 Note that a modulation of the amplitude of the typically frontocentrally maximal N1 wave should
21 not result in a parietally higher change. No significant *Percept* effect was obtained for the N2
22 component.
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36 ANOVAs of the P1 and N1 amplitudes elicited by the *B* tones yielded significant main effects of
37 *Percept*, again, reflecting a positive displacement of the segregated compared to the integrated
38 ERP responses. No significant effects including the *Percept* factor were found for the N2
39 elicited by the *B* tones or any of the components elicited by the standard *A2* tones.
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44 The ANOVAs of the N1 and N2 amplitudes measured with respect to the preceding P1 peak
45 revealed no significant effect of *Percept* for any of the tones (*A1*, *B* and *A2*), suggesting that the
46 effects of perceptual organization found for the measurements taken with respect to the pre-
47 pattern baseline for these three components are not independent of each other.
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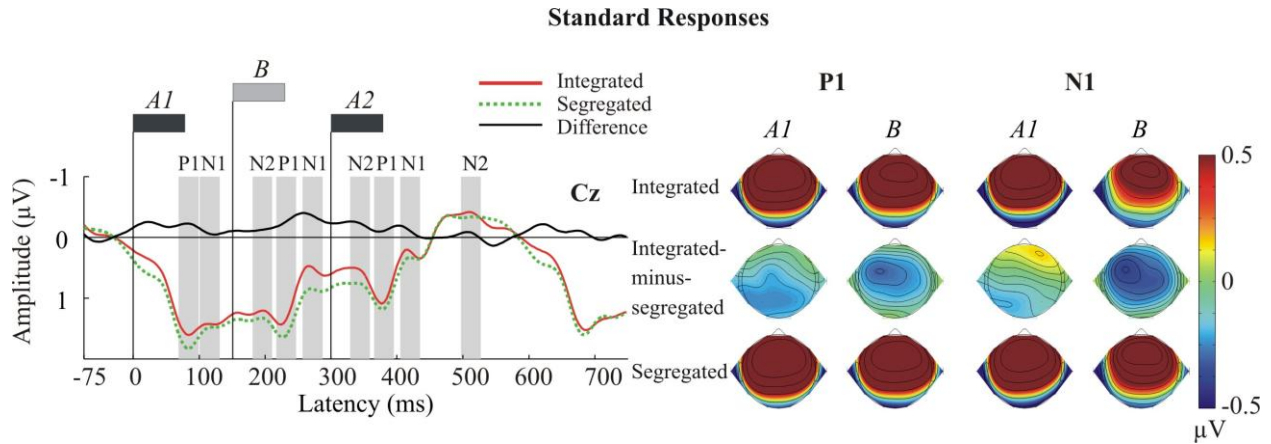


Figure 2. Left panel: ERP responses elicited by the standard tones at Cz (red continuous line: integrated, green dotted line: segregated, black continuous line: *integrated-minus-segregated* difference waveform). Tone onsets are marked by vertical lines and the tones themselves by horizontally oriented rectangles, separately for the *A1*, *B* and *A2* tones. ERP measurement windows for the standard-pattern responses are marked by gray vertical bars with the name of the corresponding component on top. Right panel: Scalp topographies for the integrated (top), *integrated-minus-segregated* (middle), and segregated (bottom) P1 and N1 amplitudes (measured in the same windows as for the statistical analyses) elicited by the standard *A1* (left) and *B* tones (right). Maps were spline interpolated with a smoothing factor of 10^{-7} . Common calibration for the color maps is shown on the right side.

Table 1. Significant results of the ANOVAs for the standard *A1*, *A2*, and *B* tones, separately. ANOVA factors are listed in Methods. The “Reference” column refers to whether the amplitudes were measured with respect to the baseline or the mean amplitude of the preceding P1 response. Degrees of freedom (df), F values, significance levels (p), Greenhouse-Geisser correction factors (where applicable), and η^2 effect sizes are given for each significant effect.

Tone	Component	Reference	ANOVA factor	df	F	p	G-G ϵ	η^2
standard <i>A1</i>	P1	Baseline	Anterior–posterior	2,36	68.90	0.001	0.60	0.79
		Baseline	Laterality	2,36	15.85	0.001	0.76	0.47
		Baseline	Percept	1,18	6.57	0.05		0.27
		Baseline	Anterior–posterior × Laterality	4,72	4.50	0.05	0.51	0.20
	N1	Baseline	Anterior–posterior	2,36	79.68	0.001	0.61	0.82
		Baseline	Laterality	2,36	12.62	0.001	0.70	0.41

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		Baseline	Anterior–posterior × Laterality	4,72	7.15	0.001	0.65	0.28
		Baseline	Anterior–posterior × Percept	2,36	4.60	0.05	0.56	0.20
		Baseline	Laterality × Percept	2,36	3.91	0.05	0.87	0.18
		P1	Anterior–posterior	2,36	20.56	0.001	0.56	0.53
	N2	Baseline	Anterior–posterior	2,36	38.75	0.001	0.59	0.68
		Baseline	Laterality	2,36	6.45	0.01	0.73	0.26
		Baseline	Anterior-posterior × Laterality	4,72	2.79	0.05	0.82	0.13
		P1	Anterior–posterior × Laterality	4,72	3.07	0.05	0.68	0.15
standard B	P1	Baseline	Anterior–posterior	2,36	57.57	0.001	0.58	0.76
		Baseline	Laterality	2,36	7.337	0.01	0.698	0.29
		Baseline	Percept	1,18	8.336	0.01		0.317
	N1	Baseline	Anterior-posterior	2,36	29.18	0.001	0.56	0.62
		Baseline	Laterality	2,36	9.00	0.01	0.91	0.33
		Baseline	Percept	1,18	11.31	0.01		0.39
		P1	Anterior-posterior	2,36	22.97	0.001	0.598	0.56
		P1	Anterior-posterior × Laterality	4,72	2.95	0.05	0.68	0.14
	N2	Baseline	Anterior–posterior	2,36	4.80	0.05	0.60	0.21
		Baseline	Laterality	2,36	4.97	0.05	0.94	0.22
		P1	Anterior-posterior	2,36	74.13	0.001	0.65	0.80
		P1	Anterior-posterior × Laterality	4,72	3.26	0.05	0.79	0.15
standard A2	P1	Baseline	Anterior–posterior	2,36	22.92	0.001	0.59	0.56

	Baseline	Laterality	2,36	4.65	0.05	0.90	0.21
N1	Baseline	Anterior–posterior	2,36	25.11	0.001	0.58	0.58
	P1	Anterior-posterior	2,36	4.59	0.05	0.558	0.20
N2	Baseline	none					
	P1	Anterior-posterior	2,36	25.42	0.001	0.58	0.59
	P1	Laterality	2,36	18.62	0.001	0.76	0.51

Responses to the deviant tones

A significant interaction was found between *Percept*, *Anterior-posterior*, and *Laterality* for the amplitude of the P1 elicited by the deviant tones. The scalp distributions of the integrated-minus-segregated differences (Figure 3, bottom panels) mirror the results of the post-hoc tests showing that the difference was smallest over right anterior electrodes (Tukey HSD with $df= 72$: all p values $< .001$).

No significant effects were obtained for the N1 amplitude that included the *Percept* factor.

For N2, significant main effects of *Percept* and *Deviant-type* were found and both of these factors showed significant interaction with the *Anterior-posterior* factor. The N2 component elicited by deviants during integrated percept was more negative than that for deviants during segregated percept, and *moderate deviants* elicited more negative responses than *small deviants*. The interaction between *Percept* and *Anterior-posterior* (Figure 3, bottom panels) was due to larger central and parietal than frontal N2 amplitude differences between the integrated and segregated responses (Tukey HSD with $df= 36$: all p values $< .001$). *Deviant-type* had a larger effect frontally than over central and parietal regions, causing the interaction with the *Anterior–posterior* factor (Tukey HSD with $df= 36$: all p values $< .001$).

The ANOVA for the P3a elicited by the *moderate deviants* yielded a significant main effect of *Percept* (higher P3a amplitudes for segregated than integrated deviants) and an interaction between *Percept* and *Anterior–posterior* as well as between *Percept* and *Laterality*. These interactions (Figure 3, bottom right panel) were caused by the P3a amplitude difference being larger centrally and parietally than frontally (Tukey HSD with $df= 36$: all p values $< .001$) as

well as over the midline than laterally (Tukey HSD with $df=36$: all p values $< .001$). Note that the scalp distribution of the percept-dependent differences in the N2 and P3a latency ranges are 1) quite similar to each other and 2) quite different from that of either component (hence the significant interactions between the *Percept* and the electrode location factors; see Figure 3). This again suggests that the effects of perceptual organization on these two components are not independent of each other.

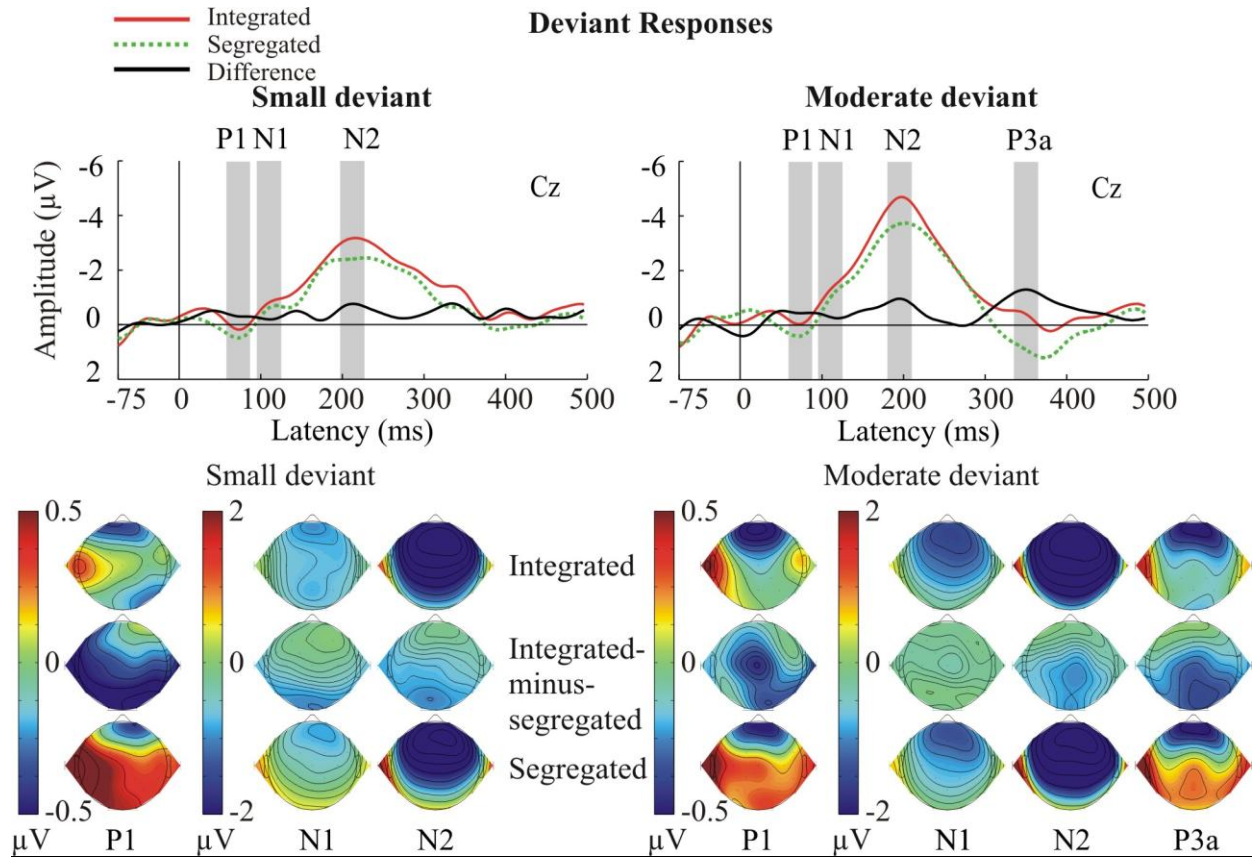


Figure 3. Top panels: Central (Cz) ERP responses (red continuous line: integrated; green dotted line: segregated; black: *integrated-minus-segregated* difference waveform) elicited by the *small* (left panel) and *moderate* deviants (right panel). ERP measurement windows for the deviant responses are marked by gray vertical bars with the name of the corresponding component on top. Bottom panels (left panel: *small deviants*, right panel: *moderate deviants*): Scalp distributions for P1 (extreme left), N1 (left), N2 (middle), and P3a (right, only for the *moderate deviants*), separately for the integrated (top), *integrated-minus-segregated* (middle), and segregated (bottom) waveforms. Maps were spline interpolated with a smoothing factor of 10^{-7} . Separate color map calibrations are provided for P1 (left to the P1 maps) and for the other three components (between the P1 map and the other maps).

Table 2. Significant results of the ANOVAs for the deviant tones. ANOVA factors are listed in Methods. ANOVA type ‘Omnibus’ refers to the ANOVA including both *small*- and the *moderate-deviant* amplitudes; ‘Moderate’ refers to the ANOVA for the P3a amplitudes elicited by *moderate deviants*. (No similar ANOVA was conducted for *small deviants*, because there were no sign of P3a being elicited by these deviants.) Degrees of freedom (df), F values, significance levels (p), Greenhouse-Geisser correction factors (where applicable), and η^2 effect sizes are given for each significant effect.

ANOVA type	Component	ANOVA factor	df	F	p	G-G ϵ	η^2
Omnibus	P1	Anterior–posterior	2,36	15.88	0.001	0.71	0.47
		Laterality	2,36	4.574	0.05	0.89	0.20
		Anterior-posterior \times Laterality \times Percept	4,72	2.982	0.05	0.84	0.14
	N1	Anterior–posterior	2,36	21.95	0.001	0.57	0.55
		Laterality	2,36	5.13	0.05	0.88	0.22
	N2	Anterior–posterior	2,36	46.22	0.001	0.53	0.72
		Laterality	2,36	21.43	0.001	0.94	0.54
		Percept	1,18	6.03	0.05		0.25
		Deviant type	1,18	22.07	0.001		0.55
		Anterior-posterior \times Deviant type	2,36	15.39	0.001	0.56	0.46
Anterior–posterior \times Laterality		4,72	6.52	0.01	0.7	0.27	
	Anterior–posterior \times Percept	2,36	5.93	0.05	0.6	0.25	
Moderate	P3a	Anterior–posterior	2,36	17.02	0.001	0.56	0.49
		Percept	1,18	4.63	0.05		0.2
		Anterior–posterior \times Laterality	4,72	3.26	0.05	0.74	0.15
		Anterior–posterior \times Percept	2,36	7.97	0.01	0.59	0.31

Discussion

We studied the ERP correlates of processing regular and frequency-deviant sounds in a perceptually bistable stimulus configuration focusing on the stages at which sound processing is modulated by the consciously perceived sound organization. The perceptually bistable stimulation allowed testing the processing of the same acoustic input while perceived sound organization varied.

We found that modulations of both early and late ERP components co-varied with the consciously experienced perceptual organization. Specifically, we found percept-dependent changes in the latency range of the P1, N1, N2, and P3a ERP components. Early (P1 and N1) effects were observed for both regular (both P1 and N1 elicited by the *A1* and *B* tones) and frequency-deviant tones (P1). These results suggest that the currently dominant representation of the auditory environment interacts with perceptual processes already at a very early stage.

For the regular tones, the amplitude of the P1 component elicited by the segregated *A1* and *B* tones was more positive than that elicited by the integrated ones. This result is consistent with that of Gutschalk et al. (2005), who found that the P1m component was enhanced when participants reported two streams compared to when they reported one. However, in contrast to Gutschalk et al. (2005) who found that the N1m was higher during the segregated percept, we found that the N1 amplitude was lower for the segregated than for the integrated percept. In fact, our data may be better described as showing a common slow ERP difference waveform overlapping both P1 and N1, than as separate modulations of these ERP responses. This is because, except for their amplitude, the scalp distributions obtained in the two latency ranges for the integrated-minus-segregated difference appear to be very similar, while differing between the *A1* and *B* tones (see Figure 2, right panel). Further, the integrated-minus-segregated difference for the N1 wave is more pronounced parietally than frontally or centrally, as supported by the significant interaction between the Anterior-posterior and the Percept factors, whereas the N1 scalp distribution has a clear fronto–central maximum. This interpretation is also supported by

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4 the results of the analysis of the N1 component measured from the preceding P1 peak, which did
5 not show any percept-dependent effects. Therefore the difference we found between the
6 integrated and segregated N1 components is more likely to have resulted from an early,
7 relatively long-lasting (ca. 60-140 ms) percept-dependent ERP effect, a slow positive
8 displacement of the segregated with respect to the integrated response, rather than from the
9 modulation of the N1 component itself. This slow displacement with a clearly different generator
10 from the well-known obligatory auditory components may reflect the influence of higher levels
11 of the auditory system on the interpretation of the incoming sounds, such as would be model
12 selection assumed by hierarchical predictive coding models (Friston, 2010; Wacongne,
13 Changeux, & Dehaene, 2012).
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23 A possible source of the contrasting results may stem from Gutschalk et al.'s (2005) instructing
24 their participants to follow either the A tones or the B tones when perceiving two streams,
25 whereas the current instructions did not vary with the experienced percept. Gutschalk et al.'s
26 (2005) instructions may have differentially influenced the N1 amplitude during the perception of
27 the segregated vs. the integrated organization through differences in attention, as the N1 is
28 strongly modulated by attention (Hillyard, Hink, Schwent, & Picton, 1973). An
29 attention-increased N1 during the segregated percept in Gutschalk et al.'s (2005) experiment
30 could have obscured the small opposite effect observed in the current study. Another possible
31 explanation of the contrast between the current and Gutschalk et al.'s (2005) results is that the
32 N1m mainly reflects the tangentially oriented auditory cortical sources of N1, whereas the N1 as
33 measured with EEG also includes contributions from radially oriented auditory cortical
34 generators as well as from generators located outside the auditory cortex, such as the
35 non-specific N1 (Näätänen & Picton, 1987).
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48 For the deviant tones, we found a similar percept-dependent modulation of the P1, suggesting
49 that Winkler et al. (2005) likely failed to find this effect because of using omissions as deviants
50 (i.e., the deviant event did not include an external stimulus). Therefore, the difference in results
51 between Gutschalk et al. (2005) and Winkler et al. (2005) was probably not brought about by the
52 investigation of standard vs. deviant sounds, but by the specific type of deviance used by
53 Winkler et al. (2005). In summary, the ERP responses elicited by regular and frequency-deviant
54 sounds showed early modulations by the perceived sound organization. Studies on binocular
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4 rivalry also showed that the neural correlates of perceptual organization appear as early as the P1
5 and N1 latency range. For example, Valle-Inclan et al. (1999) found that stimuli presented to the
6 dominant eye elicited higher ERP responses compared to stimuli presented to the suppressed eye
7 under rivalrous conditions. Their percept-dependent ERP effects started at 70 ms from stimulus
8 onset (see also Roeber et al., 2008; Vesper, O'Shea, Schroger, Trujillo-Barreto, & Roeber, 2008).
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14 Late ERP (N2 and P3a) effects of the perceptual organization were only found for deviant
15 sounds. When experiencing the segregated organization, deviants elicited smaller N2 response
16 than when experiencing integration. The P3a elicited by *moderate deviants* was larger while
17 participants reported segregation than integration. These results indicate that the percept
18 influenced the evaluation of the deviant sounds. Because both N2 and P3a are regarded as
19 electrophysiological correlates of sound evaluation processes, the N2 finding might be explained
20 by considering that when integration is perceived, the A2 tone (the position in which the deviants
21 occurred) defines the end of the repeating pattern. In contrast, while perceiving segregation, an
22 isochronous sequence of A tones is heard and the information about the cyclical pattern is lost.
23 This interpretation is supported by Hill and colleagues (Hill, Bishop, & Miller, 2012), who
24 concluded that the relative position of a tone within a sequence provides more important
25 information for auditory grouping than its spectral information. Deviations at the end of a pattern
26 might be regarded by the brain as more important than that in an arbitrary position of a
27 temporally unstructured sequence. This could have resulted in the more negative N2 response for
28 the integrated than for the segregated deviants. Thus the enhanced N2 response for the integrated
29 compared with the segregated deviants may reflect that the former were more informative for
30 sound grouping. The N2 finding is similar to that observed by Winkler et al. (2005), who found a
31 frontocentrally negative difference peaking at 176 ms from the expected onset of rare omitted
32 tones, which was larger when listeners experienced the stimulus sequence as integrated than
33 when they perceived the same sounds as segregated.
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52 Our P3a results suggest that during perceiving the segregated organization, *moderate deviants*
53 may have become more attention-catching compared with those encountered while experiencing
54 the integrated organization. Perceiving streams with uniform frequencies may have made
55 frequency-deviants more salient than finding the same when tones with different frequencies
56 have been grouped together. Winkler et al. (2005) found no significant percept-related effect on
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4 the P3a amplitude, perhaps because omissions do not have sound features that could have
5 differentially interacted with the perceived homogeneity of the two sound organizations.
6 Alternatively, it is also possible that the P3a modulation was not separate from that of the N2, as
7 were suggested by the observed percept-dependent scalp-distribution changes.
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11 In summary, we found that the perceived sound organization influences the evaluation (N2) and
12 attentional processing (P3a) of stimulus deviance. We found enhanced N2 response for *moderate*
13 as compared with *small deviants* and that *moderate* but not *small deviants* elicited the P3a.
14 However, we did not obtain an interaction between the amount of deviance and the perceived
15 sound organization (see Table 2). Based on Helson's adaptation level theory (1964) one would
16 expect small deviations to become more salient during the segregated percept (where the
17 frequency range of the groups are narrow) than during the integrated percept (where the
18 frequency range is wider), whereas larger deviations would be processed more similarly. In
19 contrast, we found no interaction between the amount of deviance (deviant-type) and perceptual
20 organization for the N2 component, and an effect opposite of what would be predicted by
21 Helson's adaptation level theory for the P3a component. One possibility is that because both
22 deviants fell outside the regular range of frequencies they acted similarly under the two sound
23 organizations (i.e., a sound outside the normal feature range). A better test would have been
24 provided by two deviants with the same amount of deviation, but one falling outside, the other
25 inside the *A-B* range. If Helson's adaptation theory applies to the processes involved in deviance
26 detection, then the two deviants could be expected to elicit similar effects under segregation (as
27 in this case, the whole range frequency in each group is a single value), but different effects
28 under integration (in which one deviant is within, the other is outside the frequency range of the
29 regular sounds).
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50 **Conclusions**

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53 In conclusion, our results showed multiple interactions between the processing of incoming
54 sounds and the currently dominant representation of the sound sequence. This conclusion is in
55 line with previous ones suggesting that sounds are immediately evaluated within their context
56 (Kilian-Hütten, Valente, Vroomen, & Formisano, 2011; Sussman, 2007; Winkler, 2007;
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4 Winkler, Denham, & Nelken, 2009). The percept-related differences found for the regular and
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6 frequency-deviant tones suggest that the current percept influences both the early processing of
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8 sounds (reflected in the P1 and N1 components) and the evaluation of deviance (reflected in the
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10 N2 and P3a components), whereas the sensitivity of the auditory system to the amount of
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12 frequency deviation does not necessarily change with the perceptual organization.
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21
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24 realized using Cogent 2000 developed by the Cogent 2000 team at the FIL and the ICN.
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26 Topographies were plotted with the aid of a plug-in for EEGLab (Delorme & Makeig, 2004)
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28 written by Andreas Widmann, University of Leipzig.
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Table 1

Table 1. Significant results of the ANOVAs for the standard *A1*, *A2*, and *B* tones, separately. ANOVA factors are listed in Methods. The “Reference” column refers to whether the amplitudes were measured with respect to the baseline or the mean amplitude of the preceding P1 response. Degrees of freedom (df), F values, significance levels (p), Greenhouse-Geisser correction factors (where applicable), and η^2 effect sizes are given for each significant effect.

Tone	Component	Reference	ANOVA factor	df	F	p	G-G ϵ	η^2
standard A1	P1	Baseline	Anterior–posterior	2,36	68.90	0.001	0.60	0.79
		Baseline	Laterality	2,36	15.85	0.001	0.76	0.47
		Baseline	Percept	1,18	6.57	0.05		0.27
		Baseline	Anterior–posterior × Laterality	4,72	4.50	0.05	0.51	0.20
	N1	Baseline	Anterior–posterior	2,36	79.68	0.001	0.61	0.82
		Baseline	Laterality	2,36	12.62	0.001	0.70	0.41
		Baseline	Anterior–posterior × Laterality	4,72	7.15	0.001	0.65	0.28
		Baseline	Anterior–posterior × Percept	2,36	4.60	0.05	0.56	0.20
		Baseline	Laterality × Percept	2,36	3.91	0.05	0.87	0.18
		P1	Anterior–posterior	2,36	20.56	0.001	0.56	0.53
	N2	Baseline	Anterior–posterior	2,36	38.75	0.001	0.59	0.68
		Baseline	Laterality	2,36	6.45	0.01	0.73	0.26
		Baseline	Anterior–posterior × Laterality	4,72	2.79	0.05	0.82	0.13
		P1	Anterior–posterior × Laterality	4,72	3.07	0.05	0.68	0.15
	standard B	P1	Baseline	Anterior–posterior	2,36	57.57	0.001	0.58
Baseline			Laterality	2,36	7.337	0.01	0.698	0.29
Baseline			Percept	1,18	8.336	0.01		0.317

	N1	Baseline	Anterior-posterior	2,36	29.18	0.001	0.56	0.62
		Baseline	Laterality	2,36	9.00	0.01	0.91	0.33
		Baseline	Percept	1,18	11.31	0.01		0.39
		P1	Anterior-posterior	2,36	22.97	0.001	0.598	0.56
		P1	Anterior-posterior × Laterality	4,72	2.95	0.05	0.68	0.14
	N2	Baseline	Anterior-posterior	2,36	4.80	0.05	0.60	0.21
		Baseline	Laterality	2,36	4.97	0.05	0.94	0.22
		P1	Anterior-posterior	2,36	74.13	0.001	0.65	0.80
		P1	Anterior-posterior × Laterality	4,72	3.26	0.05	0.79	0.15
standard A2	P1	Baseline	Anterior-posterior	2,36	22.92	0.001	0.59	0.56
		Baseline	Laterality	2,36	4.65	0.05	0.90	0.21
	N1	Baseline	Anterior-posterior	2,36	25.11	0.001	0.58	0.58
		P1	Anterior-posterior	2,36	4.59	0.05	0.558	0.20
	N2	Baseline	none					
		P1	Anterior-posterior	2,36	25.42	0.001	0.58	0.59
		P1	Laterality	2,36	18.62	0.001	0.76	0.51

Table 2

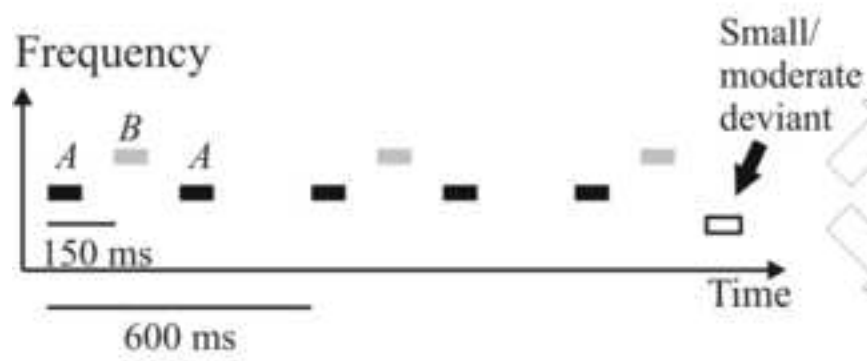
Table 2. Significant results of the ANOVAs for the deviant tones. ANOVA factors are listed in Methods. ANOVA type ‘Omnibus’ refers to the ANOVA including both *small-* and the *moderate-deviant* amplitudes; ‘Moderate’ refers to the ANOVA for the P3a amplitudes elicited by *moderate deviants*. (No similar ANOVA was conducted for *small deviants*, because there were no sign of P3a being elicited by these deviants.) Degrees of freedom (df), F values, significance levels (p), Greenhouse-Geisser correction factors (where applicable), and η^2 effect sizes are given for each significant effect.

ANOVA type	Component	ANOVA factor	df	F	p	G-G ϵ	η^2
Omnibus	P1	Anterior–posterior	2,36	15.88	0.001	0.71	0.47
		Laterality	2,36	4.574	0.05	0.89	0.20
		Anterior-posterior \times Laterality \times Percept	4,72	2.982	0.05	0.84	0.14
	N1	Anterior–posterior	2,36	21.95	0.001	0.57	0.55
		Laterality	2,36	5.13	0.05	0.88	0.22
	N2	Anterior–posterior	2,36	46.22	0.001	0.53	0.72
		Laterality	2,36	21.43	0.001	0.94	0.54
		Percept	1,18	6.03	0.05		0.25
		Deviant type	1,18	22.07	0.001		0.55
		Anterior-posterior \times Deviant type	2,36	15.39	0.001	0.56	0.46
		Anterior–posterior \times Laterality	4,72	6.52	0.01	0.7	0.27
		Anterior–posterior \times Percept	2,36	5.93	0.05	0.6	0.25
	Moderate	P3a	Anterior–posterior	2,36	17.02	0.001	0.56
Percept			1,18	4.63	0.05		0.2
Anterior–posterior \times Laterality			4,72	3.26	0.05	0.74	0.15
Anterior–posterior \times Percept			2,36	7.97	0.01	0.59	0.31

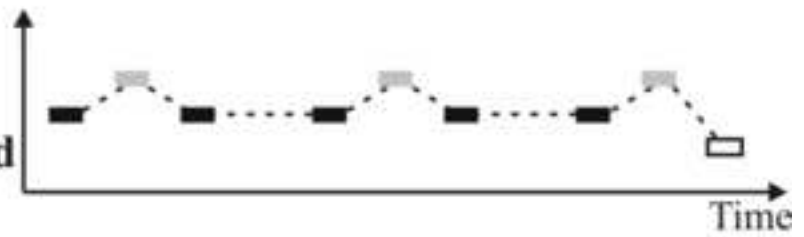
	Laterality × Percept	2,36	3.74	0.05	0.89	0.17
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Figure 1
[Click here to download high resolution image](#)

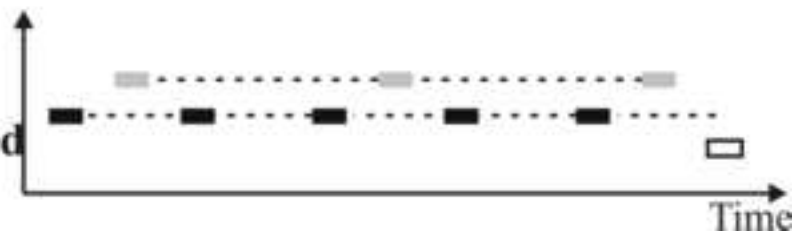
Experimental design



Integrated



Segregated



Possible percepts

Figure 2
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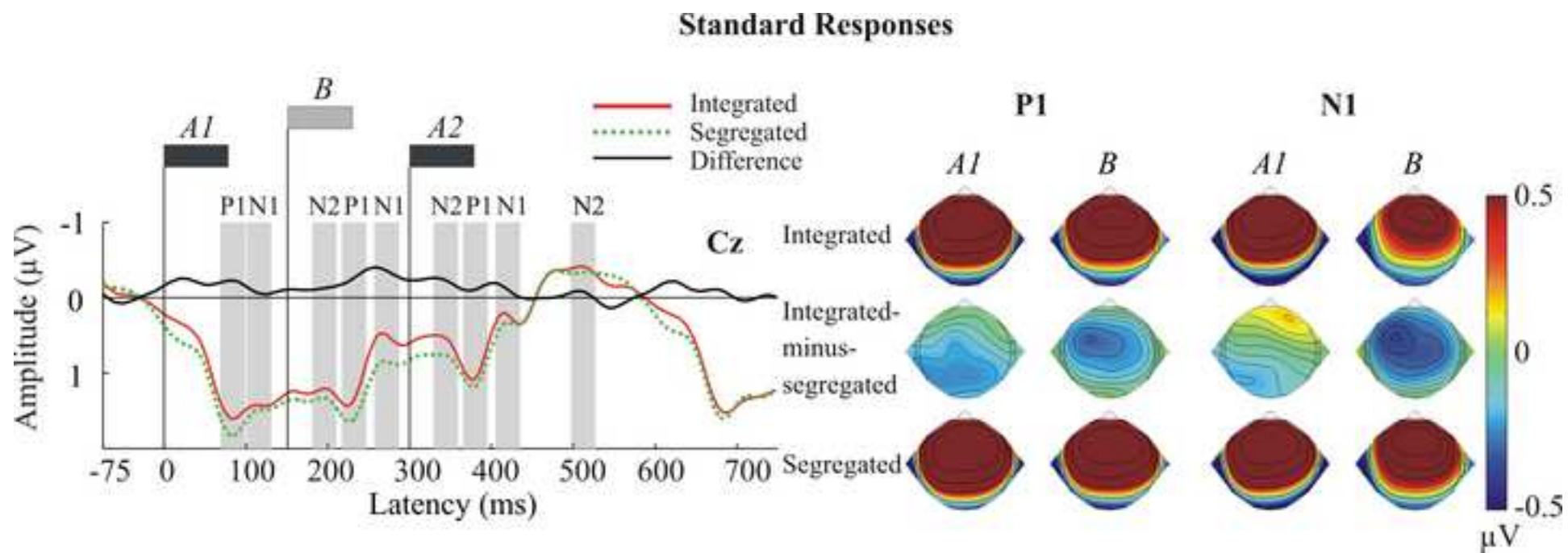


Figure 3
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Deviant Responses

— Integrated
- - Segregated
— Difference

