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Neural plasticity associated with recently versus often heard objects

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ABSTRACT

In natural settings the same sound source is often heard repeatedly, with variations of the spectro-temporal and spatial characteristics. We have investigated how such repetitions influence sound representations and in particular how the auditory cortex keeps track of recently vs often heard objects. A set of 40 environmental sounds was presented twice, i.e. as prime and as repeat, within each of 16 experimental blocks, while subjects categorized the corresponding sound sources as living vs non-living. Electrical neuroimaging analyses were applied to auditory evoked potentials (AEPs) comparing primes vs repeats (effect of presentation) and the four sections (à 4 blocks each; effect of section). Dynamic analysis of distributed source estimations revealed i) one cluster within the left temporal convexity showing a significant main effect of presentation at 164-215ms post-stimulus onset; and ii) a cluster of significant main effect of section, in the right temporo-parietal junction at 166-213ms. Thus, spatio-temporal dynamics of neural activity encode the temporal history of exposure to sound objects. Rapidly occurring plastic changes within the semantic representations of the left hemisphere keep track of objects heard a few seconds before, independently of the more general sound exposure history. Progressively occurring and more long-lasting plastic changes within networks coding for perceptual, semantic and spatial aspects of sound objects within the right hemisphere keep track of multiple exposures.

Highlights

Human auditory cortex encodes differently recently vs often heard objects

Left but not right temporal cortex encodes recency independently of exposure history

Right temporo-parietal activity encodes multiple exposures but not recency

Keywords

Repetition priming, sound object, environmental sound, semantic representation, auditory evoked potential (AEP), human auditory cortex.

Introduction

Repetition priming constitutes a useful tool to probe the nature of representations at different stages of processing streams (Grill-Spector et al. 2006) and was proposed to induce, through multiple repetitions, lasting changes at different levels of cognitive representations (Schacter et al., 2004) and to induce long-term memory (Hauptmann and Karni, 2002). Small numbers of repetitions of the same (visual) stimuli have been found to modulate behavioral priming (Wiggs and Martin, 1998) and to progressively increase repetition suppression. In animals, response suppression at the neural level continued to decrease with repeated presentations, but this decrease became smaller across successive repetitions as stimuli became familiar (Li et al., 1993). In functional magnetic resonance imaging (fMRI) experiments, activations tended to decrease monotonically with the number of repetitions, often reaching a plateau after 6 to 8 repetitions (Grill-Spector and Malach, 2001; Henson et al., 2000; Sayres and Grill-Spector, 2006). Although the progressive changes due to repeated stimulus exposure are well documented (in the visual domain), it is not known whether the adaptation through multiple repetitions allows the brain to keep track of recent repetitions among the multiple presentations.

In the auditory domain, repetition priming was shown to improve recognition of environmental sounds (Chiu and Schacter, 1995; Chiu, 2000; Stuart and Jones, 1995) and to decrease neural activity in specific regions along the ventral auditory pathway, including the non-primary auditory areas and the temporal convexity (Bergerbest et al., 2004; Altmann et al., 2010; De Lucia et al., 2010b). Electrophysiological studies identified the critical time window for repetition suppression at 156-215ms post-stimulus onset (Murray et al., 2008b) or at P2m (Altmann et al., 2008).

A naturally occurring sound source, often referred to as sound object (Griffiths and Warren, 2004; Nelken, 2004), is characterized by its identity and its location. The former is processed along the ventral/”What” pathway through hierarchically organized levels of perceptual, semantic, and complex auditory scene analysis (Leaver and Rauschecker, 2010; Scott, 2005; Murray et al. 2006; De Lucia 2010a). Relatively little is known about how multiple repetition exposures influence the perceptual and semantic representation levels within the auditory “What” pathway. Repetition suppression following one or few repetitions has been repeatedly demonstrated using acoustically identical environmental sounds in fMRI (Bergerbest et al., 2004) or magnetoencephalography and electroencephalography (Altmann et al. 2008; Murray et al. 2008b). Perceptual and the semantic contributions to repetition priming of environmental sounds have been shown in a recent fMRI study to yield similar behavioral effects and similar suppression within the ventral/”What” pathway, suggestive of similar mechanisms for both (De Lucia et al., 2010b).

We report here on neural modulation associated with multiple repetitions of the same sound object. Based on previous human (Grill-Spector and Malach, 2001; Henson et al., 2000; Sayres and Grill-Spector, 2006) and non-human visual studies (Li et al., 1993) we have postulated that progressive changes of neural activity in distinct parts of the auditory cortex reflect multiple exposures to the same sound object. We further hypothetized that distinct modulations of neural activity differentiate recent repetitions, i. e., repeats occurring within seconds of primes, among the multiple presentations. To test these hypotheses electrical neuroimaging was applied to auditory evoked potentials comparing primes and repeats separated by ~10s and the changes induced by 32 presentations over ~2 hours.

Materials and methods

Subjects

Twelve right-handed men (mean (±SD) lateralization index = 84.08 (±6.30); (Oldfield, 1971) aged 20-38 years (mean (±SD) = 26.3 (±5.5) years) without any history of neurological or psychiatric illness all with normal hearing participated in the study. They provided written informed consent and were remunerated modestly for their participation in this study. This study was approved by the Ethics Committee of the Faculty of Biology and Medicine at the University of Lausanne.

Experimental procedure

Participants completed a total of 16 blocks, each of which comprised two presentations of 40 meaningful and easily identifiable environmental sounds. The whole experiment lasted approximately 2.2 hours. The sounds were 500ms in duration, including a 50ms linear rise and fall time; (16 bit stereo; 22.5kHz digitization) and were normalized according to the root mean square of their amplitude. Half of the sounds referred to living (baby crying, bird, cat, coughing, chicken, clearing throat, cow, crow, dog, donkey, frog, gargling, laughter, owl, pig, rooster, scream, sheep, sneezing, whistling), and the other half to man-made sound sources (accordion, bicycle bell, car horn, cash register, church bell, cuckoo clock, doorbell, door closing, flute, glass shattering, guitar, harmonica, harp, organ, piano, police siren, saxophone, telephone, trumpet, violin; as already used by Murray et al., 2006). The task was a two alternative forced choice in which participants had to classify as rapidly and as accurately as possible each sound as living or man-made by pressing one of two buttons of a serial response box using the index and middle finger of the right hand (as in previous EEG studies: Bergerbest et al. 2004; Murray et al., 2008b; De Lucia et al., 2010a). Response accuracy remained constant and response times tended to decrease throughout the experiment, excluding progressive alterations in alertness or fatigue. There were several reasons for having subjects perform this task. First, an active task provided behavioral data that could be used to assess priming. Second, the behavioral data allowed for an assay of whether effects could be explained by increased fatigue over the course of the experiment, which would presumably manifest as either/both slowing of response times and increased errors. Finally, precisely this task has been used in all prior electrical and hemodynamic imaging studies of repetition effects involving environmental sounds (Bergerbest et al. 2004; Murray et al., 2008b; De Lucia et al., 2010a) and also in many studies of repetition effects in the visual modality (e.g. Cattaneo et al., 2010; Wagner et al., 1997; Wig et al., 2005). The use of this task here therefore facilitates comparison of our results with other studies.

The 16 blocks of the experiment were grouped into 4 sections (S1, S2, S3 and S4 comprising, respectively, blocs 1-4; 5-8; 9-12; 13-16; Fig. 1). Within each block, sounds were presented with a pseudo-random inter-stimulus onset interval of 1600ms to 2400ms (in 100ms steps equally distributed across conditions). The initial and the repeated presentations of a given sound object were either acoustically different (exemplars a-b, b-a) or identical (a-a, b-b); the four possibilities accounted each for 25% of the pairs within a block and were pseudo-randomly distributed across the four blocks comprising each section. The stimuli were delivered with an interaural intensity difference of 53dB ±3dB favoring the left (L) or right (R) ear through insert earphones (ER-4P; www.etymotic.com) at a sound pressure level of 88dB ±3dB for the leading ear (measured with a CESVA SC-L sound pressure meter; cesva.com). The spatial origins of the initial and the repeated presentations of a given object within a block were either the same or different (R-R, L-L, R-L, L-R; the 4 possibilities accounted each for 25% of the pairs within a block and were mixed pseudo-randomly). For a given sound object, each of the four spatial combinations was presented once within a section.

The rationale behind varying the exemplar and location of the stimuli in this way was to emulate real-world situations wherein objects appear at different locations and change their low-level features. This variability also forced subjects to attend to a wide portion of auditory space and also to minimize using low-level acoustics to perform the task. An additional consideration was that varying the stimuli in this way minimized effects of neural habituation to low-level acoustic features (either in terms of frequency and/or space). The relationship between the acoustic nature of the repeated exemplar (identical or not) and its position with respect to the initial presentation (same or different) was pseudo-randomized and balanced across sound objects and subjects. Finally, in order to avoid systematic bias arising from order presentation across subjects, the presentation order of the blocks was determined by a Latin square design. Sections were chosen as units of analysis, since within each section (but not within each block) each sound object was presented in the four possible pairs of acoustic exemplars and in the four possible pairs of lateralizations.

The blocks within a section and the sections were separated by six minute breaks, during which the participants were exposed to other auditory stimuli (series of four pure tones) which were irrelevant to the experimental task. In addition, the time lag between repetitions and the number intervening items was kept constant across participants and ranged from 2 to 12 sec. (0 to 5 distinct intervening items, none of them were exemplars of the same auditory object) for the factor presentation. Regarding the factor section, the temporal interval between the initial presentations of the same object (in 2 consecutive blocks) ranged from 6 to 8 minutes; the interval between the first presentations of an object in 2 consecutive sections was ~34 minutes. The use of pairs where the initial and the repeated presentations of a given sound object were acoustically identical vs. different or where they had the same vs. different lateralization did not influence significantly response times; a 2 x 2 x 2 repeated measure

ANOVA with factors of Acoustical-nature (same, different), Presentation (initial, repeated) and Lateralization-within-prime-repeat-pairs (same, different) did not reveal any significant main effect or interactions (main effect of Acoustical-nature: $F_{(1,11)}=0.19$; $p=0.68$, main effect of Presentation: $F_{(1,11)}=2.37$; $p=0.15$, main effect of Lateralization-within-prime-repeat-pairs: $F_{(1,11)}=3.92$; $p=0.07$, Acoustical-nature and Presentation interaction: $F_{(1,11)}=0.98$; $p=0.35$, Acoustical-nature and Lateralization-within-prime-repeat-pairs interaction: $F_{(1,11)}=0.20$; $p=0.67$, Presentation and Lateralization-within-prime-repeat-pairs interaction: $F_{(1,11)}=3.31$; $p=0.10$, and Acoustical-nature, Presentation and Lateralization-within-prime-repeat-pairs interaction: $F_{(1,11)}=0.04$; $p=0.84$).

Our study aimed at comparing the behavioral and electrophysiological effects of increasing the repetition number of auditory objects. To do so, we used a 2 X 4 within-subject experimental design with factors of presentation (within block initial vs. repeated presentation; hereafter IP and RP, respectively) and section (S1, S2, S3, S4).

EEG recordings and pre-processing

Continuous EEG was recorded at 1024Hz through a 160 channel Biosemi ActiveTwo system (Biosemi, Amsterdam, Netherlands). EEG pre-processing and analyses were performed using Cartool (Brunet et al., 2011). EEG epochs spanning 100ms pre- to 500ms post-stimulus onset were averaged, and auditory evoked potentials (AEPs) were calculated for the eight conditions (IP/S1, RP/S1, IP/S2, RP/S2, IP/S3, RP/S3, IP/S4, and RP/S4). Trials with eye blinks or transient noise were rejected offline using a semi-automated ± 60μV criterion at any channel. The average number of accepted epochs per condition was 142 ± 4 (mean ± s.e.m.), and there was no significant difference in the number of accepted trials across the eight experimental conditions ($F_{(7,5)}=2.76$, $p=0.14$). Prior to group averaging, data at artifact channels from each subject were interpolated using 3-dimensional splines (Perrin et al., 1987). Data were then recalculated against the average reference and band-pass filtered between 0.68 and 40Hz. Data were baseline corrected over the 100ms pre-stimulus period during group-averaging.

Global field power analysis

The instantaneous global field power (Lehmann and Skrandies, 1980; Murray et al., 2008a; Koenig and Melie-Garcia, 2010) was analyzed to identify modulations in the strength of the electric field recorded at the scalp. Global field power is calculated as the standard deviation across all electrodes at a given instant in time (i.e. the root mean square across the average-referenced electrode values). Global field power modulations were analyzed using time point-wise 2 x 4 repeated measures ANOVA with factor Presentation (IP, RP) and Section (S1, S2, S3, S4). To reduce the risk of false positive results arising from multiple tests, we used a temporal criterion of >20 consecutive time frames.

Source estimations and analyses

The present analyses are based on distributed source estimations; a similar approach which is routinely used in magnetoencephalographic studies (Ahlfors et al., 2010; Michel and Murray, 2012). Here, we used what has become colloquially known as the “LAURA inverse solution”, which is the combination of a minimum norm inverse solution and local auto-regressive average regularization approach (Grave de Peralta Menendez et al., 2004b; Grave de Peralta Menendez et al., 2001; Michel et al., 2004). LAURA is based on electromagnetic theory emanating from the Maxwell equations stating that the strength of a source falls off with the inverse of the squared distance for potential fields (cubic distance for vector fields). Here, homogeneous coefficients in all directions were used. The solution space included 3005 nodes, selected from a 6 × 6 × 6 mm grid equally distributed within the gray matter of the Montreal Neurological Institute average brain. The head model and lead field matrix were generated with the Spherical Model with Anatomical Constraints (SMAC; Spinelli et al., 2000). As an output, LAURA provides current density measures; the scalar values of which were evaluated at each node. Prior work has documented and discussed in detail the spatial accuracy of this inverse solution (e.g. Brodbeck et al., 2011; Gonzalez Andino et al., 2005a; Gonzalez Andino et al., 2005b; Grave de Peralta Menendez et al., 2004a; Groening et al., 2009; Martuzzi et al., 2009; Vulliemoz et al., 2009; Guggisberg et al. 2011). Source estimations were calculated for each time frame (TF), each experimental condition and each subject. Then, the data were down-sampled from 1024Hz to 512Hz to reduce the number of statistical tests. Data were corrected using the maximal pre-stimulus current density value at each solution point, i.e. the scalar value of each solution point at each TF post-stimulus onset was reset to zero when it was below the highest scalar value reached during the 100ms pre-stimulus onset period at the corresponding solution point. This procedure reduces contamination of the source estimations and the related statistical effect by ghost source activity, before the statistical analyses. The corrected scalar value of the activity at each solution point and for each time frame were submitted to the same procedure as for the waveform analysis (i.e. time point-wise 2 x 4 repeated measures ANOVA with factor presentation (IP vs. RP) and section (S1 vs. S2 vs. S3 vs. S4); (see Ortigue et al., 2005; Plomp et al., 2010; Britz and Michel, 2010; Knebel et al., 2011). To reduce the risk of false positive results arising from multiple tests, we used a node-wise significance threshold of p-value < 0.01, a temporal criterion of >20 consecutive TFs (~39ms), and a spatial criterion of 15 contiguous solution points for significant effects. This last criterion was determined using the AlphaSim program (available at http://afni.nimh.nih.gov) and assuming a spatial smoothing of 6 mm FWHM. This program applies a cluster randomization approach. This criterion indicates that there is less than 1% probability of a cluster of at least 15 contiguous nodes each meeting the $p<0.01$ at any given timeframe. In other words, we first selected among the 769280 ANOVAs (i.e. the activity of 3005 nodes X 256 TFs), those resulting in a p-value of maximally 0.01. Then, the number of positive results was reduced according to the temporal criterion, so that only effects occurring at a specific location for at least 20 consecutive TFs were retained. Finally, the spatial criterion was applied so that among the remained positive results, only those belonging to a cluster of at least 15 contiguous solution points, at each time frame, were retained.

Results

Behavioral results

All subjects readily categorized all stimuli as living vs. man-made and tended to be more rapid with increasing numbers of repetitions (Table 1). The performance in respect the initial and repeated presentations in the four sections was analyzed with a 2 x 4 repeated measure ANOVA with factors of Presentation and Section. For accuracy none of the main effects (Presentation ($F_{(1,11)}=0.18$; $p=0.68$); Section ($F_{(3,9)}=0.06$; $p= 0.98$)) nor the Interaction ($F_{(3,9)}=0.04$; $p = 0.99$) were significant. For response times, the main effect of Section was significant ($F_{(3,9)}=4.42$; $p<0.05$), the Interaction marginally so ($F_{(3,9)}=3.41$; $p=0.07$), but not the main effect of Presentation ($F_{(1,11)}=2.74$; $p=0.13$). Accuracy and response times were similar to those in other studies using environmental sounds (Lebrun et al. 1998; Saygin et al. 2003; Bergebest et al. 2004; Murray et al. 2006; De Lucia et al. 2009; De Lucia et at al. 2010a).

Global field power

Global field power waveforms are shown in Figure 2; they illustrate data quality, as evident in the superimposed baseline activity, and they a sense of how the timing of effects in the source estimations corresponds with canonical AEP components observed at the scalp. The time frame-wise 2 x 4 repeated measures ANOVA with factors of Presentation (IP, RP) and Section (S1, S2, S3, S4), performed on global field power modulations, revealed a significant main effect of Section (Fig. 2) over the 172-199ms post-stimulus onset period. There was no evidence for period exhibiting a significant main effect of presentation or interaction between the factors.

Electrical neuroimaging results

The time frame-wise 2 x 4 repeated measures ANOVA with factors of Presentation (IP, RP) and Section (S1, S2, S3, S4) performed on source estimations was applied to all solution points. This analysis revealed a cluster of solution points exhibiting a significant main effect of Presentation and a cluster of solution points exhibiting a significant main effect of Section (Fig. 3). There was no evidence for clusters exhibiting a significant Interaction between these factors.

A significant main effect of Presentation was present over the 164-215ms post-stimulus onset period in two clusters on the left temporal convexity (Fig. 3). One cluster was located on the posterior part of the superior temporal gyrus. The other, larger cluster spread over the middle part of the middle temporal gyrus and sulcus to the posterior part of the inferior temporal gyrus as well as to the fusiform and parahippocampal gyri (Talairach et al. 1988). This effect was driven by significantly stronger activity during the initial than the repeated presentation of the sound, irrespective of section.

A significant main effect of Section was found in a cluster on the right temporo-parietal cortex over the 166-213ms post-stimulus onset period (Fig.3). It comprised the posterior part of the superior temporal gyrus and sulcus, the planum temporale, the primary auditory cortex, the parietal operculum as well as the supramarginal and the angular gyri (Talairach and Tournoux, 1988). This effect was driven by a significant decrease of activity over the sections of the experiment.

Our results suggest that during a specific time window 166-213ms post-stimulus onset, the two hemispheres code differently for recently vs. often heard sounds. To test this hypothesis we compared the mean neural activity within the above described clusters in the left and the right hemisphere (in red and in blue, respectively in Fig. 3) with a 2 x 2 x 4 repeated measures ANOVA with the factors Hemisphere (left, right), Presentation (IP, RP) and Section (S1, S2, S3, S4). The interaction between the factors Hemisphere and Presentation was significant ($F_{(1,11)}=8.48$; $p<0.05$); post-hoc analysis revealed a significant difference between IP and RP within the left ($p<0.001$) but not within the right hemispheric cluster (see Supplementary Figure). These results speak in favor of a specific involvement of the left hemisphere in the detection of recently heard objects. Conversely, the interaction between factors Hemisphere and Section was not significant ($F_{(3,9)}=0.77$; $p=0.54$) leaving the possibility open that not only the right but also the left hemisphere contribute to long-term habituation to frequently heard objects.

Discussion

Our results speak in favor of differential sound object representations within the auditory cortex, as a function of the temporal history of exposure to these objects. In particular, the fact that an object has been heard recently, i.e., within the preceding 2-12 s, is encoded differently than the track record of multiple exposures over time, as here e. g. 32 exposures over ca 2 hours. Recently heard sounds, independently of the number of previous exposures, were found to be encoded by a modulation of a left-sided network, whereas often heard sounds by a modulation in an essentially right-sided network. The corresponding time windows were very similar for the two types of temporal history, in the 164-215ms post-stimulus onset range. When compared to other stages of recognition of environmental sounds, the time history of exposure is encoded later than the initial sound object categorization, which starts as soon as 70-100ms post-stimulus onset, about at the same time as the differentiation of human vs. animal vocalizations, and before the finer discrimination of sound objects in action vs. non-action related (Murray et al. 2006; De Lucia et al. 2010a).

Neural plasticity related to recently heard objects

Repeated exposure to recently heard objects yielded a repetition suppression at 164-215ms post-stimulus onset on the posterior part of the superior temporal gyrus, the middle part of the middle temporal gyrus and sulcus, the posterior part of the inferior temporal gyrus as well as on the fusiform and parahippocampal gyri of the left hemisphere. The suppression effect included regions of the temporal convexity that were shown to carry the semantic representations within the auditory ventral/What stream (Leaver and Rauschecker, 2010; Scott, 2005). Its location and time window were similar to those reported in previous studies of repetition priming with the same (Doehrmann et al., 2008; Murray et al., 2008b) or acoustically different exemplars of non-lateralized environmental sounds (De Lucia et al., 2010b). Together, these studies suggest that keeping track of recently heard objects taps into the plasticity of associative-semantic (rather than perceptual-discriminative) representations, where positional information was shown not to influence encoding (Bourquin et al., 2012 submitted).

Neural plasticity related to multiple presentations of a sound object

Progressive repetition suppression for often heard objects, here up to 32 presentations of acoustically identical or different, left- or right-lateralized exemplars over a 2.2 hour period, was present at 166-213ms post-stimulus onset involving the posterior part of the superior temporal gyrus and sulcus, the planum temporale, the primary auditory cortex, the parietal operculum as well as the supramarginal and angular gyri on the right side. This effect cannot be readily explained in terms of fatigue or alertness because subjects became progressively faster during the course of the experiment. The region corresponds to the intersection between the dorsal/Where and the ventral/What streams (Alain et al., 2001; Anourova et al., 2001; Arnott et al., 2004; De Santis et al., 2007; Maeder et al., 2001). It includes parts of networks which were reported to code for semantic, perceptual and spatial features of sound objects. The right superior temporal gyrus was shown to decrease the BOLD signal during repeats of acoustically identical (Bergebest et al. 2004) or different (De Lucia et al. 2010b) environmental sounds or during repeats of spectral or amplitude envelopes of animal vocalizations (Altmann et al., 2010). In a study with localized animal vocalizations the right planum temporale and the posterior part of the superior temporal gyrus was found to respond to location changes, and the temporo-parietal junction and the inferior parietal lobule to location vs animal changes (Altmann et al., 2007).

Whereas the progressive decrease of neural activity with increasing repetitions was statistically significant only within the temporo-parietal region on the right side, there was a (not significant) tendency towards progressive decrease during a similar time period within temporal clusters on the left side (Fig. 3). This difference of clearly progressive adaptation to multiple presentations on the right side and no or at the best a very sluggish adaptation on the left side was observed with 32 presentations. We cannot exclude that even more numerous repetitions would not reveal a progressive decrease on the left side; further experiments are needed to elucidate this issue.

Conclusion

To our knowledge this is the first demonstration of spatio-temporal brain dynamics which keep track of the temporal history of exposure to sound objects. Our results indicate that rapidly occurring plastic changes within the left hemisphere keep track of object heard a few seconds before, independently of the more general sound exposure history. Progressively occurring and more long-lasting plastic changes within a network centered on the right hemisphere keep track of sound exposure history over a larger time scale, including numerous repetitions.

Plastic changes which occur after multiple presentations of lateralized sound objects involve perceptual and semantic stages of the auditory ventral/What stream as well as spatial representations within the dorsal/Where stream of the right hemisphere. Plastic changes that occur after recent exposure to the same sound object appear to be limited to parts of its semantic representation within the left auditory ventral/What stream. Unlike plastic changes associated with multiple repetitions, they concentrate on the “common denominator” of the stimuli (here the semantic representation) and do not encompass perceptual or spatial features of the stimuli, which tended to vary between primes and repeats.

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Table

Table 1. Accuracy and response times to initial (IP) and repeated presentations (RP) in the four sections (S1, S2, S3, S4). Mean and standard error of the mean are indicated.

	Accuracy (%)		**Response time (ms)**	
	IP	**RP**	**IP**	**RP**
S1	95 (±0.01)	95 (±0.01)	716 (±25)	693 (±24)
S2	96 (±0.01)	94 (±0.01)	685 (±28)	689 (±32)
S3	96 (±0.01)	95 (±0.01)	681 (±27)	680 (±26)
S4	96 (±0.01)	95 (±0.01)	665 (±23)	655 (±21)

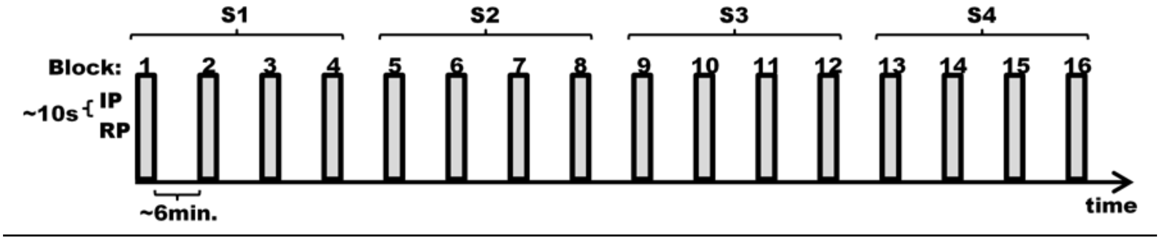


Figure 1. Schematic representation of the experimental paradigm. Sixteen blocks (1 – 16) each of which comprised initial (IP) and repeated presentations (RP) of 40 environmental sounds were grouped into 4 sections (S1, S2, S3, S4). The interval range between IP and RP of the same sound object (within a bloc) was 2-12 s; between the IPs of the same sound object within two subsequent blocks 6-8 minutes; and between the first presentations of an object in a section lasted ~34 minutes.

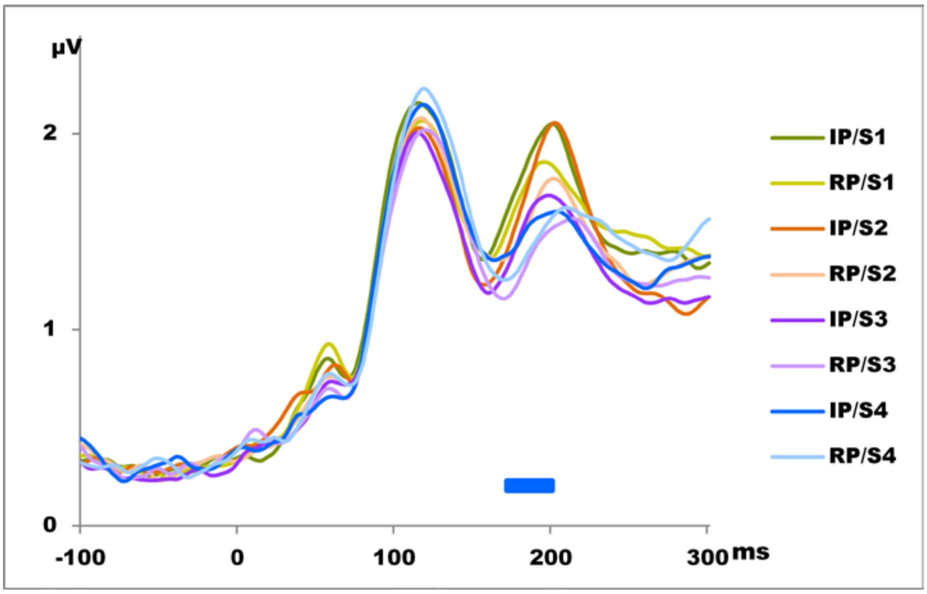
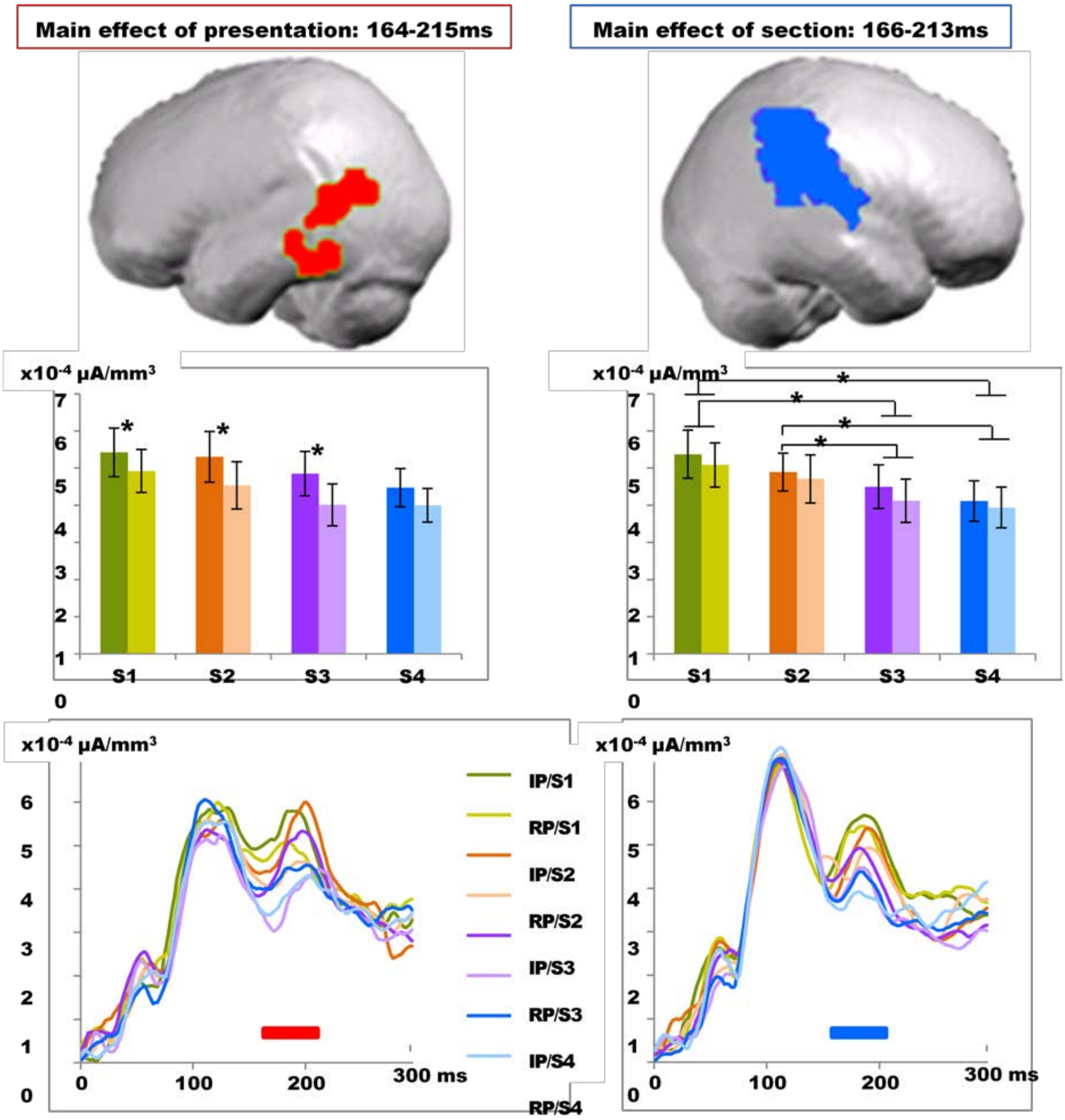


Figure 2. Mean global field power waveforms. The group-averaged waveforms are displayed for each section (S1, S2, S3, S4) as well as for initial and repeated presentations (IP, RP) within a section. Blue bar indicates time period of significant effect of section.


Main effect of presentation: 164-215ms

Main effect of section: 166-213ms

Figure 3. Significant modulation of neural activity occurred in respect to main effect of Presentation at 164-215 ms post-stimulus onset on the left temporal convexity (top row: red cluster) and to main effect of Section at 166-213 ms post-stimulus onset on the right temporo-parietal convexity (blue cluster). Mean neural activity within the corresponding cluster and time frames during initial (IP) and repeated presentations (RP) is shown for the four sections (S1, S2, S3, S4; middle row); asterisks denote significant difference ($p<0.05$). The time course of neural activity in the corresponding cluster is illustrated in bottom row; periods of significant main effects are highlighted with red and blue bars.