



NATIONAL RESEARCH UNIVERSITY  
HIGHER SCHOOL OF ECONOMICS

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BASIC RESEARCH PROGRAM

WORKING PAPERS

SERIES: PSYCHOLOGY  
WP BRP 55/PSY/2015

This Working Paper is an output of a research project implemented at the National Research University Higher School of Economics (HSE). Any opinions or claims contained in this Working Paper do not necessarily reflect the views of HSE

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## **SHORT-TERM PLASTICITY IN AUDITORY CORTICAL CIRCUIT EVOKED BY MONETARY INCENTIVE DELAY TASK<sup>3</sup>**

To choose optimally, people must consider both the potential value and the probability of a desired outcome. This idea is reflected in the expected value theory, which considers both the potential value of different courses of action and the probability that each action will lead to a desired outcome. Accordingly, during decision-making people choose an alternative with the highest expected value. The dominant neurobiological models of decision-making assume that the sensory inputs to the decision-making neural networks are stationary. However, many cognitive studies have demonstrated experience-induced plasticity in the primary sensory cortex, suggesting that repeated decisions could modulate the sensory processing. We investigated experience-induced plastic changes in the neural representation of the acoustic cues coding different expected values using a repeated monetary incentive delay task (MID-task; Knutson et al., 2005). Subjects participated in two extensive sessions of an audio-version of the MID-task. Next, we investigated electrophysiological correlates of the experience-induced plasticity of the primary auditory cortex by comparing the mismatch negativity (MMN) component before and after the MID-task sessions. We found that after extensive MID-task training, the stimuli with largest expected value evoked larger MMN responses (as compared to the baseline oddball session) that probably reflects a more fine-grained stimulus discrimination of highly valued stimuli. After extensive MID-task training acoustic cues coding intermediate expected values evoked larger P3a component (as compared to the baseline oddball session), that can indicate a stronger involuntary attention switching toward moderately valued stimuli. Overall, our results show that continuing valuation during the MID-task evokes a short-term plastic changes in the auditory cortices associated with the improved stimulus discrimination and the involuntary attention towards auditory cues with the high expected value.

Keywords: expected value, auditory cortex, neuroplasticity, EEG, mismatch negativity, MMN, P300

JEL Classification: Z

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<sup>3</sup> This work was supported by RFBR research project № 14-06-00349a and was partially supported by the subsidy granted to the National Research University Higher School of Economics by the Government of the Russian Federation for the for the implementation of the Global Competitiveness Program.

## Introduction

People continuously learn values associated with the environment. To choose optimally, they must consider both the potential value of different courses of actions and the probability that each action will lead to a desired outcome. In 1654, Blaise Pascal formalized this idea as the expected value (EV) theory, which has played a prominent role in both economic and psychological theory (von Neumann and Morgenstern, 1944; Bandura, 1977). Here EV is the value of any course of action that could be determined by multiplying the expected gain by the likelihood of receiving that gain. Moreover, the value-maximization approach suggests that people choose an alternative with a maximal EV. Despite its limitation, the EV theory has been widely used being probably the first theory which accurately describes how rational, value-maximizing individuals choose between different options. Neuronal mechanisms involved into computation of both EV and its two subcomponents (probability and magnitude) were widely investigated during last two decades (Glimcher et al., 2009). Importantly, the dominant neurobiological model of decision-making (Rangel et al., 2008) assumes that sensory processing of options and the evaluation of options are independent: the neuroeconomics model of decision-making implicitly suggests that sensory inputs to decision-making (valuation) neural networks are stationary. However, experience-induced plasticity is vital for human brain and provides the possibility to learn and adapt to constantly changing sensory environment. Experience-induced brain plasticity is well-established and neuroplastic changes could be found long after the developmental period (Buonomano and Merzenich, 1998). For example, in the motor cortex and sensory cortices of different modalities, learning leads to the increase in the number of neurons that represent the learned stimuli or induces the spatial rearrangement in neurons populations topography (Nudo et al. 1996; Recanzone, Merzenich, and Schreiner 1992; Recanzone, Schreiner, and Merzenich 1993; Recanzone et al. 1992). An experience-driven improvement in quality of stimuli perception is called *perceptual learning* and can be used to explore plasticity in sensory cortices (Gilbert, Sigman, and Crist 2001). Here, we hypothesized that repeated valuation of auditory cues coding different EVs induce perceptual learning and an experience-induced brain plasticity of the auditory cortex.

Numerous ERP studies have shown training-induced changes in neuroplasticity of auditory function (Atienza, Cantero, and Quiroga 2005; Kujala and Näätänen 2010; Shtyrov, Nikulin, and Pulvermüller 2010) which could be explained by reorganization of neuronal populations and changes in sensitivity and processing of relevant information. For example, frequency discrimination training increases the cortical representation area of the corresponding frequencies (Recanzone, Schreiner, and Merzenich 1993) because more neurons become responsive to trained

frequencies. An experience-induced brain plasticity was robustly demonstrated using the mismatch related negativity (MMN) (see Näätänen et al. 2007, for a review). MMN is evoked by the presentation of an oddball or deviant stimuli, embedded in a stream of repeated stimuli, the standards (Näätänen et al. 2007). MMN is normally elicited in the interval of 150–250 ms after the onset of a deviant stimulus. The MMN component can be elicited out of the focus of attention and is thought to be the result of a preperceptual, pre-attentive process able to detect alterations in a regular sound sequence (Näätänen, 1990; Winkler et al., 1996). Changes in the amplitude and latency of MMN seem to reflect the more fine-grained stimulus discrimination indicating sensory cortex neuroplasticity. Magnetoencephalography (MEG) recordings have shown that training-dependent MMN is generated in the auditory cortex (Alho et al., 1996; Tervaniemi et al., 2001). Further studies have demonstrated presence of changes in MMN amplitude not only right after discrimination training, but also several days later (Atienza et al., 2002, 2005; Kraus et al., 1995; Menning et al., 2000; Tremblay et al., 1998), suggesting a training-dependent long-term effect on pre-attentive sensory processing in the auditory cortex. For example, musicians represent an ideal model of plastic changes in the human brain (Tervaniemi et al., 2001): detection of changes (as indicated by MMN's amplitude) in a highly complex auditory pattern is facilitated by musical expertise. MMN was also used to study plasticity of the auditory system related to speech discrimination (Kraus et al., 1995, 1996), as well as related to the learning of the native language in infancy (Cheour et al., 1998), or a foreign language in adulthood (Winkler et al. 1999). Overall, the MMN amplitude was found enhanced and/or its latency was shortened as a consequence of training or due to long-term experience. Thus, previous studies have robustly demonstrated that the training-induced change of the MMN amplitude is a good marker of experience-induced neuroplasticity. Here we hypothesize that repeated valuation of auditory cues coding high EV could lead an experience-induced brain plasticity of the auditory cortex and the more fine-grained discrimination of auditory high EV cues as manifested in the change of the MMN amplitude.

Experience-induced effects of EV on auditory processing could also affect P300 – a positive ERP component, known to be induced by infrequent stimulus presentation (Sutton et al., 1965). P300 consists of two sub-components: the P3a with latency around 230–300 ms and fronto-central distribution, and the P3b, which occurs later (300 - 400 ms) in parietal sites. The P3a has been associated with neural activity related to involuntary shifts of attention to changes in the environment (Escera et al., 1998, Rinne et al., 2006). P3a response has been linked to both short- and long-term plasticity changes as a result of auditory training (Atienza et al. 2004; Draganova et al. 2009; Uther et al. 2006). Here we hypothesize that repeated valuation of auditory cues coding

high EV could lead to an increase in P3a amplitude indicating the involuntary shifts of attention towards high EV cues.

In the current study we investigated experience-induced plastic changes in the neural representation of acoustic cues coding different EVs, using repeated monetary incentive delay task (MID-task; Knutson et al., 2005). The MID-task is widely used to study neural responses to cues coding monetary outcomes with different EVs. During the two-day experiment subjects participated in two extensive sessions of an audio-version of the MID-task. Next, we investigated electrophysiological correlates of the experience-induced plasticity of the primary auditory cortex by comparing ERPs (MMN and P3a) to stimuli with different EVs before and after MID-task sessions.

## Methods

### Subjects

Twenty-nine healthy right-handed subjects (mean age 23 years, range 20–27 years, 17 males) participated in the two-day study after giving a written informed consent. Out of them, fourteen (7 males, 21-27) participated in the EEG part of the experiment. Experiment was approved by the local Ethics Committee.

### Stimuli

Three sinusoidal tones (523, 1046 and 1569 Hz with the fundamental frequency corresponding to C5 of the Western musical scale, intensity 70 dB) were used in the oddball paradigm as the standard stimuli (Fig. 1).

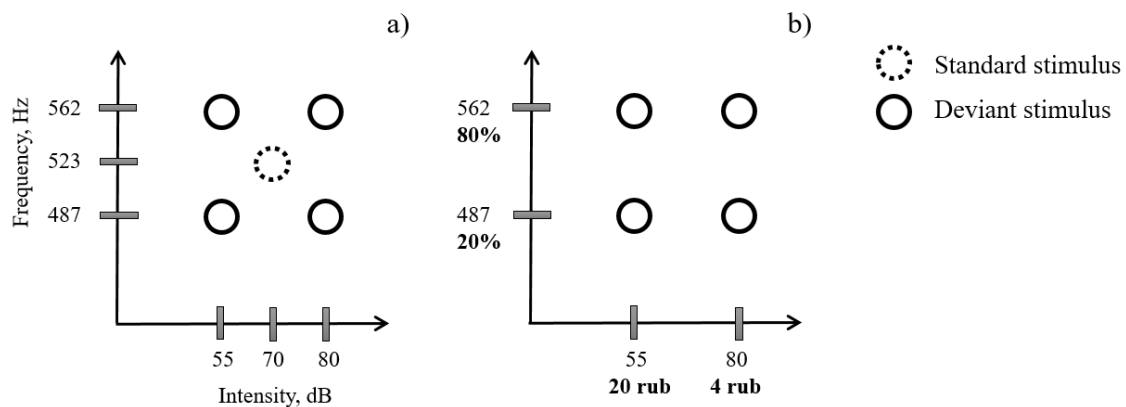


Figure 1. Physical parameters of acoustic stimuli. a) Stimuli in the oddball paradigm. b) Physical parameters of stimuli used in the MID task. Frequency of the sound encoded probability of the positive outcome, while intensity of the sound indicated magnitude of the positive outcome.

Deviant tones (Fig. 1) differed from standard both in frequency and intensity according to a probabilistic design (an increment or decrement were equally probable) which resulted in four distinct deviants. Deviants differed from standards in frequency by  $+10/8$  and  $-10/8$  semitones of the Western musical scale (fundamental frequencies 562 Hz for the higher and 487 Hz for lower deviant tones). The intensity of the deviants was either smaller or bigger than the standard (70 dB) by 15 dB and 10 dB, respectively (55 and 80 dB). All tones had a duration of 200 ms (including 5 ms rising and falling times). Stimuli were generated with the help of the PRAAT software. Four deviant odd-ball stimuli were also used in the auditory MID task, where they were assigned the economics connotation: probability was reflected in the sounds' frequency and magnitude – in

sounds' intensity (Fig.1, b). Some deviants coded high and low reward probability (80 and 20%, correspondingly while others - high and low magnitude (4 or 20 rubles, correspondingly).

### **Study design**

At the beginning of each experiment the ability of participants to discriminate auditory stimuli (standard tones) was tested during a recognition task: participant were instructed to classify tones by pressing the corresponding button. The EEG session started when the subject successfully identified 8 out of 10 last sounds. *After the 1<sup>st</sup> odd-ball session*, subjects performed two 25-min MID tasks in two consecutive days followed by the last odd-ball task.

*Oddball task.* To record MMN before and after MID training, subjects participated in the passive oddball task where infrequent deviant tones were randomly interspersed with a standard tone presented with a standard probability ( $P_{std}$ ) of 0.8. (Fig.1, b) with a  $800 \pm 100$  ms onset-asynchrony (SOA). 8. Each deviant type ( $Dev_{11F1}$ ,  $Dev_{11F2}$ ,  $Dev_{12F1}$ ,  $Dev_{12F2}$ ) was presented as every fourth, fifth or sixth tone with the same probability ( $P_{dev} = 0.2/4 = 0.05$ ). Two successive deviants were always of different types (e.g.,  $Dev_{12F2}$ -- Std-- Std -- Std --  $Dev_{11F1}$ —Std -- Std -- Std -- Std -- Std --  $Dev_{12F1}$  -- Std -- Std -- Std -- Std -- Std --  $Dev_{11F1}$ --Std-....). The stimuli were delivered in 30-min sequences: 2400 tones per sequence, each of the 4 deviants was presented 120 times, all sequences started with four successive standards.

*Auditory version of MID-task.* During the auditory version of MID task, participants were exposed to tones (auditory cues) indicating that they might win money (4 or 20 rubles) with certain probability (20% or 80%), then wait for a variable anticipatory delay period (2000-2500 ms), and finally respond to rapidly presented target with a single button press (Fig. 2). After a short delay, subsequent feedback notified subjects if they had won or lost money together with their cumulative total (outcome, 2000 ms). Probability of win was manipulated by altering the average target duration through an adaptive timing algorithm that followed subjects' performance, such that they would succeed on 80% of high-probability trials and 20% of low-probability trials overall.

The initial time of target MID presentation was based on reaction times collected during the training session. Prior the MID performance participants were instructed with regard to a.m. principles of the EV encoding in acoustic features.

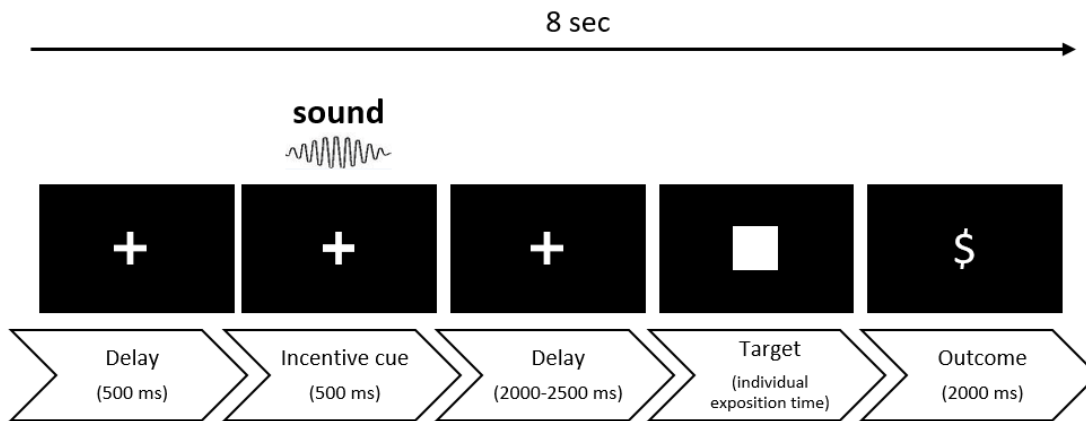


Fig. 2. Trial scheme of auditory version of MID-task

### EEG recordings and data analysis

To study experience-induced plastic changes we recorded MMN and P3a components before and after two-days training in MID-task. EEG was recorded using 30 active electrodes (Brain Products, Germany) at a sampling rate of 500 Hz, according to the extended version of 10–20 system: Fp1, Fp2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T7, T8, P7, P8, Fz, Cz, Pz, Oz, FC1, FC2, CP1, CP2, FC5, FC6, CP5, CP6, TP9, TP10. Active channels were referenced against the mean of two mastoids electrodes, in order to display the maximal MMN response at frontal electrode sites. The electrooculogram (EOG) was recorded with electrodes placed at the outer canthi and below the left eye.

The EEG was offline filtered (passband 1–30 Hz, notch filter – 50 Hz). Epochs of 600 ms including a 100 ms pre-stimulus period was separately averaged for different trial types. The mean voltage of the pre-stimulus period served as a baseline for the amplitude measurement. Epochs including voltage changes exceeding 75 mV at any channel were omitted from the averaging in order to exclude artifacts. Impedance was confirmed to be less than 5 k $\Omega$  in all electrodes prior to recordings. Baseline correction was performed using a time window of -100 to 0 ms. For each deviant condition we computed the MMN, defined as the difference between averaged ERP following standard and deviant stimuli. MMN peak amplitudes were measured from the most negative peak occurring at 80–250 ms post stimulus-onset at an electrode located at Cz. The P3a component was identified as the most positive deflection between 180-300 ms post stimulus-onset at the same electrode.



To test effects of the Day (Day1, Day2) and Condition (four combinations of reward magnitude and gain probability: 4rub 20%; 4rub 80%; 20rub 20%; 20rub 80%) factors on the amplitudes of the MMN and P3a, separate two-way analyses of variance ANOVA were conducted. The LSD post-hoc test was used to compare differences among trial types ( $P < 0.05$ ) in case of a significant interaction.

## **Results**

We identified negative deflection on the difference waveforms as MMN component. MMN amplitude was clearly larger in case of trials with largest EV (20 rub \* 80%; 562 Hz, 55dB):  $-3.37 \pm 0.39$  mV on day 1 and  $-4.39 \pm 0.45$  mV on day 2. No changes in MMN component amplitude were found in other types of trials. For trials with smallest EV (4 rub \* 20%; 487 Hz, 80 dB) MMN amplitude was  $-3.31 \pm 0.39$  mV on day 1 and  $-2.77 \pm 0.42$  mV on day 2. In case of intermediate EV, for 4 rub \* 80% (487 Hz, 80 dB) on the first day mean MMN amplitude was  $-3.43 \pm 0.37$  mV and  $-3.65 \pm 0.4$  mV on day 2. For trials with another intermediate EV 20 rub \* 20% (562 Hz, 55 dB) amplitude was  $-3.9 \pm 0.44$  mV on day 1 and  $-3 \pm 0.39$  mV on day 2.

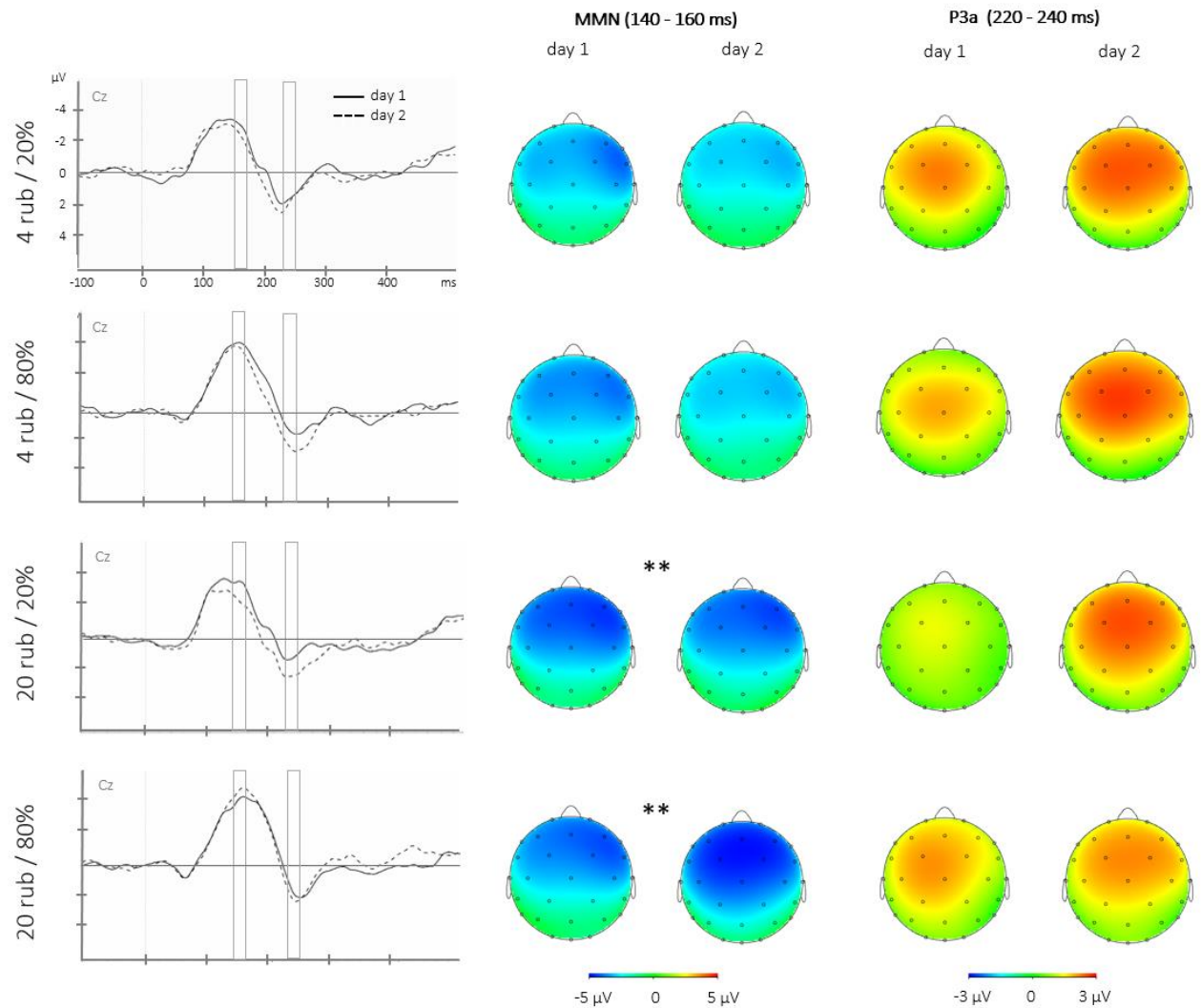


Figure. 4. Grand-averaged deviant-minus-standard difference curves superimposed for two oddball conditions at Cz: before- (solid line) and after-MID-task (dashed line) (Left) and their topographies for MMN (Middle) and P3a time range (Right). Vertical bars on left ERP plots indicate integration time intervals (140-160 ms and 240-260 ms for MMN and P3a correspondingly). ERPs and topographies are presented for all 4 combinations of magnitude and probability, constituting EV (4 rub/20%, 20 rub/80%, 20 rub/20%, 4 rub/80%, 20 rub/80%). Asterisks mark significant changes of ERP amplitude between two recording days.

The two-way repeated measures ANOVA of MMN amplitude revealed no significant effects of *Day* and *Condition*. However, a significant interaction between factors was found ( $F(3; 39) = 4.74$ ;  $p=0.01$ ). A Post-hoc comparison of the MMN amplitude in Day1 and Day 2 across different EV showed significant increase of the MMN amplitude in case of the highest EV = 20 rub\*80% (562 Hz, 55 dB) ( $p = 0.01$ ) and significant decrease in case of lower EV = 20 rub\*20% (487 Hz, 55 dB) ( $p = 0.02$ ) (Fig 4).

We identified a positive frontal-parietal deflection around 250 ms as the P300 component. Changes in P300 were the largest in trials with intermediate EV: 4 rub \* 80% and 20 rub \* 20%.

For the '4 rub \* 80%' condition, mean P3a amplitude was  $1.35 \pm 0.31$  mV and  $1.35 \pm 0.31$  mV for Day1 and Day2, correspondingly. For trials with the 20 rub \* 20% EV, the amplitude of P300 was  $2.26 \pm 0.55$  mV and  $3.21 \pm 0.48$  mV for the Day 1 on the Day2 correspondingly. For trials with the smallest EV (4 rub \* 20%) amplitude did not differ across two days:  $2.16 \pm 0.54$  mV on day 1 and  $2.87 \pm 0.34$  mV on day 2. In trials with the largest EV (20 rub \* 80%) no difference in P300 was observed between two days:  $2.06 \pm 0.51$  mV (Day1) and  $1.74 \pm 0.45$  mV (Day2).

The two-way repeated measures ANOVA of P300 amplitude revealed a significant influence of factor Day ( $F(1; 13) = 5.37$ ;  $p = 0.04$ ) and Condition ( $F(3; 39) = 2.98$ ;  $p = 0.04$ ), but no significant interaction between factors.

ERP topographies (Fig.4) for difference curves obtained on Day 1 and Day 2 show distribution of the potential in two time windows. MMN component was pronounced mainly in fronto-central sites, with no change in distribution across two days. However, the P300, registered mainly in central areas on first days, became more frontally distributed on second day.

## Discussion

To investigate the experience-induced plasticity of the auditory cortex as a function of the EV encoded in acoustic tones we specifically focused on changes in MMN and P3a components between two consecutive oddball experiments separated by an extensive training in MID-task sessions.

The analysis of ERPs revealed the experience-induced plasticity of the auditory cortex: significant enlargement of amplitude for both the MMN and P3a to tones coding larger EVs as compared to small EV. Tones that encoded largest EV evoked plastic changes in auditory cortex underlying preattentive stimuli discrimination: the MID-task induced enlargement of the MMN amplitude for stimuli with the largest EV (20 rub \* 80 %). We suppose that relatively small changes in MMN amplitude (less than 1 mV) could be related to initially good discrimination of frequency and intensity of deviant sounds (Novak et al., 1990; Tiitinen et al., 1997). This interpretation is well supported by results obtained in the sound identification test at the beginning of each experimental session.

MMN is usually implicated into involuntary switching of attention to sound changes, and this automatic attention shift may result in conscious awareness of deviant stimulus. The MMN has been successfully used as an electrophysiological measure of plasticity in the central auditory system associated with the automatic discrimination. Initial poor identification of differences

between deviant and standard stimuli results in absent or very low-amplitude MMN (Sams et al. 1985; Tiitinen et al. 1994). For example, absence of discrimination corresponded to absence of MMN, while MMN emerged following an active learning to discriminate deviant pattern (Näätänen et al. 1993b; Novak et al., 1990; Tiitinen et al., 1997). Moreover, the MMN amplitude correlated with accuracy of performance. Thus, repeated valuation of auditory cues coding different EVs in MID task evoked an experience-induced brain plasticity of the auditory cortex manifested in the enlarged MMN.

We also found that MID training modulated the P3a response evoked by two types of cues coding intermediate EVs (4 rub\* 80% and 20 rub\*20%).

From literature it is known that the P3a has a multisource nature: its activity was found in the orbitofrontal cortex, lateral prefrontal areas, and posterior cortices (Bledowski et al., 2004; Løvstad et al. 2011; Knight and Scabini, 1998). The P3a amplitude effects seem to reflect alterations in stimulus evaluation, involuntary switch of attention for infrequent sounds (for review, see Polich 2007), as well as attention switch and automatic novelty detection stemming from changes in frontally based working memory representations (Escera et al., 1998; Friedman et al., 2001). Our P3a results implicate the involvement of fronto-central areas well corroborating the involuntary change of attention hypothesis of P3a (Escera et al., 1998, Rinne et al., 2006). We hypothesize that training-induced P3a enhancement obtained in our study can be associated with the EV of auditory cues due to a top-down process. The enhancement of P3a amplitude seems to represent the involuntary attention switch towards stimuli encoding intermediate EVs. This might reflect training-dependent plasticity resulting in the enhanced change detection (Seppänen et al., 2012), which in its turn facilitates processing of auditory stimuli. Thus, repeated valuation of auditory coding moderate EVs led to an increase in P3a amplitude indicating the involuntary shifts of attention towards those acoustic tones.

Overall, our results show that continuing valuation of auditory cues coding different EVs evokes a short-term plastic changes in auditory cortices associated with the improved stimulus discrimination and the involuntary attention toward the auditory cues with the high expected value. Observed signatures of neuro-plasticity of the auditory cortex may play an important role in learning and decision-making processes through facilitation of future perceptual discrimination of valuable external stimuli. Overall, results indicate the sensory processing of options and the evaluation of options are not independent as has been assumed by the dominant neuroeconomics model of decision-making.

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