NATIONAL RESEARCH UNIVERSITY HIGHER SCHOOL OF ECONOMICS

As a manuscript

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SENSORY NEUROPLASTICITY ELICITED BY AUDITORY CUED MONETARY OUTCOMES

Summary of the dissertation
for the purpose of obtaining academic degree
Doctor of Philosophy in Psychology

Academic supervisor:
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Moscow 2021

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INTRODUCTION

Research problem

The traditional decision-making theory assumes that individuals' choices are driven by values that are associated with prospective outcomes. Numerous neurobiological studies have implicated the involvement of dopaminergic neurons in the valuation stage of the decision-making process and in behavioral adaptations. Interestingly, popular neurobiological models of decision making acknowledge the key role of learning in reward-based decisions, but they indirectly assume that the primary sensory inputs to dopaminergic (decision making) networks are stationary and independent from previous decisions. However, many cognitive studies have demonstrated experience-induced plasticity in the primary sensory cortices, indicating that repeated decisions could modulate sensory processing, which, in turn, could modulate follow-up decisions. The electroencephalography (EEG) research reported here focused on the plastic changes in the auditory sensory cortex reflected in the modulation of the auditory event-related potential (ERP) component called mismatch negativity (MMN) elicited in a passive oddball task following learning to associate a particular sound cue with monetary outcome during a separate monetary incentive delay (MID) task which was originally conceived to study valuation in the brain. In response to the gains and losses of the MID task, one can record the feedback-related negativity (FRN) component of ERP which reflects the learning-associated reward prediction error (RPE) processing. MID tasks are frequently used to study valuation processes in the visual domain. We developed an auditory version of the MID task in order to use the auditory MMN tool to test sensory plasticity. Thus, our first study focused on the feedback-locked FRN and cue-locked dN200 responses recorded during our original auditory version of the MID task and their sensitivity to the probability and magnitude of reward outcomes. FRN was modulated by both magnitude and probability of the outcome, whereas dN200 amplitude was not affected by the outcome parameters predicted by the cues. On the other hand, the cue-locked dN200 component correlated with the feedback-locked FRN component which is associated with a negative RPE. Our second experiment used two oddball task sessions interspersed by two MID task sessions where sound cues encoded parameters of the

monetary reward. We found that after 2 days of training in the MID task, incentive cues evoked a larger P3a (compared with the baseline condition), indicating there was an enhancement of the involuntary attention to the stimuli that predict rewards. At the individual level, the training-induced change of mismatch-related negativity was correlated with the amplitude of the feedback-related negativity (FRN) recorded during the first MID task session. The third study focused on the changes in the MMN amplitude as a result of the association of the auditory cues with the particular monetary losses. The MMN magnitude significantly increased in the second oddball session for the sound cue that encoded a big monetary loss in the context of a small monetary loss but did not change in other conditions as well as in the control condition. Individual changes in the MMN correlated with the individual sensitivity of the FRN component to the magnitude of experienced loss. Taken together, our research supports the hypothesis of plasticity of the sensory input to associative cortices, demonstrates that FRN amplitude is sensitive to the magnitude of outcome both in gain and loss domains, and connects plastic changes in MMN with the parameters of individual FRN component that is associated with reward prediction error processing.

Decision making and sensory plasticity

The traditional decision-making theory assumes that individuals' choices are driven by values that are associated with prospective outcomes. Numerous neurobiological studies have implicated the involvement of dopaminergic neurons in the valuation stage of the decision-making process (Schultz, 2006) and in behavioral adaptations (Bromberg-Martin et al., 2010). Interestingly, popular neurobiological models of decision making (Rangel et al., 2008; Wang, 2012) acknowledge the key role of learning in reward-based decisions, but they indirectly assume that the primary sensory inputs to dopaminergic (decision making) networks are stationary and independent from previous decisions. On the other hand, many cognitive studies have demonstrated experience-induced plasticity in the primary sensory cortices (Atienza et al., 2005; Kujala and Näätänen, 2010; Shtyrov et al., 2010; Pantev and Herholz, 2011), indicating that repeated decisions could modulate sensory processing, which, in turn, could modulate follow-up decisions. Although the

idea that the sensory cortex directly participates in learning during classical conditioning is not novel in psychophysiology and well supported by experimental evidence (Galambos et al., 1955), relatively little is known about the neural reorganization in auditory cortical areas related to stimuli with assigned economic values. We assume that similar to plasticity during the learning of speech or music, neuroplastic changes could also manifest when stimuli are being associated with economic values: for example, a slot machine sound could become associated with pay-out during the first visit to a casino. In our series of studies, we tested the hypothesis that the repeated associations of a stimulus with a monetary outcome may evoke plasticity in an individual's sensory processing. Furthermore, we explored the neural activity underlying value-based learning and its link to the plastic changes in the sensory cortices.

Mismatch negativity

The mismatch negativity component of auditory event-related potation is one of the widely used ERP components to study sensory plasticity.

MMN was found in 90th as an electrophysiological signature of a pre-attentive process that detects alterations in a regular sound sequence (Näätänen, 1990; Winkler et al., 1996). It can be evoked by an oddball or a rare deviant auditory stimulus embedded in a sequence of frequently presented standard stimuli or by using a roving standard paradigm in which a deviant sound becomes a standard one after some repetition, thus allowing as many stimuli as possible to be accommodated (Shestakova et al., 2013). The MMN is frequently explained in terms of predictive coding, which is a general theory of perceptual inference (Garrido et al., 2009; Carbajal and Malmierca, 2018). According to this theory, the brain actively learns the regularities of the sensory input and models an internal representation of this information. When the model's prediction of the forthcoming stimulus is violated, the mismatch signal is generated (Paavilainen et al., 1999; Näätänen et al., 2005; Winkler, 2007). Importantly, the amplitude of the MMN is modulated by previous experiences and correlates with behavioral discrimination performance (Ref). In addition to indexing, sensory memory traces (Näätänen and Michie, 1979; Cowan et al., 1993) changes in the amplitude of MMN can also indicate the presence of long-term or

permanent memory traces, for example, those for mother-tongue speech sounds (Winkler et al., 1999; Tremblay et al., 1997). Thus, previous studies have robustly demonstrated that training-induced changes of the MMN amplitude are reliable markers of experience-induced neuroplasticity.

As it can be elicited irrespective of whether a participant is paying attention to the task or not (Näätänen and Michie, 1979; Shtyrov et al., 2010), MMN has become a widely used instrument in studies of various auditory functions: from automatic auditory discrimination to higher-order cognitive processes (e.g. language and speech), as well as training-induced plasticity (Shtyrov et al., 2010; Kraus et al., 1996; Menning et al., 2000). In our series of research, we explored changes in MMN amplitude as a correlate of plastic changes in auditory sensory cortices.

Feedback-related negativity and reward prediction error

Tightly interwoven with reinforcement learning (RL) theory (Bush and Mosteller 1951), decision theory assumes that individuals' choices are driven by the values attached to prospective outcomes (Steele and Stefansson 2015). The magnitude and probability of outcomes are integrated to form the expected value (Bandura 1977; Von Neumann and Morgenstern 1944). For example, the temporal difference model of RL (Rescorla and Wagner 1972) indicates that an individual assigns high values to the states that predict future rewards when encountered unexpectedly. Therefore, the reward prediction error (RPE) reflects the discrepancy between obtained and expected outcomes: unexpected unfavorable outcomes (i.e., monetary losses) produce negative RPEs, whereas unexpected favorable outcomes (i.e., monetary gains) result in positive RPEs. Subsequently, with the seminal work of Wolfram Schultz (1997), RL theory has come to play an important bridging role between economics (e.g., Camerer and Ho 1999; Erev and Roth 1998), psychology (Rescorla and Wagner 1972), and neuroscience (Schultz 1997). The dopaminergic system has been proposed to broadcast a "prediction error" signal of precisely the form needed in reinforcement algorithms to drive convergence toward a standard dynamic programming value function (Barto and Sutton 1982). Since then, the dopaminergic RPE hypothesis has been tested with the use of a variety of

neuroimaging techniques, including electroencephalography (EEG) (Düzel et al. 2009; Holroyd and Coles 2002; Knutson et al. 2005; O'Doherty et al. 2001; Pessiglione et al. 2006; Talmi et al. 2012). Using the event-related potential (ERP) approach to the obtained and expected outcomes in the EEG experiment, Holroyd and Coles (2002) suggested that the feedback-related negativity (FRN) component of ERP can code an RPE learning signal that modifies performance on the task. FRN is a relatively negative defection in the ERP following losses or error feedback compared with wins or positive feedback. Two main interpretations have been proposed to explain the nature of this negative difference wave, FRN, which occurs approximately 250–350 ms after feedback onset. FRN can represent a negative ERP component, elicited by an unfavorable outcome (Ullsperger et al. 2014). Alternatively, this negative defection can be explained by a positive ERP component, elicited by a favorable outcome, which is the reward positivity (RewP) (Proudft 2015). Consequently, FRN/RewP should be strongly modulated by the expectations of positive outcomes. While the interpretation of FRN/RewP is still under debate, a general agreement exists on its involvement in context-sensitive feedback evaluation underlying RPEs. In addition, electro- and magnetoencephalographic (E/MEG) and functional magnetic resonance imaging (fMRI) studies suggested the causal role of dopaminergic activity in the cingulate cortex and the surrounding medial prefrontal cortex in FRN generation (Agam et al. 2011; Emeric et al. 2008; Miltner et al. 1997; Walsh and Anderson 2012; Warren et al. 2015). The sensitivity of FRN to the valence of the outcome constitutes the main proof of the hypothesis that FRN might be an encoder of RPE's sign (Holroyd and Coles 2002; Luu et al. 2000). A number of recent studies reported that FRN responds to the contextually most salient information and thus reflects an unsigned prediction error (Hauser et al. 2014; Oliveira et al. 2007; Talmi et al. 2012, 2013). A recent meta-analysis (Sambrook and Goslin, 2015) refuted this hypothesis and clearly demonstrated the main effect of valence and the interaction of RPE size and valence. Thus, FRN is sensitive to the size of the RPE, which can be manipulated by changing two components of expected value, namely, magnitude and probability. While the majority of neuroimaging studies suggest that FRN is more sensitive to the probability of outcomes than to their magnitude (Walsh and Anderson 2012), evidence also shows

that the outcome magnitude exerts a modulatory effect on FRN (Sambrook and Goslin 2015).

Monetary incentive delay task

One of the paradigms that can be utilized to study FRN is a monetary incentive delay task (MID). The MID task is an elegant tool to study the different stages of RL from reward anticipation to its delivery (Knutson et al. 2000, 2005). It can be used to delineate the neural mechanisms of performance monitoring during behavioral acts with different expected values and RPEs. Initially, the MID task was used in fMRI studies on the neural processing of gains and losses (Knutson et al. 2000). Subsequent EEG and MEG studies utilized the MID task to examine the neural dynamics of reward processing with a temporal resolution in the millisecond range (Broyd et al. 2012; Doñamayor et al. 2012; Thomas et al. 2013). The MID task introduces incentive cues that signal both the magnitude and the probability of prospective outcomes. It enables the investigation of the effects of these two components of expected value on neural activity associated with the processing of incentive cues and feedback (Knutson et al. 2005). In the classic MID task, visual stimuli, such as circles, squares, and triangles, are utilized as incentive cues that code the probabilities and magnitudes of outcomes. We developed an auditory version of the MID task (Figure 1b) that relied on the sounds of different physical characteristics as incentive cues to construct robust associations between auditory stimuli and monetary outcomes.

Figure 1. Schematic illustration of the experiment and its components. (**a**) The overall structure of the experiments. (**b**) Structure of a probe in the MID task. (**c**) An example of sound sequences in the roving oddball task. Published in Gorin et al., 2020.

Taken together, the research described here includes a consequent set of experimental studies, developed to examine the possibility of the sensory cortices plasticity as a result of learning during monetary games. In the first study, we developed an auditory version of the MID task, validated its applicability in the EEG research, and used it to build cue-outcome associations. In the second study, we focused on the changes in auditory ERPs during the passive oddball task after two sessions of the MID task in the gain domain. In the third study, we switched to the loss domain and modified the task to separate effects of magnitude of an outcome and context of the monetary game. Therefore, we consequently performed research that demonstrated that monetary outcomes associated with certain stimuli may affect their processing in the future.

Research goals

1. Develop a research paradigm to study brain plasticity associated with financial outcomes in the economic game in the auditory modality using electroencephalography.

2. Study plastic changes in auditory ERP responses to the oddball stimuli associated with the monetary rewards varying in expected value using the newly developed combined MID-oddball paradigm approach.

3. Study plastic changes in auditory ERP responses to the oddball stimuli associated with the monetary losses varying in monetary value using the newly developed combined MID-oddball paradigm approach.

Overview

In the following overview, we provide a short description of the research. In the first part (Study 1, Attachment A of the thesis) we performed an experimental study of the auditory cue-related N200 component and feedback-related FRN component to check if their magnitudes were affected by the parameters of the expected reward. In the second study (Study 2, Attachment B of the thesis) we ran an EEG experiment to study plastic changes in the auditory ERP components (MMN and P3a) as a result of the cue-reward association during the monetary game and their correlation with the feedback-related ERP. In the third experiment (Study 3, Attachment C of the thesis) we studied plastic changes in the MMN component as a result of the cue-loss association during the monetary game in different contexts and their correlation with the sensitivity of the FRN component to the loss magnitude.

Methodology

In the series of experiments, we developed two versions of the auditory monetary incentive delay task, using them along with the auditory oddball tasks. To collect the data, in all experiments we used BrainVision actiCHamp amplifier (Brain Products GmbH) with a sample rate set at 500 Hz. All subjects were right-handed, with normal or corrected-to-normal vision. They did not report any history of psychiatric or neurological problems, and they all reported to be right-handed. The study was approved by the local

ethics committee. All participants gave their written informed consent prior to their participation and received rewards for the participation.

KEY RESULTS

Part I (EEG Study I). We hypothesized that FRN component will be modulated by the parameters of the reward; we also expected that the dN200 component would appear as a response to the predictive cue coding more and less desirable outcomes. We showed that feedback-locked FRN was modulated by both the magnitude and the probability of outcomes during an auditory version of the MID task (Figure 2). Furthermore, the cue-locked dN200, which is associated with the update of information about the magnitude of prospective outcomes, correlated with the standard feedback-locked dFRN, which is associated with the processing of favorable and unfavorable outcomes (RPE). The results further expand our knowledge of the interplay between the processing of the evaluation of ongoing predictive events and future outcomes and the following revision of these predictions during outcome delivery.
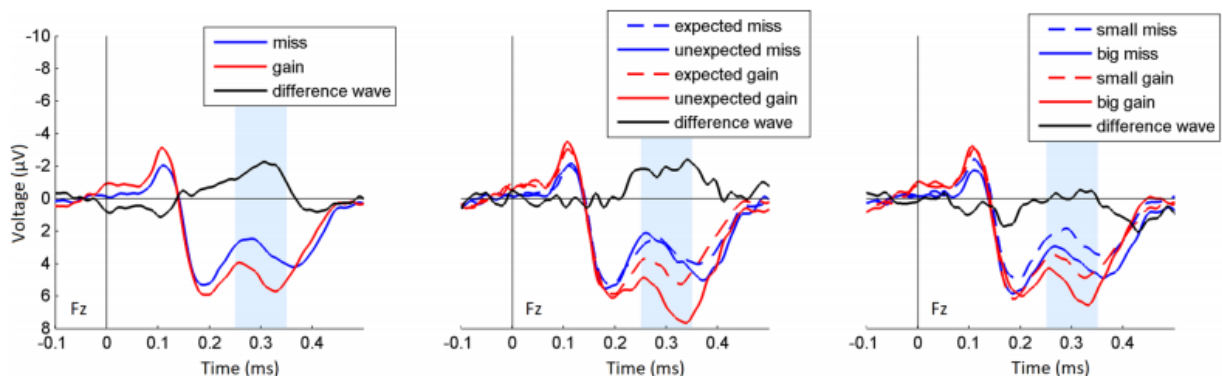
Figure 2. Grand-averaged visual ERP waveforms (Fz) superimposed for different types of feedback (upper row). Difference waveforms were calculated separately for valence (misses − gains), probability ((unexpected misses − unexpected gains) − (expected misses − expected gains)), and magnitude ((big misses − big gains) − (small misses − small gains)) of the outcomes. The width of the blue bars corresponds to the 250–350-ms time window within which the differences between corresponding ERPs were measured and plotted in the form of difference waveforms.

Part II (EEG Study II). We tested hypothesis whether repeated exposure to the stimuli that signal different incentive values in the MID task changes their sensory processing

when tackled in the oddball tasks. In the absence of the group MMN effect, we observed learning-related changes of the P3a, indicating a stronger reallocation of attention to the incentive cues (Figure 3). The correlational analysis of individual MMN amplitudes with the MID-session FRN responses revealed that a stronger RL signal was associated with more fine-grained discrimination of the incentive cues. Our results showed that plastic changes associated with better discrimination could be sensitive to the continuing valuation of incentive cues that leads to enhanced involuntary attention switching.
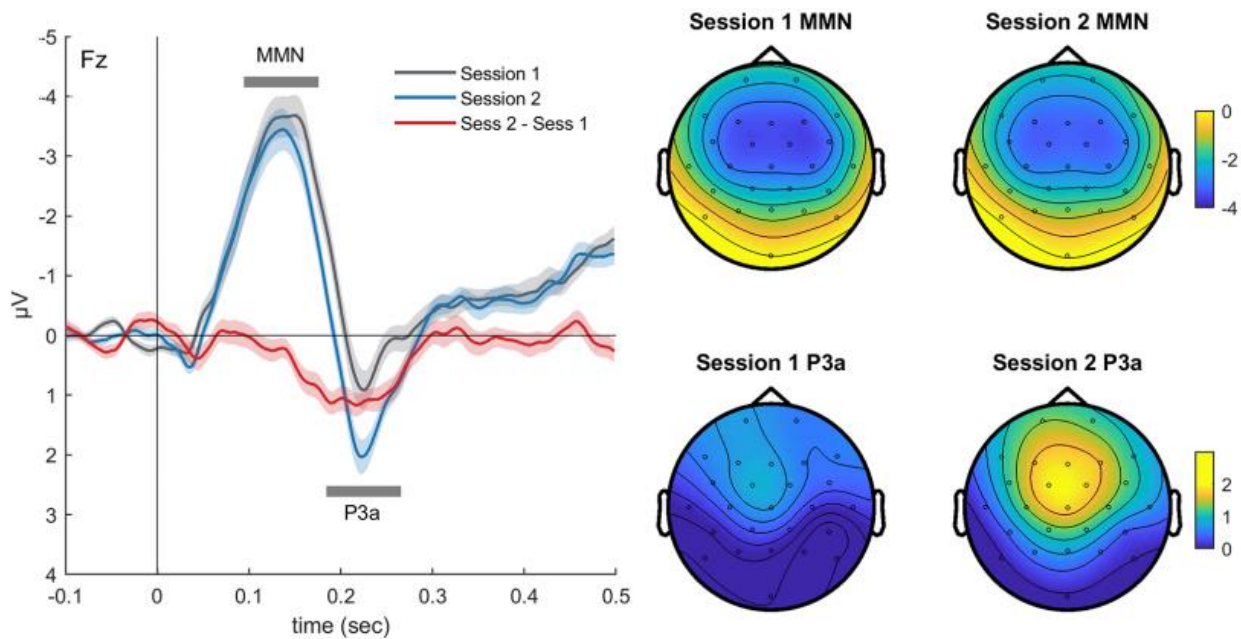
Figure 3. Difference waveforms (Fz, left) derived by averaging the ERPs across four conditions, and corresponding scalp topography (right) of the mismatch negativity (MMN) and P3a during oddball sessions 1 and 2. The shaded area around curves represents the standard error of the mean. The topographic maps indicate the voltage distribution of the mean amplitude in the 110–130-ms (MMN) and 220–240-ms (P3a) time windows.

Part III (EEG Study III). We hypothesized that repeated MID task in the loss domain would lead to the plastic changes in MMN recorded during the passive oddball session. The game had three contexts, in two of the subjects were able to lose a comparable amount of money (low or high) from trial to trial, whereas in the third context consecutive losses could widely differ. As a result, we observed significant growth of the MMN for the acoustic cue that predicted larger loss in the third context, where

sufficient learning was necessary for successful performance (Figure 4). The magnitude of differences, dMMN, significantly correlated with the individual sensitivity of the FRN to the loss amount (dFRN) (Figure 5). We also analyzed the source distribution of the signal using the standard head model and found that the major part of the activity was located in the temporal cortex, supporting our hypothesis of the plasticity in the auditory sensory cortex.
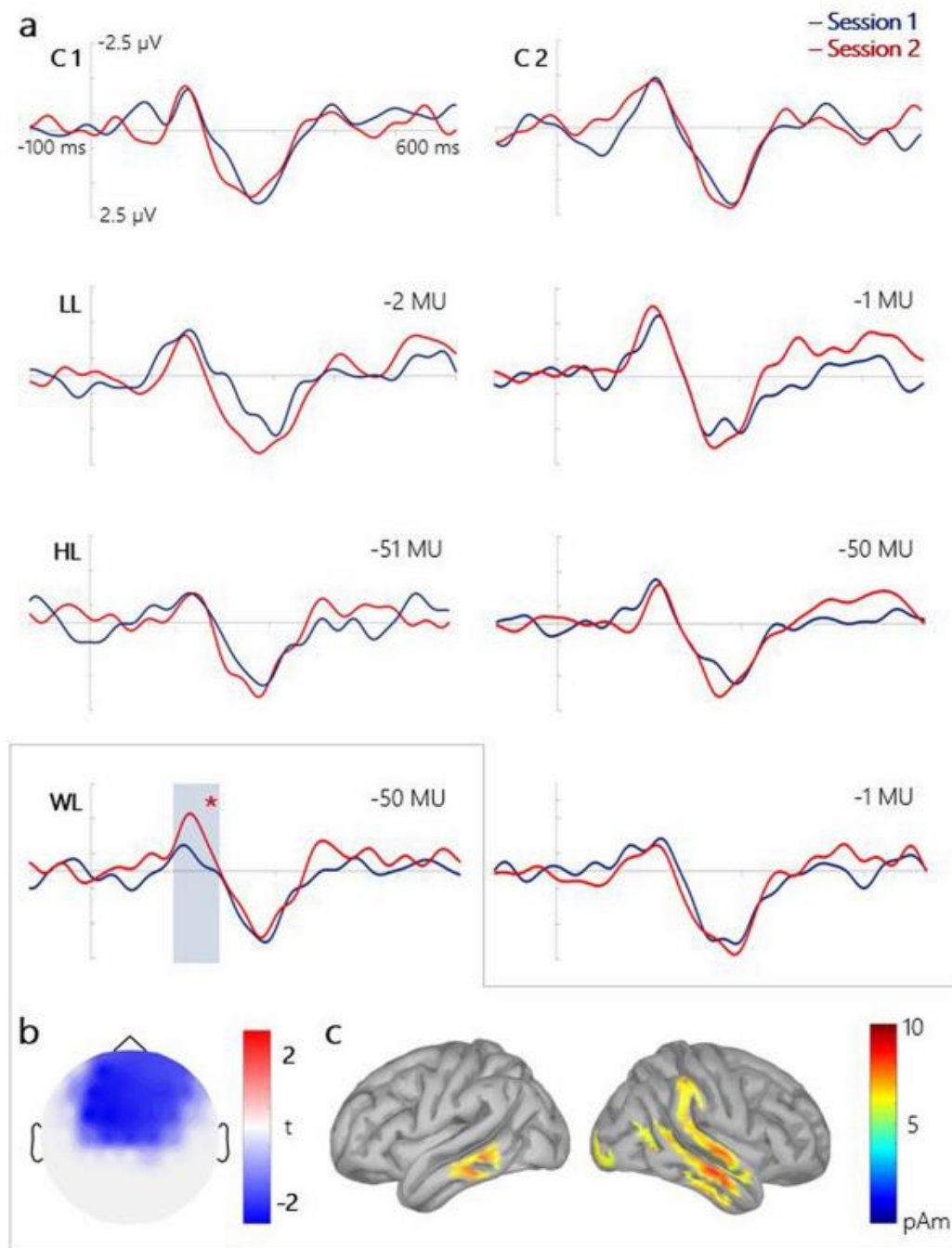

Figure 4. Evoked responses in the oddball task. (**a**) Grand-averaged difference waves (deviant *minus* standard) for the first and second sessions at the Cz electrode site. C1 and

C2—high- and low-frequency control sounds. *LL* 'low losses' context, *LL-trials*; *HL* high losses' context, *HL-trials*; *WL* widely varying losses' context, *WL*-trials. (**b**) Cluster t-map for the dMMN (MMN in session 2 *minus* MMN in session 1) in response to large losses (− 50 MU) in WL-trials. (**c**) Source reconstruction of the dMMN in response to monetary cues that code large losses (− 50 MU) in WL-trials (186 ms post-stimulus).
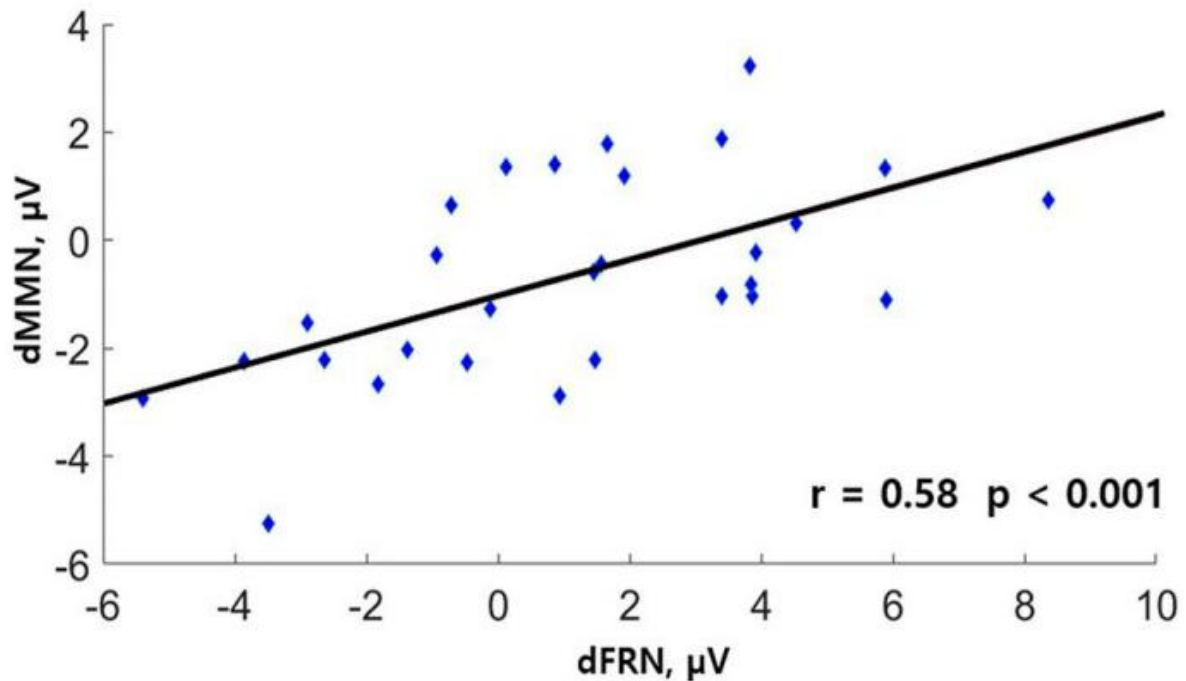

Figure 5. Correlation between the dMMN signature of cortical plasticity and the dFRN signature of reinforcement learning signals for the WL-trials.

Taken together, this series of experiments focused on the plastic changes and dynamics of auditory ERP components and changes in the FRN component that is connected to the reward prediction error processing. We study modulation of the FRN by the magnitude of expected outcome in gain and losses domains, and by the probability – in the gain domain. We also studied how auditory ERPs change as a result of cue-outcome association and found that in the loss domain changes in the MMN component were most prominent only if the sound cue predicted big loss in the context of much smaller. We localized the source of the differential activity in the temporal cortices. Taken together, our results support our initial hypothesis of neuroplasticity of the sensory inputs to the

reward processing associative cortices and extend our knowledge in the field of reward processing dynamics.

Theoretical novelty

Our results support the hypothesis of neuroplasticity of the sensory input to the neural ensembles that process the expected utility of stimuli and extend knowledge about sensitivity of the FRN component to the rewards, losses, and their magnitudes.

Methodological novelty

We developed a set of experimental paradigms that used auditory modality to associate stimuli and outcomes in the MID task that allowed us to manipulate magnitudes and probabilities of losses or rewards and combined this modified MID task with the oddball task to study induced plastic changes in auditory ERPs.

Empirical novelty

For the first time, we demonstrated significant changes in the auditory sensory ERP component as a result of the cue-outcome association during a monetary game and connected them to the parameters of the feedback-related ERP component.

Theoretical significance

The presented results complement most of the available decision-making models, demonstrating plastic changes in sensory areas as a result of the association of stimulus and monetary reinforcement. In addition, we have shown that plastic changes can be associated with the signal of processing the result of an action, thus being consistently associated with decision-making models.

Practical significance

As a result of scientific work, a number of experimental paradigms have been developed, which have shown their worth as a tool for studying sensory plasticity in neuroeconomic problems.

Contribution of the author

The author was directly involved in all stages of the research: development and programming of the experiment, collection and analysis of data, interpretation of results and preparation of articles, work with literature.

Provisions for the defense

1. The RPE signal, a feedback-locked FRN was modulated by both the magnitude and the probability of outcomes during an auditory version of the MID task. Furthermore, the cue-locked dN200, which is associated with the update of information about the magnitude of prospective outcomes, correlated with the standard feedback-locked dFRN.

2. In the gain domain, we observed learning-related changes in the oddball task (P3a component) as a result of the MID task. MMN changes were not significant but correlated significantly with the FRN amplitude.

3. In the loss domain, we observed learning-related changes in the MMN component as a result of the cue-loss association during the MID task. The amplitude of the changes correlated significantly with the FRN signal.

First-tier publications[1]

1. Krugliakova E., Klucharev, V., Fedele, T., Gorin, A., Kuznetsova, A., & Shestakova, A. Correlation of cue-locked FRN and feedback-locked FRN in the auditory monetary incentive delay task // Experimental brain research. – 2018. – T. 236. – №. 1. – C. 141-151.

2. Krugliakova, E., Gorin, A., Fedele, T., Shtyrov, Y., Moiseeva, V., Klucharev, V., & Shestakova, A. The monetary incentive delay (MID) task induces changes in sensory processing: ERP evidence // Frontiers in Human Neuroscience. – 2019. – T. 13. – C. 382.

3. Gorin, A., Krugliakova, E., Nikulin, V., Kuznetsova, A., Moiseeva, V., Klucharev, V., & Shestakova, A. Cortical plasticity elicited by acoustically cued monetary losses: an ERP study // Scientific reports. – 2020. – T. 10. – №. 1. – C. 1-14.

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[1] First-tier publications include papers indexed in the Web of Science (Q1 or Q2) or Scopus (Q1 or Q2) databases, as well as peer-reviewed collections of conferences that appear in CORE rankings (ranks A and A*).

Conference reports

1. Annual Meeting of the Society for Neuroeconomics, October 6 – 8, 2017 (Toronto, Canada). Report: *Short-term plastic changes in the primary sensory cortex elicited by monetary outcomes*

2. Annual Meeting of the Society for Neuroeconomics, September 26-28, 2014 (Miami, USA). Report: *Short-term plasticity in auditory cortical circuit evoked by monetary incentive delay task*

3. Annual Meeting of the Society for Neuroeconomics, October 4 – 6, 2019 (Dublin, Ireland). Report: *tDCS-induced modulation of the feedback-related negativity in the MID task*

CONCLUSION

Initially, we hypothesized that the sensory input to associative cortices could be modulated by the association of a stimulus with a particular outcome. To check the hypothesis, we modified the MID task and accommodated it to the auditory modality, where we encoded the probability and magnitude of the outcome by frequency and intensity of the cues. EEG results demonstrated that the FRN signal has been modulated by monetary features of the outcome. We further analyzed ERP results in the two passive oddball sessions – prior to and after MID sessions and focused on the MMN and P3a components of the auditory ERP recorded in the oddball condition. The results indicated that the P3a component changed its amplitude as a result of the MID task, but MMN changed insignificantly. Nevertheless, individual changes in MMN correlated with the magnitude of FRN in the monetary game. To simplify the game, we fixed the probability (and intensity of the sounds). Since people are more sensitive to losses, we modified the task and switched it to the loss domain. As a result, we demonstrated that the MMN amplitude increased for the cue that encoded bigger monetary loss, that this growth has been correlated with individual parameters of FRN, and that sources of this differential signal were spread over the temporal cortices. Our results supported our initial hypothesis and may inspire further studies of the plasticity of the sensory cortex as a result of economic games.

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to my advisor, Doctor Anna Shestakova, for giving me the opportunity to conduct and complete the Ph.D. study at the Centre for Cognition and Decision Making.

My sincere thanks go to Elena Krugliakova, who is my coauthor on all of the studies for the extremely valuable contribution.

I would like to thank Prof. Vasily Klucharev for his valuable comments and help while designing, conducting, and describing these studies.

Many thanks to Alexandra Kuznetsova, who helped a lot during data collection and processing.

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