Effect of emotional context in auditory-cortex processing

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Abstract

We examined how emotional context influences processing of emotionally neutral acoustic stimuli in the human auditory cortex. Nine subjects performed a simple discrimination task. In the positive-emotional trials correct performance was awarded with money, whereas in the negative-emotional trials, correct performance resulted in avoidance of the loss of money. Auditory stimuli were identical in both trial types. An event-related brain potential (ERP) N100 deflection, generated in the auditory cortex, was significantly larger in the negative as compared to the positive-emotional trials. This result demonstrates that emotional context influences early sensory-specific cortical processing. In addition, we found some evidence in favor of assumption that processing of positive visual feedback was faster in negative-emotional trials. This was reflected in the tendency for the latency of visual ERPs to be shorter in the latter case. We suggest that our results indicate that the systemic organization at all stages of deployment of behavior depends on emotional context. Dynamics of learning the discrimination task was also dependent on emotional context.
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1. Introduction

We recently suggested a unified concept of consciousness and emotion, emphasizing that behavior is active and goal-directed, rather than responding to external stimuli (Alexandrov 1999; Alexandrov and Sams, 2005). Formation of new memories (functional systems; Anokhin, 1973) during development results in increasing differentiation of organism–environment relations (*e.g.* Alexandrov, 1989; Edelman, 2003; Werner and Kaplan, 1956; Witkin et al., 1962). We argue that systems that are formed later in ontogenesis are more differentiated than systems formed earlier. Any behavioral act is a simultaneous realization of many less and more differentiated systems. We suggest that emotions are dynamic systemic characteristics that are prominent at the least differentiated systemic levels (Alexandrov and Sams, 2005).

The lowest, earliest, and most general level of differentiation of behavior is to approach "good things" and to avoid "bad things" (Dennett, 1993; Schneirla, 1959). We connect emotion to these most ancient and low-differentiated levels of the organization of behavior (for similar views, see Cacioppo and Gardner, 1999; Davidson et al., 1990; Panksepp, 2000; Schneirla, 1959; Zajonc, 1984). Different emotions are associated with different types of actions (Alexandrov and Sams, 2005; Davidson et al., 1990; Frijda and Swagerman, 1987; Schwarz, 1990). Approach is associated with positive-valence emotions and avoidance with negative-valence emotions. The experiments described in this paper demonstrate that neural processing of acoustic stimuli depends on emotional valences.

There is evidence that approach and avoidance behaviors are not organized symmetrically. It has been suggested that there is more diversity in negative than in positive emotion states (Wundt, 1897; Damasio, 1994). As Claeys and Timmers (1993, p. 118) put it: "...the universe of different negative behaviours is cut in smaller pieces than the universe of different positive

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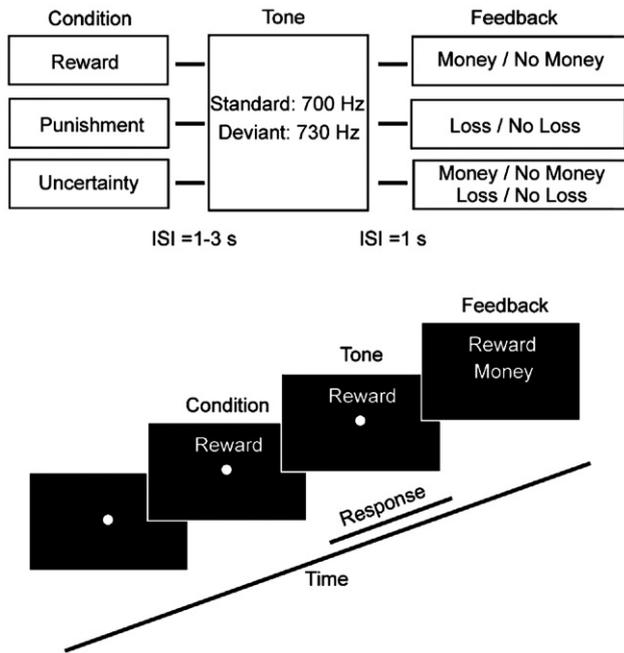*E-mail address:* yuraalexandrov@yandex.ru (Y.I. Alexandrov).

Fig. 1. Upper part of the figure shows the structure of the experiment. Picture indicates trials (trial types), acoustic stimuli and feedback stimuli used in the study. Lower part demonstrates an example of a positive-emotional trial.

behaviours". More systems belong to the avoidance rather than to the approach domain of memory (Alexandrov and Sams, 2005). Feeding behavior (approach) in young altricial tree-hole pied flycatcher nestlings may be elicited by a wide range of low-to medium-frequency sounds. However, the exact characteristic of the triggering sounds makes a difference for avoidance (defensive) behavior. A range of high-frequency sounds can elicit freezing, but in addition the sounds must be organized to rhythmical patterns (Alexandrov and Alexandrov, 1993; Khayutin et al., 1997). Therefore, avoidance requires a more detailed analysis of the physical properties of the environmental cues than approach.

In the present study, we tested whether identical auditory stimuli activate the human auditory cortex differently when they are involved in discrimination tasks of different emotional valences. Our theoretical approach suggests that neural mechanisms related to even processing of identical stimuli in the sensory-specific cortex are partly different depending on the emotional context of the behavior. Our subjects used outwardly identical behavioral acts in discriminating acoustic stimuli to get a reward or to avoid punishment. As argued above, the systemic organization of these two behaviors should be different. We further hypothesize that if more functional systems (neuronal populations) are involved in the negative-valence domain, then stronger auditory-cortex activity to physically identical stimuli is expected in avoidance than in approach trials.

ERPs were recorded during a modified oddball task. Subjects were instructed to detect an infrequent auditory stimulus in two different trial types. In the positive-valence trials, correct performance was awarded with money. In the negative-valence trials, correct performance meant that the subjects did not lose money. Trial types differed in behavioral

goals (win vs. avoid losing), and therefore in valence. We also included uncertainty trials where subjects were not informed of the type of the condition before the discrimination task. We expected that ERPs to identical acoustic stimuli differ in emotionally different behavioral contexts. We have analyzed both N100 and P300, but focused more on the auditory N100 deflection, known to reflect processing in the auditory cortical areas.

2. Materials and methods

2.1. Participants

Ten male right-handed volunteers, aged 21–25 years, participated in the study. None of them reported neurological impairments. The principles of Helsinki Declarations were followed. The data of one non-native speaker of Finnish was excluded from the analysis because cue and feedback words were in Finnish (see below).

2.2. Stimulus presentation and task

Two auditory stimuli (35 db HL) were presented via headphones. Visual stimuli were presented on a computer screen located 1.5 m in front of the subjects sitting comfortably in the armchair. Stimulus presentation was controlled with Presentation software (Version 0.43, Neurobehavioral Systems Inc.). A black fixation point ($0.1° \times 0.1°$) was constantly presented on the screen.

Each trial (Fig. 1) started by presentation of a cue word indicating one of the three trial types (punishment, reward or uncertainty — in Finnish palkinto, rangaistus or epävarmuus). The cue word ($12.9° \times 2.5°$) was present on the top of the screen during the entire trial. After the cue, an auditory stimulus (700 Hz or 730 Hz, duration 100 ms) was presented. The interval between the onsets of the visual cue and the auditory stimulus varied randomly from 1 to 3 s, in 50-ms steps.
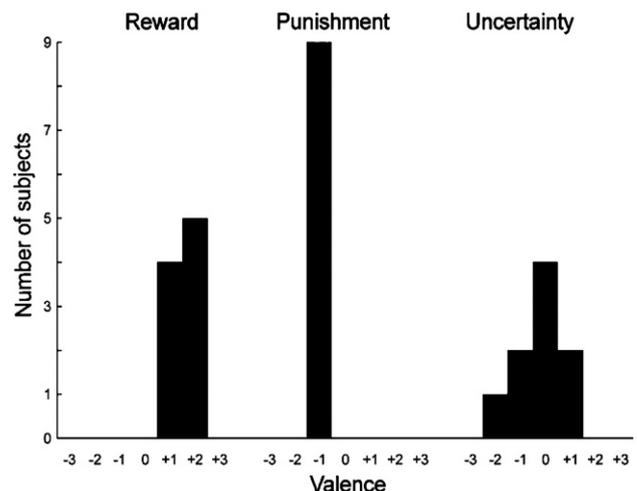

Fig. 2. Results of the subjective evaluation of the trial types used in the study. (Emotional valence was measured using Likert scale from very emotionally negative −3 to very emotionally positive +3.)

Auditory stimulus was followed by one of four visual feedback stimuli (money, no money, loss, no loss — in Finnish rahaa, ei rahaa, häviö, ei häviö) with a 1-s delay. The interval between the trial onsets varied randomly from 4.5 s to 9.5 s, in 50-ms steps.

Subjects were instructed to press a reaction key as quickly as possible in response to the infrequent high tone target stimuli ($p = 0.1$) and not to respond to the frequent standard stimuli ($p = 0.9$). Subjects learned the task during short training session (10–20 trials) before the experiment. Subjects received credits for correct responses and lost them for mistakes. In the end of the experiment, the credits were converted to money. On average, subjects earned 35 euros starting from a 20 euro initial account.

During the task subjects could win credits (reward trials), lose credits (punishment trials) or the trial was ambiguous (uncertainty trials). The order of the trial types was randomized and they were presented with equal probabilities. Correct detection of both target and standard stimuli in reward trials was rewarded by one credit and indicated by giving feedback "money". Mistakes triggered the feedback "no money". In punishment trials, subjects tried to avoid losing accumulated credits. Correct detection triggered feedback "no loss" indicating that subject's account didn't change. Mistakes resulted in feedback "loss" (subtraction of one credit from the account). In uncertainty trials, subjects were randomly exposed to punishment or to reward trials. Therefore, they did not know the nature of the trial before they received feedback. Correct detection in uncertainty trials randomly triggered "money" or "no loss" feedbacks whereas mistakes randomly triggered feedbacks "no money" or "loss". Trial types were randomized and presented with equal probabilities.

2.3. Evaluation of valence of the experimental trials

Immediately after the EEG recording, subjects evaluated their feeling associated with each experimental trial type using a seven-step Likert scale, spanning from −3 ("I find this trial type emotionally very negative") to +3 ("I find this trial type emotionally very positive"), whereas zero (0) indicated "neutral" feeling. In addition to valence, these ratings reflect also intensity of emotion (Anderson et al., 2003; Canli et al., 2000; Lang et al., 1993; Phan et al., 2003).
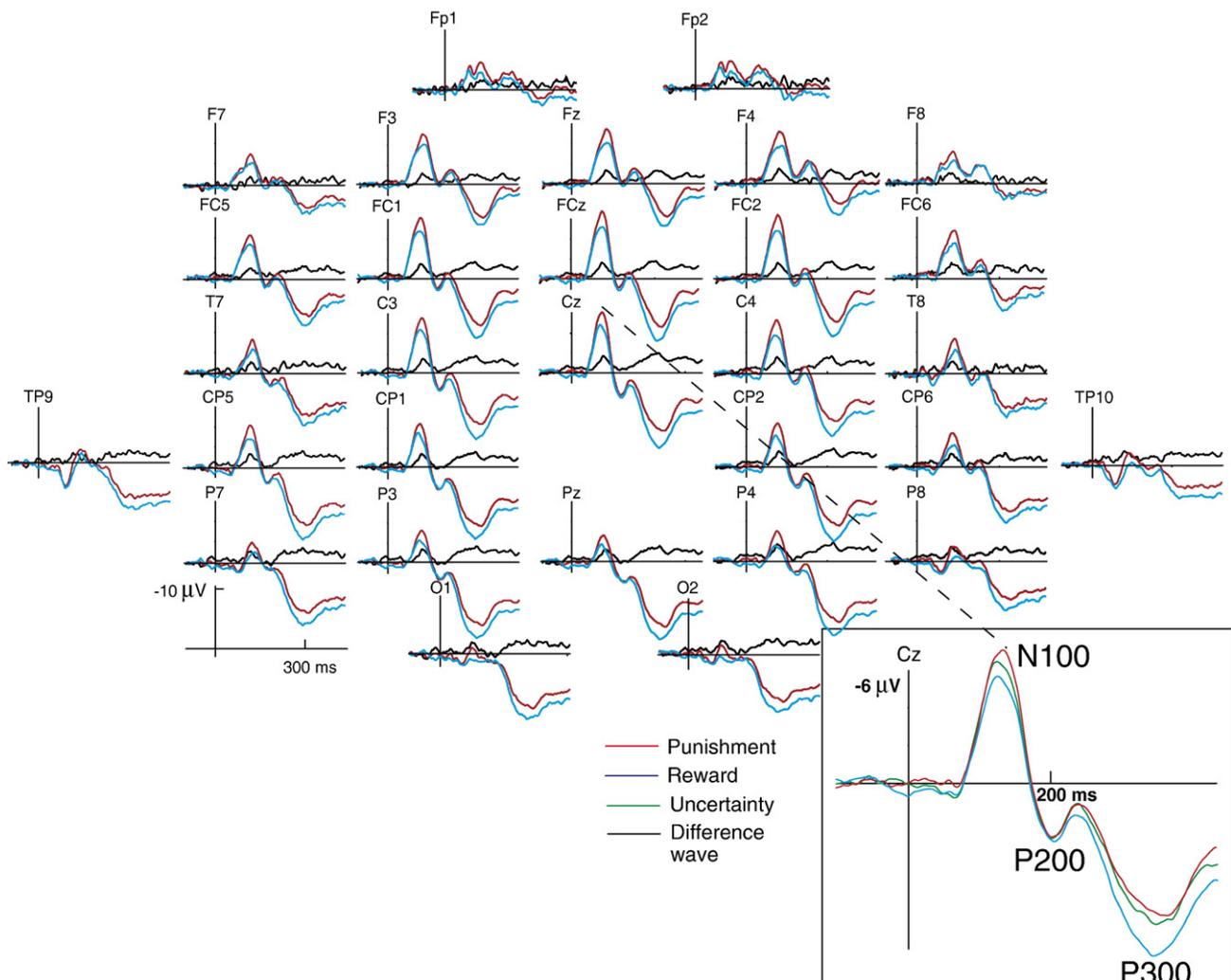

Fig. 3. Grand-average ERPs to the acoustic standard stimuli in the punishment and reward trials. The amplitude of N100 was larger in punishment as compared to reward trials whereas P300 was largest in reward trials. The inset also shows the ERPs in the uncertainty trials.
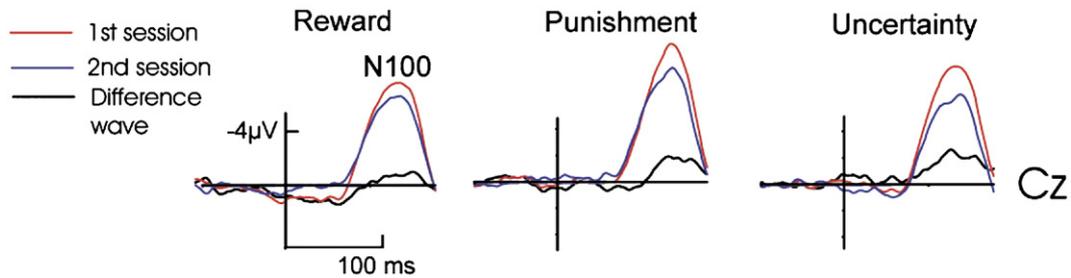
Fig. 4. Grand-average auditory N100 responses to the acoustic standard stimulus in the first and second sessions, measured from Cz. Note that the amplitude difference between the sessions is dissimilar in different trial types. Learning effects indicated by a decrease of N100 amplitude at the second session were larger in punishment than in reward trials.

2.4. EEG recording and analysis

EEG was recorded with 30 silver/silver chloride electrodes embedded in an electrode cap (BrainCap, Brainproducts GmbH) according to the extended version of 10–20 system: Fp1, Fp2, F3, F4, FCz, C3, C4, P3, P4, O1, O2, F7, F8, T7, T8, P7, P8, Fz, Cz, Pz, FC1, FC2, CP1, CP2, FC5, FC6, CP5, CP6, TP9, TP10. Reference electrode was at the tip of the nose. The impedance of the electrodes was below 5 kΩ. EEG was amplified with BrainAmp amplifier (Brainproducts GmbH). Analogue signal (0.016–250 Hz) was sampled at 1000 Hz. Vertical and horizontal eye movements (EOG) were monitored with electrodes placed above and below the left eye. If the amplitude of the EEG or EOG epoch exceeded ±60 μV, it was automatically rejected from further analysis. Mean number of rejected trials was 23 per trial type. EEG was segmented offline

to 600-ms blocks, starting 100 ms before the auditory stimulus onset. Segments were filtered at 1–25 Hz, baseline corrected and averaged.

ERPs were averaged separately to acoustic standard stimuli in reward, punishment and uncertainty trials. In addition, ERPs were averaged to the following visual feedback stimuli: "money" (reward trials), "no money" (reward trials), "no loss" (punishment trials), "loss" (punishment trials), "money" (uncertain trials), "no money" (uncertain trials), "no loss" (uncertain trials), and "loss" (uncertain trials). The mean number of trials averaged for different stimulus types was 134. The experiment consisted of two sessions, separated by a short break. To study how learning of the task influences the results, ERPs were also averaged separately for the first and second sessions. In these sessions, the mean number of averaged trials was 67. ERPs to deviant acoustic stimuli, and

Fig. 5. Grand-average ERPs to the visual feedback stimuli. Responses to "no loss" and "money" feedback stimuli were averaged across uncertainty and punishment trials. Inset shows responses to "no loss" and "money" feedback stimuli separately for uncertainty and punishment trials recorded at O2. The amplitude of N160 to both types of positive feedback ("money", "no loss") was smaller in uncertainty than in punishment and reward trials.

to "loss" and "no money" feedbacks were not calculated due to a small number of trials.

Amplitudes of auditory ERPs were quantified by calculating the mean values in area around the latency of interest (120–140 ms for N100 component and 320–350 ms for P300 component). Statistical analyses were carried out using a 2-way or 3-way ANOVA with *Electrode site* (30 locations), *Session* (part 1 and 2) and *Trial types* (punishment, reward, uncertainty) as within-subject factors (Statistica 6.0, StatSoft). Significance values were Geisser–Greenhouse corrected. ERPs in the two sessions were analyzed separately (within-subject factor *Session*). Differences were considered significant at $p \leq 0.05$. Specific predictions were checked by testing planned comparisons of least squares means corrected using Bonferroni's method.

Power in EEG alpha band indicates subjects' arousal (Cajochen et al., 2000; Coull, 1998) and sustained attention (Herrmann and Knight, 2001) level. We measured the EEG frequency distribution with FFT analysis in punishment, reward, and uncertain trials from a period starting with trial cue onset and ending with auditory stimuli presentation. The mean value of power in alpha band (7.5–12.5 Hz) was measured in the three trial types.

3. Results

3.1. Behavioral results

Subjective evaluation of the valence of the experimental trial types is presented in Fig. 2. Evaluations differed significantly in punishment and reward trials (Fisher exact test, $p < 0.0001$). All subjects evaluated punishment trials as emotionally negative (−1) and reward condition as positive (+1 or +2). As expected, uncertainty trials were evaluated more inconsistently.

The number of mistakes in punishment, reward, and uncertainty trials, $5.5 \pm 1.2\%$, $5.2 \pm 1.0\%$, and $5.8 \pm 1.1\%$ (mean±sem), did not differ significantly. Reaction times (RTs) to the acoustic stimuli did not differ in different trials ($F(1,8) = 0.2$, $p = 0.80$). However, mean RTs were significantly shorter in the second (448 ± 13.7 ms) than in the first (476 ± 10.7 ms) part of the experiment (main *Session* effect: $F(1,8) = 25.7$, $p < 0.001$). ANOVA showed a trend toward interaction effect *Session* × *Trial types* ($F(1,8) = 2.1$, $p = 0.15$, partial Eta squared 0.35). Planned comparisons revealed the strongest learning (*Session*) effect in punishment trials (42 ms shorter RT in the second session; $p < 0.05$) and a weaker non-significant effect in uncertainty (29 ms shorter RT in the second session) and in reward (14 ms shorter RT in the second session) trials.

3.2. Auditory ERPs

Auditory stimuli elicited a wave peaking in grand averages at around 130 ms, followed by a positive wave peaking at around 200 ms (P200) (Fig. 3). We identified negative wave as N100 component. N100 amplitude was clearly larger in the punishment than in the reward trials, and intermediate in the uncertainty trials. ANOVA revealed a significant main effect of *Trial types* ($F(2,16) = 6.0$, $p < 0.02$). Planned comparisons

showed that the amplitude difference between punishment and reward trials was significant ($t = 22.2$, $p < 0.01$). The small amplitude differences between punishment and uncertainty and between reward and uncertainty trials were not statistically significant.

N100 amplitude was smaller in the second session as compared to the first one (3-way ANOVA, factor *Session*: $F(1,8) = 9.6$, $p < 0.02$, see Fig. 4). The difference was statistically significant only in punishment and uncertainty trials (planned comparisons: $t = 8.2$, $p < 0.05$; $t = 5.5$, $p < 0.05$ correspondingly).

Overall, we demonstrated that identical auditory stimuli activate the human auditory cortex differently when they are involved in discrimination tasks of different emotional valences.

The amplitude of the positive parietal–occipital deflection (identified as P300 component) at 330 ms (Fig. 3) was significantly affected by emotional trials (main *Trial types* effect: $F(2,16) = 5.2$, $p < 0.05$). P300 was largest in reward trials, intermediate in uncertainty trials, and smallest in punishment trials (Fig. 3). Planned comparison revealed a trend of significant difference between reward and punishment trials ($t = 10.2$, $p = 0.1$).

Present behavioral results and ERP effects in uncertainty trials were intermediate to punishment and reward trials. Subjective reports showed high inter-subject variability (Fig. 2). Rusalov (1979) has shown that cognitive styles used in uncertainty situation vary in accordance with subject's personality. Moreover, brain activity patterns correlate well with individual differences in subjective evaluation of intensity and valence of emotions so that subjects giving different evaluation have also different structures of brain activity (Anderson et al., 2003; Canli et al., 2000; Knutson et al., 2001). We suggest that mean ERP results in uncertainty trials in our study indicates highly variable individual responses.

3.3. ERPs to visual feedback

ERPs to visual feedback stimuli consisted of early positive deflection peaking in grand averages at about 100 ms followed by negative (160 ms) and positive (230 ms) deflections (Fig. 5). ERPs to "money" and "no loss" feedback were analyzed using a 3-way ANOVA with factors *Electrode*, *Trial types* and *Feedback*. Amplitude of all ERP deflections to positive feedback stimuli (main factor *Feedback*: "money" *vs.* "no loss") did not differ from each other. However, latency of N160 wave to "no loss" feedback in punishment trials (152 ± 5 ms) was 10 ms shorter than that to "money" feedback in reward trials (162 ± 3 ms; 2-way ANOVA, *Feedback* × *Trial types*: $F(1,8) = 5.00$; $p = 0.056$). The amplitude of N160 to both types of positive feedback ("money", "no loss") was somewhat smaller in uncertainty than in punishment and reward trials ($F(1,8) = 4.8$; $p = 0.0598$).

3.4. EEG frequency analysis

In order to compare the level of arousal in all emotional trial types we performed the frequency analyses. The mean power of

alpha-band activity did not differ in the different *Trial types* (F $(2,16)=0.60$, $p=0.56$). Interaction between *Trial types* and *Electrode* was also not significant.

4. Discussion

Manipulation of valence of the experimental conditions worked as intended. Punishment condition was experienced as emotionally negative whereas reward condition as emotionally positive. Evaluation of uncertainty condition was a mixture of these two.

4.1. ERPs to auditory stimuli

As typically, N100 was of opposite polarity at temporal locations Tp9 and Tp10, indicating two contributing sources in the left and right supratemporal auditory cortex. The source of N100 was reliably localized in auditory cortex in the number of previous EEG and MEG studies using sources analysis (Giard et al., 1994; Huotilainen et al., 1998; Perrault, Picton, 1984; Sams et al., 1985; Woldorff et al., 1993). In our study the valence of condition had a significant influence on the amplitude of auditory N100. The amplitude was larger in punishment than in reward condition. Effect of emotional context revealed in present experiments is consistent with the idea that brain represents sensory-specific information in accordance with a current task goal (Wheeler et al., 2000). Our finding is in line with fMRI data showing that responses to acoustic conditioned stimuli in auditory cortex are modulated by the visual context that signaled the likelihood of receiving an aversive unconditioned stimulus (Armony and Dolan, 2001). Our results are also in agreement with single cell studies that have demonstrated modifications in evoked activity of the auditory cortical cells to the same tonal stimulus depending on the reinforcement type (Beaton and Miller, 1975). In the first condition, monkeys were rewarded for key releases to all tonal stimuli irrespective of their frequency, while in the second condition key releases to tones with certain frequencies were unrewarded. A quarter of all neurons showed different activity to the same signals depending on the condition. Recently, Brosch et al. (2005) also demonstrated that responses to identical auditory stimuli in the monkey auditory cortex are affected by the behavioral context.

The difference does not show a similar polarity reversal at mastoidea as does the N1 deflection (Fig. 3). To estimate the source location of the difference wave, we modeled it with current dipoles. The small size of the difference wave made modeling of its source quite difficult. We localized the difference waves of three subjects with the most prominent difference waves using BESA 5.1 (dipole model with two symmetrical sources). All effects were localized close to the auditory cortex (Brodmann areas 41/13): subject N1 (goodness of fit=87.5%) 40.9–15.1 30.7 (Talairach coordinates); subject N2 (goodness of fit=71.2%) 40.9–19.6 19.2; subject N3 (goodness of fit 80.3%) 32.1–19.5 17.9. Dipoles had quite variable hemispheric asymmetry. This cross-subject variability probably explains the complex pattern of the grand-averaged

waveforms. The results of source localization give the additional support to our hypothesis that the emotional context influences processing of emotionally neutral acoustic stimuli in the human auditory cortex in the areas close to the source of N1 component.

In most studies, emotion influence is studied with help of emotional stimuli. Lewis and Critchley (2003) suggest that Erk et al. (2003) were the only ones to use neutral (visual) stimuli (see also Erk et al., 2005) to study how emotional context modulates recognition and memory encoding. Stimuli of different valences are also physically different; such differences may partly explain different patterns of brain activity. In contrast to the aforementioned majority of studies in the present investigation, we studied the effect of emotional valence on the responses to neutral and physically identical auditory stimuli. This was also done by Surakka et al. (1998), who studied the effect of visually-induced emotions on processing of auditory stimuli. The amplitude of the mismatch negativity, a specific response to a change in acoustic stimulus sequence generated largely in the auditory cortex, was smaller during positive than during negative emotions. However, they found no emotion-related change in the amplitude of auditory N100. In the study of Surakka et al. (1998), the subjects did not attend to the acoustic stimuli as in the present experiment, which could explain the discrepancy between the present results. Pessoa et al. (2002) have shown that fMRI responses generated in different brain structures (*e.g.* the calcarine fissure, the middle occipital and fusiform gyri, and the right superior temporal sulcus) reflected the valence of the visual stimuli only when subjects attend to the pictures. Cuthbert et al. (1998) found that the amplitude of the auditory N100 deflection to identical acoustic stimuli was larger when the subjects viewed negative-valence than positive-valence pictures. However, this was found only when the auditory stimuli were so strong that they elicited a startle response, *i.e.* they were emotional.

Joseph LeDoux (1998, p. 1234) pointed out that the majority of the recent work in affective neuroscience has concentrated on automatic, evolutionary programmed stimulus processing, but have not examined «"willful" actions». Our subjects certainly performed such actions directed to achieving different goals depending on the varying emotional context: to avoid punishment (punishment trials) or to accumulate rewards (reward trials).

Our results indicate that brain mechanisms involved in processing of identical auditory stimuli are different quite early on in the processing stage depending on the emotional context. It is possible that auditory-cortex neurons coordinate their activity with different sets of activated neurons in approach and avoidance trials. Previous studies showed that different sets of neurons in the monkey cingulate cortex are active during the outwardly similar instrumental act when it is performed to avoid pain or to obtain a reward (Koyama et al., 2001; Nishijo et al., 1997). Paton et al. (2006) have shown that different neuron sets in primate amygdala are active during presentation of visual stimuli with positive and negative values.

Our N100 finding is in line with numerous data showing generally the greater impact of negative than positive events on

behavior (see for a review Baumeister et al., 2001; Peeters and Czapinski, 1990). We hypothesize that larger N100 in negative trials reflects higher differentiation of domain of memory, elements of which subserve withdrawal behaviors and therefore activation of more memory nodes. Increase in N100 amplitude might reflect involvement of a larger number of neurons in the auditory cortex. This proposition fits well the single unit recording data demonstrating that significantly more neurons were activated in rabbits' primary visual area in response to light flash when it signaled an avoidance behavior than in situation when the same flash signaled a feeding behavior (Shvyrkov, 1990; Shvyrkova and Shvyrkov, 1975). However, due to low spatial resolution of ERP method we can't completely exclude the possibility that different level of activity of neurons involved in both approach and avoidance behavior makes a contribution to variation of the ERPs amplitude. It is well known that level of attention may be larger in avoidance situation (see below) and that the firing rate of animals' auditory-cortex neurons increases with increase of attention (*e.g.* Benson & Heinz, 1978). Changes of firing rate occurred at latencies as early as 20 ms. Also attentional modulation of early sensory processing (larger magnetic brain responses in the latency ranges 20–50 ms and 80–130 ms) was shown in human auditory cortex (supratemporal plane) (*e.g.* Woldorff et al., 1993).

It could be argued that N100 modulation was due to a higher level of attention or arousal in punishment trials (Cuthbert et al., 1998; Pessoa et al., 2002; Smith et al., 2003). However, we did not find differences in number of mistakes, RTs and alpha-band power between the trial types that would indicate an attentional effect. Additionally, N100 modulation was opposite to that for P300 (see below for discussion) that argues against general attention or arousal effect. Therefore, we suggest that our results are genuinely related to emotional valence but not the above mentioned unspecific factors per se.

Negative information "receives more thorough processing" than positive information (Baumeister et al., 2001, p. 340). There are more words in ordinary language designating negative-emotional states than positive ones (Averill, 1980; Baumeister et al., 2001; Kanouse and Hanson, 1972). There is universal human tendency to use emotionally positive words more frequently than negative words due to the "Pollyanna principle: look on (and talk about) the bright side of the life" (Boucher and Osgood, 1969, p. 1). Nevertheless categories for positive emotions are less differentiated than those for negative ones (Averill, 1980).

The greater complexity of cognitions during negative states is well known. Negative affective states elicit more cognitive effort and require allocation of more processing resources. They require more time, more careful and detail-oriented strategies, and force individual to categorize information more narrowly, store it in "smaller chunks" or "pieces" and make "more discrete judgments" than positive affects (Charles et al., 2003; Clore et al., 1994; Ortony et al., 1983; Ohira et al., 1998; Peeters and Czapinski, 1990; Robinson-Riegler and Winton, 1996; Schwarz, 1990). More fine-grained distinctions can be made within emotionally negative behaviors than within positive

ones. This allows people to cut the universe of different negative behaviors in smaller units than the universe of positive emotions (Claeys and Timmers, 1993, p.113; Clore et al., 1994; Lewica, 1988; Raghunathan and Pham, 1999).

We suggest that such fine-gained differentiation is related to the necessity to be more careful in selection of behavioral act during negative states and even use specific cognitive styles (more "detail-oriented"). Processing of negative stimuli has greater informational value (Peeters and Czapinski, 1990) because it leads to the selection of responses with larger number of degrees of freedom, *i.e.* to a greater reduction of uncertainty.

Even when our N100 result seems to be specific to the valence of the experimental trial types but not to be due to different levels of attention and arousal, the specificity of emotionally negative states could be related to higher level of attention in other types of experiments. Higher differentiation and higher level of attention in negative state may be different descriptions of the systemic organization of behavior. Higher differentiation in negative-emotional states is certainly connected with more *accurate*, *attentive*, and *concentrated* performance in this state (Schwarz 1990, pp. 545, 548, 550; Claeys and Timmers, 1993, p. 119; Erk et al., 2005, p. 836; Peeters and Czapinski, 1990, p. 46). It may be that in negative-emotional states higher systemic differentiation, requiring the necessity to be more careful and thorough, spending more time and even using specific cognitive styles (more "detail-oriented"), is due to the necessity to select from a larger set of systems than that required by a positive-emotional state.

4.2. Difference in N100 and P300 effects

The amplitude of P300 component was significantly affected by emotional context. We observed a trend of significant difference between P300 amplitudes in punishment and reward trials. It can indicate that P300 amplitude was larger in the reward situation and, therefore, that the effect of emotional context on P300 was opposite to that on N100. This dissimilarity most probably reflects differences in the underlying neurophysiological and systemic processes. ERPs amplitude changes at 100 ms latency have been suggested to be related to "between-channel" selection while P300 is associated with "response set" (for details, see Näätänen, 1992; Näätänen and Michie 1979). It was shown that N100 and P300 effects may be independent and even opposite (Näätänen, 1992).

In systemic terms, this dichotomy corresponds to different stages of organization and deployment of behavioral acts. These stages are based on qualitatively different neural mechanisms (Aleksandrov and Maksimova, 1985; Alexandrov et al., 2000; Shvyrkov, 1990; Shvyrkov and Alexandrov, 1973).

Possible difference of N100 and P300 effects (the maximum in negative trials *vs.* the maximum in positive trials) could be explained from the mobilization–minimization hypothesis perspective (Taylor, 1991). S.E. Taylor proposed that in an emotional situation behavior consists of initial short-term mobilization stage and long-term minimization. This pattern appears to be greater for negative than for positive situations. Therefore, initially in a negative situation organisms mobilize

more recourses than in a positive one. The following minimization or "relaxation" stage is also more prominent in the negative state. As a result the "magnitude of response" during the initial short stage is larger in negative situations; whereas during the second stage it is larger in positive situations (see Fig. 1 in Taylor, 1991, p. 76).

Nevertheless, if late ERP components correspond to the beginning of a specific action (Shvyrkov, 1990, p. 72) we can assume that later effects could be relatively unstable and depended on experimental task. In contrast to our study, Ito et al. (1998) demonstrated that visual late positive potential similar to the P300 was larger to negative as compared to positive-emotional stimuli. Different modality and non-neutral stimuli used in that study can't fully explain the contradiction with our results. Indeed, in a pilot experiment (two subjects) we used unpleasant electrical shock as a feedback instead of the loss of money in the almost similar behavioral test. We observed the same effect of emotional condition on the N100 component as in the current experiment: larger amplitude in punishment trials. However, the P300 effect was similar to Ito et al. (1998) experiments: Amplitude of P300 was larger in punishment trials. Therefore the direction of P300 effect is quite unstable and could be changed by a modification of the feedback modality even despite recently demonstrated similarity of the monetary loss and the electrical shock feedbacks in the effectiveness in driving aversive conditioning (Delgado et al., 2006).

4.3. Learning effects

Previous studies demonstrated that relatively fast (within tens of minutes from the beginning of an experiment) reorganization of brain activity takes place even if effectiveness of subject's performance doesn't change (*e.g.*, van Mier et al., 1998; Raichle et al., 1994). Highly specific and rapid changes in the receptive fields of cells during learning were also shown in the primary auditory cortex (Weinberger, 2007). We found learning effects for both behavioral and electrophysiological results: RTs shortened and N100 amplitudes decreased from the first to the second half of the experiment. Learning usually results in a reduction of number of neurons involved in the behavior and corresponding decrease of brain activation (Van Mier et al., 1998; Raichle et al., 1994; Shima et al., 1996; Wirth et al., 2003).

Emotion- and mood-related memory effects are well known (*e.g.* Cahill and McGaugh, 1998). Results of some recent studies suggested a possibility of valence-specific effects on brain mechanisms of memory formation (Cahill and McGaugh, 1990; Erk et al., 2003, 2005; Seidenbecher et al., 1997). We found a trend of learning effects for RTs and parallel quite significant learning effects of N100: Learning effects indicated by a decrease of N100 amplitude and shortened RTs at the second session were larger in punishment than in reward trials. Previous studies have demonstrated a negative bias in learning. Learning is faster in punishment than in reward conditions even when intensity of emotions is equal (*e.g.* Baumeister et al., 2001). A number of studies have demonstrated more incidental

learning, stronger and more detailed memory, better recall and recognition memory for negative than for positive-emotional states (Baumeister et al., 2001; Charles et al., 2003; Finkenauer and Rime, 1998; Kensinger et al., 2002; Pratto and John, 1991; but see Erk et al., 2003; Taylor, 1991).

Carretié et al. (2003) have shown different dynamics in ERPs during perceptual learning in positive- and negative-emotional states when subjects classified pictures according to their valence. Amplitude of the ERP to positive pictures, peaking at 100 ms, decreased during the experiment, but that to negative pictures did not. The disagreement with our results could be explained by differences in experimental setup. Different trial goals and feedbacks in positive- and negative-emotional situations in our experiments contrast to the same trial goals and absence of feedback in Carretié et al. study. In addition, we used identical neutral auditory stimuli, whereas Carretié et al. (2003) used different emotional stimuli.

Interestingly, Carretié et al. (2003) also interpreted their data by a negative bias. Probably this is true for both experiments. In our experiments negative bias implies faster learning to make a simple perceptual decision in all three emotional trial types, *i.e.* selection between two identical neutral signals. In the Carretié study action was not so simple and included explicit report about valence of stimuli. Negative bias in such a situation may manifest itself as stronger maintenance of concentration (more stable N100) during recognition of just negative-emotional stimuli.

4.4. ERPs to visual feedback stimuli

Behavioral acts end with the evaluation of achieved result. Both approach and avoidance behavior can result in positive outcome. If brain systems involved in different types of emotional behavior differ, this difference should also be reflected on the "outcome" evaluation stage. Indeed, we found a tendency for the amplitude of the visual N160 deflection to the positive feedback stimulus in uncertainty *vs.* punishment and reward trials to be different. We found the latency of N160 to be shorter to positive feedback in punishment trials ("no loss") than to positive feedback in reward trials ("money"). These results suggest that processing of feedback depends on the emotional tone of trials and, more specifically, that partly different neural processes underlie processing of positive feedback in approach and avoidance behaviors.

It might be argued that shorter N160 peak latency was due to the difference in word length or familiarity of words used as feedback in punishment and reward trials (rahaa, ei häviö). However, we believe that this is not the case. Recently Hauk and Pulvermüller (2004) concluded that the effect of letter-string length is sparse and inconsistent. Furthermore, Osterhout et al. (1997) have published the only study (to our knowledge) that has shown that the peak latency of an ERP deflection depends on word length. Shorter latency for longer words was found in the time window earlier than our effect (80–125 ms) and the longer latency for longer words was later than our effect (250–450 ms). Wydell et al. (2003), found no latency difference of MEG responses, peaking around 140 ms, to long and short

words. Consistent effects of word frequency have been found in ERPs later than 250 ms (Hauk and Pulvermüller, 2004).

5. Conclusion

Our data show that early activity in the auditory cortex, triggered by identical acoustic stimuli, is stronger in punishment than in reward trials. We suggest that the result reflects higher differentiation of neuronal mechanisms subserving withdrawal behaviors and, in relation to that, activation of more neurons specialized in relation to the systems belonging to these behaviors. We also found some evidence in favor of assumption that processing of positive visual feedback stimulus in approach and avoidance trials were different. Thus, the systemic organization of neuron networks underlying behavior at different stages of its performance (from the early beginning till the evaluation of end result of the act) depends on emotional context. Furthermore, dynamics of learning the discrimination task was also dependent on emotional context.

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