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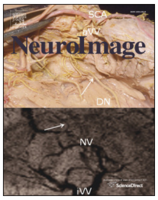

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Effects of social context on feedback-related activity in the human ventral striatum

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ABSTRACT

It is now well established that activation of the ventral striatum (VS) encodes feedback related information, in particular, aspects of feedback validity, reward magnitude, and reward probability. More recent findings also point toward a role of VS in encoding social context of feedback processing. Here, we investigated the effect of social observation on neural correlates of feedback processing. To this end, subjects performed a time estimation task and received positive, negative, or uninformative feedback. In one half of the experiment subjects thought that an experimenter closely monitored their face via a camera. We successfully replicated an elevated VS response to positive relative to negative feedback. Further, our data demonstrate that this reward-related activation of the VS is increased during observation by others. Using uninformative feedback as reference condition, we show that specifically VS activation during positive feedback was modulated by observation manipulation. Our findings support accounts which posit a role of VS in integrating social context into the processing of feedback and, in doing so, signaling its social relevance.

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Introduction

In human and non-human primates, learning from feedback usually takes place in complex social environments. Recent research has aimed at elucidating the influence of social cognition on neural mechanism of reward and feedback processing (Delgado, 2007). Evolutionarily-developed neural circuits in human and nonhuman primates have been proposed to specifically process social information on a perceptual level, generate social as well as nonsocial motivational signals and guide behaviors that utilize these signals to enhance successful adaptation to reproductive and survival demands (Chang et al., 2013). For example, striatal circuits appear to play a key role in integrating social context during feedback processing. In primates, neurons that encode information about conspecifics during a reward task were found in the striatum (Klein and Platt, 2013). Likewise in humans, striatal activity is increased during the delivery of social reward (Izuma et al., 2008; Lin et al., 2012) as well as during downward social comparison of monetary outcome (Bault et al., 2011; Dvash et al., 2010; Fliessbach et al., 2007) and is modulated by perceived collaborative behavior of co-players (Delgado et al., 2005; Le Bouc and Pessiglione, 2013). Other key reward areas like ventromedial prefrontal (VMPFC; Bault et al., 2011; Harris et al., 2007) and orbitofrontal cortex (OFC; Kringelbach and Rolls, 2003) are sensitive to social information embedded in reward and feedback tasks (Amft et al., 2014). Thus, social cues appear to have distinct characteristics that seem to supplement conventional incentives and modulate neural activation to rewarding feedback accordingly. While influences of social information on feedback related activity of the human brain were investigated in several previous studies, it remains unclear if the presence of an observer who is not explicitly engaging in social interaction may modulate processing of positive and negative performance feedback. Assuming prioritized processing of social context, which has been critical for evolutionary fitness (Chang et al., 2013), neural feedback processing should be altered by social cues. For example, in behavioral experiments the presence of observers or just the mere presentation of images of others is frequently associated with enhanced performance and increased frequency of overt behaviors across many species (Zajonc, 1965). Generally, social situations seem to induce the perception of being monitored and might therefore trigger heightened arousal and elevated preparedness to focus on the specific behavioral significance of feedback. Although the neural representations of complex social interaction phenomena have been studied in considerable depth (Rilling and Sanfey, 2011), we still know little about the more general role of social context in modulating the neural response to behaviorally relevant feedback.

Therefore, the present study investigated potential modulations of neuronal activity during processing of performance feedback by perceived presence or absence of observers by means of functional magnetic resonance imaging (fMRI). To this end, participants were informed

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that they were observed by a camera while performing a time estimation task with trial-by-trial modulations of performance feedback. We expected valence-modulated differences in feedback related activity in ventral striatum (VS), and VMPFC/medial OFC. These differences in neural activity should be more pronounced under social observation. Thus, we hypothesized that the perception of being observed by others interacts with processing of valence feedback, possibly by contributing additional significance to the feedback.

Materials and methods

Participants

A total of 20 right-handed healthy subjects participated in the experiment. All underwent an in-house medical screening. Two subjects did not comply with the task instructions resulting in high numbers of missed trials. After a short debriefing only one subject reported distrust in the cover story of observation manipulation and was excluded from further analyses. Finally, data from seventeen subjects (8 female; mean age, 37.35 years ± 12.88 years) were analyzed. No participant had a history of neurological or psychiatric disease and all subjects provided written informed consent for the study prior to the experiment proper. Handedness was assessed using the Edinburgh Inventory (Oldfield, 1971). The study was approved by the Ethics Committee of the University of Jena.

Experimental paradigm

The present study applied a modified version of the time estimation task (Miltner et al., 1997; van Veen et al., 2004). Previous fMRI-studies have reliably shown, that this task differentially recruits brain regions known to be involved in reward and feedback processing (Becker et al., 2013, in press; Mies et al., 2011; Nieuwenhuis et al., 2005; Van Veen et al., 2004). The time estimation task required participants to estimate an interval of 1 s duration as accurately as possible (Fig. 1). On each trial, an auditory cue of 50 ms duration marked the onset. Participants were instructed to press a button with their right index finger as soon as they thought an interval of 1 s had elapsed. Subsequently, subjects received positive, negative, or uninformative feedback about the accuracy of their response. Crucially, feedback was based on a performance-adaptive algorithm to balance the frequencies of the three feedback conditions across the course of the experiment. To this end, a time window centered around 1 s after cue presentation – the target time point – was defined. The training run was used to establish an individual baseline of this time window's length for every subject. In the experiment proper this baseline was used as the starting value and adjusted trial-wise according to the following criteria: in the case of an insufficiently accurate response the window is widened by 20 ms, and in the case of an accurate response the window is shortened by 20 ms. Feedback was given in the form of letters (‘A’, ‘B’ and ‘C’), which were projected onto a screen inside the scanner bore. During the remaining time, subjects were requested to fixate a cross. Letter-feedback category assignment was pseudorandomized to control for specific effects of visually presented feedback stimuli. In order to decorrelate response- and stimulus-related activation patterns, time between button press and feedback presentation (offset within a range of 3800-7000 ms) as well as the intertrial interval (offset within a range of 2600-7100 ms) was jittered (Fig. 1). Uninformative feedback was implemented to create an appropriate control condition that visually stimulated participants but provided no information about the subjects' performance (see also Nieuwenhuis et al., 2005).

Participants performed the task under two different conditions. In one condition, participants were informed that they would be video-monitored online by the experimenter by means of a camera mounted inside the scanner bore. It was emphasized that the observer would specially focus on visible physiological reactions of the participant's face (e.g. skin perfusion and pupil dilation). Subjects were told that we were piloting a task so as to optimize certain technical parameters for camera recordings which would require runs with and without a camera. During the other condition the scanner bore did not contain a camera and subjects were informed accordingly. The order of both conditions was counterbalanced across subjects. In each condition 66 trials of time estimation were completed in separate runs. Outside the scanner subjects' accurate recollection of letter assignment to feedback type was checked and subjects were debriefed.

fMRI data acquisition and analysis

Scanning was performed in a 3-Tesla magnetic resonance scanner (Magnetom Trio, Tim System 3 T; Siemens Medical Systems). After acquisition of a T1-weighted anatomical scan, two runs of T2*-weighted echo planar images consisting of 370 volumes were recorded (TE, 30 ms; TR = 2100 ms, flip angle, 90°; matrix, 64 × 64; field of view, 192 mm^2). Each volume comprised 35 axial slices (slice thickness 3 mm; interslice

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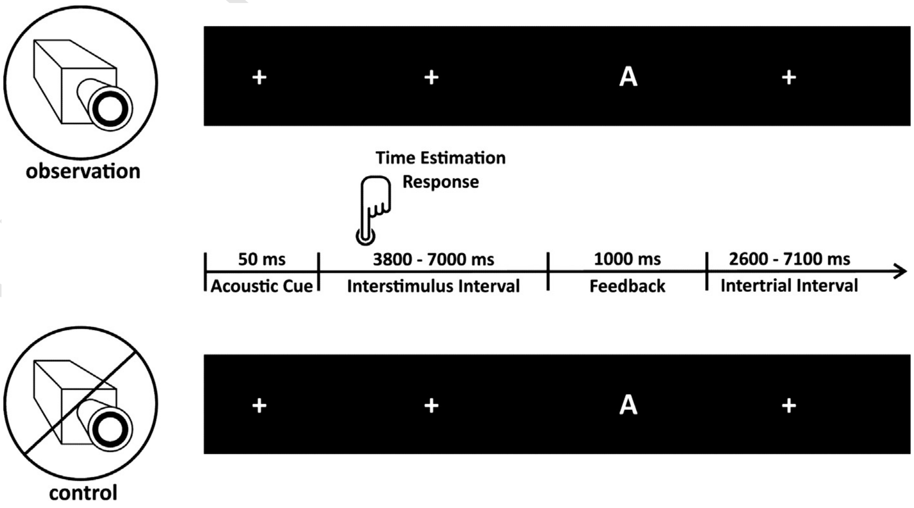

Fig. 1. Schematic illustration of a trial in the observation condition and a trial in the control condition: Each condition was symbolized by cue which indicated if the camera was turned on or off. After presentation of an auditory cue, subjects pressed a button when they felt that 1 s had elapsed. Positive (correct estimation), negative (incorrect estimation) and ambiguous (no information about estimation accuracy) feedback were presented visually after a jittered interval; the characters A, B and C served as feedback stimuli and were shown for 1 s in white against a black background. Prior to scanning, participants learned one of the six possible letter-feedback assignments. Feedback depended on an adaptive response criterion adjusted after each trial. Each condition comprised 66 trails, respectively.

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