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

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A B S T R A C T

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; 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 mm²). Each volume comprised 35 axial slices (slice thickness 3 mm; interslice
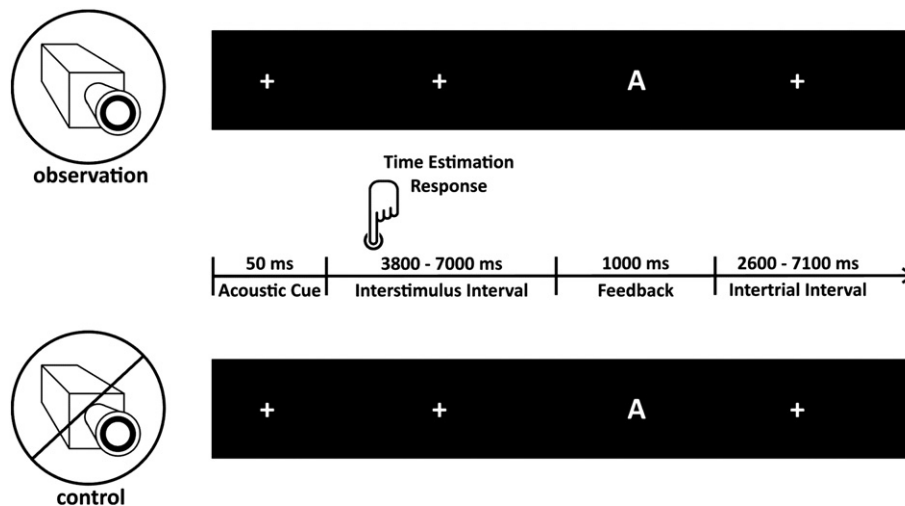

Fig. 1. Schematic illustration of a trial in the observation condition and a trial in the control condition: Each condition was symbolized by cue which indicated if the camera was turned on or off. After presentation of an auditory cue, subjects pressed a button when they felt that 1 s had elapsed. Positive (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.

gap 0.5 mm; in-plane resolution 3 × 3 mm) which were acquired with a 30° caudally tilted orientation relative to the anterior–posterior commissure line in order to reduce susceptibility artifacts (Deichmann et al., 2003). Prior to that, a shimming procedure was performed. To ensure steady-state tissue magnetization the first four volumes were discarded from analysis.

Functional MRI-data preprocessing and analysis were performed using Brain Voyager QX software (Version 2.4; Brain Innovation). First, all volumes were realigned to the first volume to minimize artifacts of head movements. Further data pre-processing comprised correction for slice time errors and temporal (high-pass filter: 10 cycles per run; low-pass filter: 2.8 s; linear trend removal) as well as spatial (8 mm full-width half-maximum isotropic Gaussian kernel) smoothing. The anatomical and functional images were coregistered and transformed to normalized Talairach-space (Talairach and Tournoux, 1988).

Statistical analyses were performed by multiple linear regression of the signal time course at each voxel. Expected blood oxygenation level dependent (BOLD) signal change for each predictor was modeled by a 2-gamma hemodynamic response function. On the first level, predictor estimates based on z-standardized time course data were generated for each subject using a random-effects model with adjustment for autocorrelation following a global AR(2) model. On the second level, predictor estimates were analyzed across subjects for the relevant contrasts. An a priori-defined whole-brain mask was used to mask out nonbrain tissue. A cluster-size threshold estimation procedure was used (Goebel et al., 2006) to correct for multiple comparisons. Significant clusters of contiguously activated voxels were determined by a Monte Carlo simulation based on 2000 iterations. After setting the voxel-level threshold to $p < .005$ (uncorrected) and specifying the FWHM of the spatial filter, the simulation resulted in a minimum cluster size of contiguously activated voxels corresponding to a false positive rate of 5% (corrected). The watershed-algorithm of Neuroelf (v0.9c; http://neuroelf.net/; i.e., the splitclustercoords function) was used to assess local maxima of clusters.

Results

Behavioral data

On average, participants received 32.5% positive, 33.4% negative and 33.2% uninformative feedback in the time estimation task. On average, in 0.9% of the trials the response deadline (2 s) was exceeded and consequentially no visual feedback was shown. As intended by algorithm implementation, presentation frequency did not differ between feedback types as the main effect of feedback ($F_{2,32} = 0.09$, $p = .775$) and condition ($F_{1,16} = 0.37$, $p = .553$) as well as the condition × feedback type interaction ($F_{2,32} = 2.30$, $p = .148$) did not reach statistical significance. We used the range of the response window as an index of accumulated performance (and response variability) levels and found no differences between observation and control conditions ($M_{CamOn} = 315$ ms (± 42 SEM); M_{NoCam} 305 ms (± 42 SEM); $t_{16} = .199, p = .845$). The temporal unfolding of the response window ranges reflects the adaptive nature of the algorithm as they show a tendency for subjects to become better with practice (i.e. $M_{Range\ starting\ value} =$
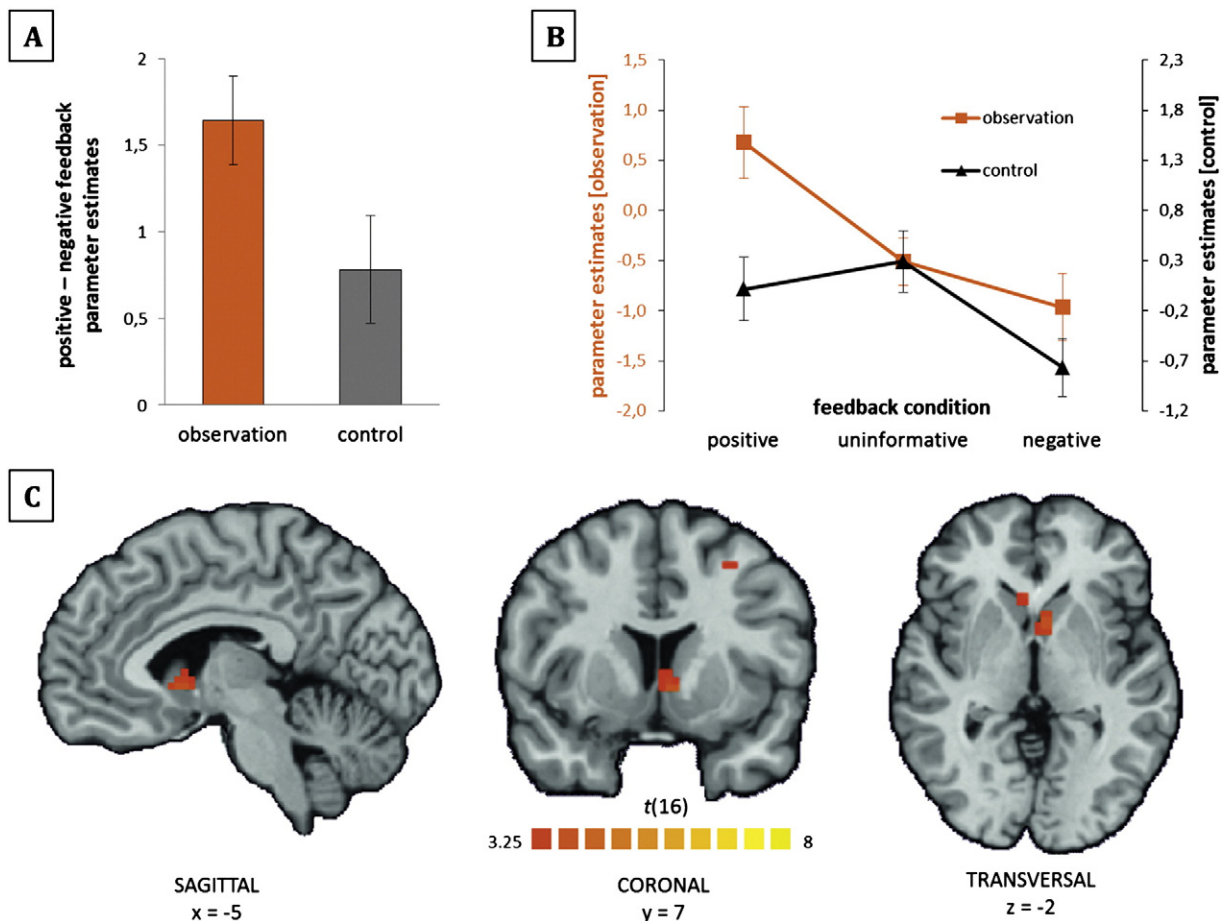

Fig. 2. Modulation of feedback-related neural activity by social context in the left ventral striatum. (A) Feedback effects (positive–negative) in the two experimental conditions (observation and control) at x = −8, y = 6, and z = −4; (B) parameter estimates (mean and SE) for different feedback types in the experimental conditions (observation and control) [parameter estimates were graphically adjusted by equalizing the point of uninformative feedback on the different scales of the two runs / observation conditions] (x = −8, y = 6, z = −4); (C) statistical parametric maps of the contrast positive > negative feedback differential for observation and control condition overlaid on a normalized brain (radiological convention).

335 ms; $M_{Range\ split-half} = 289$ ms) until performance reaches a natural difficulty threshold where improvement is unlikely; therefore, in the second half of the experiment, the error rates increase and the window becomes wider again ($M_{Range\ final\ value} = 310$ ms). Yet, these effects are not statistically significant ($F_{2,32} = .896$; $p = .418$). Further, we calculated the absolute deviation from the target time point of 1 s for every feedback trial and analyzed whether accuracy in estimation differed on average in trials after positive, negative and ambiguous feedback. As reported before (Van der Veen et al., 2011) it was positive feedback that was associated with higher accuracy on the succeeding trial than ambiguous and negative feedback ($F_{2,32} = 16.52$, $p < 0.05$; positive: M = 166.5 ms (± 72.9 SEM); negative: M = 217.3 ms (± 99.7); ambiguous: M = 187.3 ms (± 88.9)). The main effect of observation as well as the interaction of feedback type by observation did not reach significance (all F's < 2.5).

FMRI data

Analysis revealed an effect of feedback valence in the informative trials (positive relative to negative feedback) within the right VS (peaks x, y, z: 12, 14, −5; $t_{16} = 6.07$, $p < .05$, corrected, size 2700 mm³) and left VS (peaks x, y, z: −12, 8, −2; $t_{16} = 6.42$, $p < .05$, corrected, size 5940 mm³) as well as within the VMPFC pronounced in four separate clusters stretching into the anterior cingulate cortex (cluster 1: peaks x, y, z: 12, 47, −11; $t_{16} = 5.54$, $p < .05$, corrected, size 1431 mm³; cluster 2: peaks x, y, z: 9, 29, 13; $t_{16} = 3.83$, $p < .05$, corrected, size 486 mm³; cluster 3: peaks x, y, z: 0, 44, 7; $t_{16} = 3.22$, $p < .05$, corrected, size 459 mm³; cluster 4: peaks x, y, z: −9, 35, 10; $t_{16} = 3.57$, $p < .05$, corrected, size 324 mm³), indicating increased activity for positive relative to negative feedback across observation conditions (observation and control condition). Besides in VS and consistent with former studies employing the time estimation task (Becker et al., 2014; Mies et al., 2011; Nieuwenhuis et al., 2005; Van Veen et al., 2004), higher activation for positive compared to negative feedback was found in anterior insular and medial frontal cortices (Table 1). The contrast negative > positive feedback did not reveal significant clusters after correction, indicating that there is no brain region that reliably showed increased activity to negative relative to positive feedback. Differences in valence processing induced by observation manipulation were tested by means of an interaction contrast. Regions

within the right VS (peaks x, y, z: 9, 23, 1; $t_{16} = 4.19$, $p < .05$, corrected, size 594 mm³) and left VS (peaks x, y, z: −3, 8, −2; $t_{16} = 4.61$, $p < .05$, corrected, size 2214 mm³) responded stronger to positive relative to negative feedback under observation than in the control condition. To find out whether this significant interaction is driven by modulation of positive or negative feedback, the interaction of observation manipulation and positive versus uninformative feedback as well as negative versus uninformative feedback was tested. Only the interaction contrast of observation manipulation and positive versus uninformative feedback revealed significant voxels in the right VS (peaks x, y, z: 6, 17, 2; $t_{16} = 5.06$, $p < .05$, corrected, size 891 mm³) and left VS (peaks x, y, z: −12, 14, −6; $t_{16} = 4.22$, $p < .05$, corrected, size 621 mm³; Fig. 2). Thus, if one assumes a neutral baseline during uninformative trials, observation manipulation modulated the neural activity during positive feedback. Further, the interaction contrast revealed significant clusters in the middle frontal gyrus and cerebellum. Significant differences between positive and negative feedback were higher in the control condition relative to observation only within an anterior insula cluster (Table 1).

Discussion

The present study investigated the modulation of neuronal activity during processing of performance feedback by alleged presence or absence of an observer. This was established by a performance situation which ensured that social context information did not interact with the physical properties or the presentation frequencies of feedback stimuli or the performance level of subjects. While the conventional feedback effect in VS and VMPFC (Mies et al., 2011; Nieuwenhuis et al., 2005; Van Veen et al., 2004) was replicated, a differential impact of social observation was found only for the VS. Importantly, increased BOLD activity of the VS during positive as compared to negative feedback processing was found to be more pronounced when subjects were observed by another person during the task. The neural effects we observed for the observation condition were not explicable as differences in estimation thresholds as an index of the accumulated performance level; hence, subjects were not confronted with grossly different response scenarios between conditions, which might have confounded feedback information and value during observation and control. These findings suggest that even a task irrelevant social cue is sufficient to modulate VS activity during feedback processing. Using uninformative feedback as reference condition, we show that specifically neural activity during positive feedback was modulated by observation manipulation.

Association of striatal activity and reward receipt has been shown in various contexts. This included various stimulus domains (e.g. primary and secondary reinforcer) as well as different task settings (e.g. gambling and learning tasks) (Delgado et al., 2008; Diekhof et al., 2012). Studies have shown shared representation of reward value in VS across domains (money, social reward, cognitive feedback) (Daniel and Pollmann, 2010; Lin et al., 2012) and findings of more recent studies strongly imply distinct rewarding characteristics of social cues and a supplementary contribution to processing of conventional incentives (Fliessbach et al., 2007; Izuma et al., 2010). In a broader sense, the striatum seems to be involved in social cognition phenomena like joint attention (Gordon et al., 2013; Schilbach et al., 2010), altruistic behavior (Fehr and Camerer, 2007; Izuma et al., 2010) and social motivation (Le Bouc and Pessiglione, 2013).

Recent fMRI studies have illustrated the effects of context information about the performance of other participants on brain activation to reward (Bault et al., 2011; Dvash et al., 2010; Fliessbach et al., 2007). Fliessbach et al. (2007) found that VS activation to reward is elevated if the reward magnitude obtained by oneself exceeds that of a competitor, implicating that VS activation is modulated by social context information. Subsequent studies have also confirmed these observations for situations where subjects lost less money than another participant accompanied by increased striatal response compared to loss only

Table 1

Whole-brain results. Significant clusters for the contrast positive > negative feedback (whole brain level, cluster-threshold ≥ 243 mm³) and the interaction contrasts (whole brain level, cluster-threshold ≥ 297 mm³).

Area	LA	BA	mm³	x	y	z	t score
Positive > negative feedback							
Ventral striatum	R	–	2700	12	14	−5	6.07
Ventral striatum	L	–	5940	−12	8	−2	6.42
Insula	R	47	891	33	11	−14	4.60
Insula	L	13	1161	−32	5	−14	4.21
Medial frontal gyrus	R	11	1431	12	47	−11	5.54
		11	459	0	44	7	3.22
Anterior cingulate cortex	R	24	486	9	29	13	3.83
	L	24	324	−9	35	10	3.57
Superior frontal gyrus	R	9	567	21	44	33	4.55
	L	8	405	−12	35	37	4.00
Midbrain	L	–	1026	−9	−28	−17	5.00
Observation [positive > negative feedback] > control [positive > negative feedback]							
Ventral striatum	R	–	594	9	23	1	4.19
Ventral striatum	L	–	2214	−3	8	−2	4.61
Middle frontal gyrus	L	6	486	−24	14	52	3.89
Cerebellum	R	–	405	39	−80	−19	3.92
Observation [positive > negative feedback] < control [positive > negative feedback]							
Insula	R	13	297	34	12	−13	3.73

Area label, lateralization (LA), Brodmann area (BA) where applicable, cluster size in mm³, Talairach coordinates (x, y, z) and t-statistic of the contrast at the voxel of maximal activity within significant clusters are shown.

events (Dvash et al., 2010) and are demonstrating that these effects are explicitly influenced by the social context and not by the comparison per se (Bault et al., 2011). The influence of mere observation, however, has not been directly investigated, despite its relevance for modifying behavior and experience (Zajonc, 1965). Fareri et al. (2012) have investigated the influence of sharing a reward with other persons of varying closeness during a card guessing task and found increased striatal activation to rewards shared with a close person. Yet, they did not include a condition of non-shared rewards. A study by Izuma et al. (2010), however, includes a similar condition and corroborates the assumption that the VS codes social reward. Building on these results, our data demonstrate that mere presence of an observer was sufficient to increase VS activation to positive relative to negative feedback compared to the non-social condition. A parsimonious interpretation of this finding (1) corroborates that the presence of others enhances activation in a brain region reliably associated with reward processing in the human brain, and (2) implies that this reward enhancement is in effect even when social information is not in itself task-relevant. The latter aspect is strongly implied by theory (Paulus, 1983) but has not been demonstrated for activation signatures coding reward-related information. Situations during which we are observed are ample in real life and the mechanisms which direct and influence allocation of performance-relevant resources are likely to be guided by these reward-related signatures. In particular, our finding might mirror an increase in attentional relevance and rewarding potential of positive feedback during observation by others as has been implied but not directly shown by prior work (Fareri et al., 2012). Being observed by others in mastering a task successfully seems more positive and rewarding than being successful while acting alone. Our results extend this finding by demonstrating that this effect is specific to positive feedback, because the observation manipulation did not affect striatal activity to negative feedback: inclusion of an uninformative condition as gain-loss-neutral baseline allowed for dissociation of both processes, respectively. Further, the results consolidate the hypotheses that (1) specifically the striatum is highly sensitive to information about social context and (2) social information is integrated in the feedback signal. This finding is in line with assumptions about the increasing relevance of social information in phylogenesis and, in particular, with a postulated repurposing of domain-specialized neural circuits for social functions (Chang et al., 2013).

As exemplified by several studies (Baliki et al., 2013; Delgado et al., 2008; Pohlack et al., 2012; Seymour et al., 2007), the VS has repeatedly been assumed to carry a saliency signal, which is pronounced during aversive conditioning and may reflect activation of the posterior parts of the striatum (Seymour et al., 2007). Recent research has suggested that the nucleus accumbens core may contribute to both appetitive and aversive responses (Baliki et al., 2013). Our own findings are compatible with the general conceptualization of VS activation as a saliency signature, if one assumes positive feedback to be more informative and relevant than negative feedback in the time-estimation task: it has been argued that negative feedback in this particular protocol is less relevant for behavioral adjustments because it implies two directions (longer or shorter) in which to adjust, while positive feedback merely implies to reproduce a motor program (Van der Veen et al., 2011).

Another line of research has reported evidence for a policy-based action value update signal in VS rather than dorsal striatum (FitzGerald et al., 2014; Klein-Flügge et al., 2011; Li and Daw, 2011). Using sophisticated designs, these studies show that VS might carry a signal reflecting performance and behavioral relevance of a chosen response strategy and not unexpectedness of reward occurrence per se. As in the time-estimation task feedback signals appropriateness and accuracy of response timing and not the mere value of an action or stimulus, data from this task might prove fruitful for understanding this nuance of VS function. It is well established that in this kind of task feedback is needed in order to clarify an otherwise underdetermined response outcome; hence, internal representations of policy selections are most likely to be updated during feedback presentation. As one has hardly any reason to assume an inherent rewarding potential of the feedback letter stimuli per se, our results are compatible with the general assumption of policy signaling in VS.

Conclusions

In conclusion, our results demonstrate that a social observation context leads to significant differences in activation in VS to performance feedback. In particular, we have found an elevated response to positive feedback in the VS during observation by another person that explicitly did not monitor participants' performance. This suggests a general contribution of social context to processing of rewarding feedback signals beyond the specific context of social comparisons or social interactions. Accordingly, the VS activation was modulated by social information, implicating a high sensitivity of evolutionary-specialized neural systems to social context (Chang et al., 2013).

Conflicts of interest

The authors declare no competing financial interests.

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