Better you lose than I do: neural networks involved in winning and losing in a real time strictly competitive game

Mikhail Votinov1,4, Juergen Pripfl1, Christian Windischberger2, Uta Sailer1,3,4 & Claus Lamm1,*

Many situations in daily life require competing with others for the same goal. In this case, the joy of winning is tied to the fact that the rival suffers. In this fMRI study participants played a competitive game against another player, in which every trial had opposite consequences for the two players (i.e., if one player won, the other lost, or vice versa). Our main aim was to disentangle brain activation for two different types of winning. Participants could either win a trial in a way that it increased their payoff; or they could win a trial in a way that it incurred a monetary loss to their opponent. Two distinct brain networks were engaged in these two types of winning. Wins with a monetary gain activated the ventromedial prefrontal cortex, an area associated with the processing of rewards. In contrast, avoidance of loss/other-related monetary loss evoked activation in areas related to mentalizing, such as the temporo-parietal junction and precuneus. However, both types of winnings shared activation in the striatum. Our findings extend recent evidence from neuroeconomics by suggesting that we consider our conspecifics’ payoff even when we directly compete with them.

Competition between and among different living forms is one of the most important forces in evolution, and human beings are no exception. We compete for food, territory, mates, and also in all possible areas of our social life, like sports, politics, education and business. The more a certain resource is limited, the more competition arises between individuals. In the field of game theory, a mathematical model describes one type of competitive situation, called “zero-sum” game or strictly competitive game, in which one participant's gains are the result of equivalent losses for the adversary1. In this type of game, the net change in total wealth allocated to all participants is zero, because in each round the available wealth is allocated to one participant at the expense of the other. Good examples of this type of competition are gambling and sport contests. These types of competitions usually involve winners and losers and a relationship where the win of one competitor signifies a loss to the other. This setup implies that participants directly benefit from the other's misfortune.

Several neuroimaging studies have shown that activation in “mentalizing” brain networks including medial prefrontal cortex (MPFC), temporoparietal junction (TPJ) and temporal pole (TP) are involved in competition2-5. In particular, distinct regions were found to be selectively associated with cooperation and competition, notably the orbitofrontal cortex in the former and the inferior parietal and medial prefrontal cortices (MPFC) in the latter2. In addition, activation in bilateral TPJ was associated with

1Social, Cognitive and Affective Neuroscience Unit, Department of Basic Psychological Research and Research Methods, Faculty of Psychology, University of Vienna, Liebiggasse 5, A-1010 Vienna, Austria. 2MR Center of Excellence, Center for Medical Physics and Biomedical Engineering, Medical University of Vienna, Lazarettgasse 14, A-1090, Vienna, Austria. 3Department of Psychology, University of Gothenburg, PO Box 500, SE-405 30 Gothenburg, Sweden. 4Dept. of Psychiatry, Psychotherapy and Psychosomatics, RWTH Aachen University, Pauwelsstr. 30, 52074, Aachen, Germany. *These authors contributed equally to this work. Correspondence and requests for materials should be addressed to M.V. (email: mvotinov@ukaachen.de) or C.L. (email: claus.lamm@univie.ac.at)
competition during a bargaining game\(^1\), and activations in the MPFC, TPJ, right fusiform gyrus and TP were associated with the opponent’s response in a competitive domino game\(^2\). Other competition studies demonstrated engagement of the ventral striatum (VS) and the ventromedial prefrontal cortex (VMPFC), brain areas associated with the “reward” brain network\(^3\)–\(^8\).

However, there is a lack of neuroimaging studies which investigated strictly competitive games, i.e., games in which decisions affect both competitors (see however\(^9\),\(^10\) for related earlier work). Therefore, the goal of the current study was to disentangle evoked neural responses for different types of self-related and other-related monetary feedback during a real time strictly competitive game, in which each participant’s move had direct consequences both for himself/herself and the opponent.

Compared to previous studies, our experimental design enabled investigating two different types of wins and losses. Participants could either win against another participant by gaining the money at stake in that round, instead of the opponent, whose payoff in turn would be zero; or they could win by averting a monetary loss, in which case, however, the opponent would suffer from a monetary loss. Hence, there were also two mirrored types of losses for participants. One was losing without monetary consequences, but with the opponent winning money. Another one was a monetary loss, in which case the opponent won the trial, but without an increase of money. For this purpose, we implemented a simple reaction time task in the form of a modified monetary incentive delay (MID) task\(^11\) in which two participants (one in the scanner, one outside) competed to respond faster than the other in “gain” and “loss” trials, to either gain the money of that round, or to avoid its loss. We measured brain responses to the outcome of this game, i.e., during the feedback phase in which participants were informed who had responded faster in that round, and hence had won the trial.

Based on previously published fMRI studies which investigated competition and reward processing, we predicted that winning in the game would engage different brain networks, depending on the type of winning. We expected that a monetary gain trial would result in higher activation in reward processing areas, while trials in which winning incurred losses to the opponent would reveal activation in “mentalizing” areas because of an implicit coding of the aversive response of the opponent due to his or her monetary loss\(^6\),\(^12\)–\(^15\).

Furthermore, we predicted that self-related monetary losses in the game would reveal activation in the insulae, medial/anterior cingulate cortex (M/Acc), and lateral prefrontal cortex, as these areas have been associated with pain, monetary loss, and punishment in previous research\(^6\),\(^16\)–\(^19\).

Since competition in this game conceptually resembles a social interaction, we also wanted to investigate the involvement of brain structures related to the self-other distinction during the real-time strictly competitive game. More specifically, we wanted to explore which brain areas are involved in processing the feedback for the two different types of wins and losses, and clarify whether these brain areas are overlapping or distinct.

**Results**

**Behavioral data.** The ANOVA revealed a main effect of the factor outcome (F(2,136) = 54.16, p < 0.001, \(\eta^2 = 0.44\)). Post-hoc tests demonstrated that there was no significant difference in reaction time between gain (mean ± SD ; 198 ms ± 22) and loss cue trials (197 ms ± 21, \(p = 1\)), while both gain and loss cue trials resulted in faster reaction times than neutral cue trials (216 ms ± 17; \(p < 0.001\) for both comparisons).

**fMRI data.** The main effect of *wins* \((WG[3:0] + WL[0:−3]) > (LG[0:3] + LL[−3:0])\) revealed activation in bilateral striatum, VMPFC, PCC, thalamus, left OFC and occipital (visual) areas (Fig. 1a). The main effect of *losses* \((LG[0:3] + LL[−3:0]) > (WG[3:0] + WL[0:−3])\) did not reveal any significant activation.

The interaction contrast, with the participant’s monetary payoff being positive, (i.e., \((WG[3:0] − LG [0:3]) > (WL[0:−3] − LL[−3:0]))\), did not reveal activation using the more stringent voxel-wise multiple comparison correction threshold. However, using a slightly more liberal cluster level correction threshold (\(P = 0.05\), cluster selection intensity threshold of \(P = 0.001\)) revealed activation in VMPFC (Fig. 1b). Another interaction contrast, which represented non-monetary winning \((WL[0:−3] − LL[−3:0]) > (WG [3:0] − LG[0:3])\), revealed activity in the temporo-parietal lobe and precuneus (Fig. 1c).

The contrast \((WG[3:0] > LG[0:3])\), which compared winning and losing in Gain frame trials revealed activation in bilateral striatum, VMPFC, MCC and PCC (Fig. 2a). Conversely, the contrast \((WL[0:−3] > LL[−3:0])\), which compared winning and losing in Loss frame trials demonstrated activation in inferior parietal lobule (IPL), thalamus, bilateral striatum, and visual cortex (Fig. 2b). However, we did not observe activation for the losing conditions, i.e., neither for the contrast \(LG[0:3] > WG[3:0]\) nor for \(LL[−3:0]) > WL[0:−3]\).

The contrast \((WG[3:0] > LL[−3:0])\), where we compared winning with monetary gain versus losing with a monetary loss demonstrated greater activation in bilateral striatum, middle/posterior bilateral insula, VMPFC, medial prefrontal cortex (BA10), ACC, PCC, lateral OFC, and temporal pole (TP) (Fig. 2c; Table 1).

The comparison \((LL[−3:0] > WG[3:0])\) did not reveal significant activation. Only after reducing the threshold to 0.001 uncorrected we observed activation in bilateral IFG, TPJ and precuneus.
The next step was to investigate brain activation for the processing of the other type of winning. The contrast WL[0:−3] > LG[0:3] revealed activation in bilateral striatum, bilateral inferior frontal gyrus (IFG), inferior parietal lobule (IPL), TPJ, PCC, precuneus, thalamus and midbrain (Fig. 2d, Table 2). However, the opposite contrast LG[0:3] > WL[0:−3] did not reveal any activation. When reducing the threshold to $P = 0.001$ (uncorrected for multiple comparisons), however, we observed activation in bilateral middle insulae and left hippocampus.

**Conjunction analysis.** The conjunction analysis for both winning contrasts (WG[3:0] > LL[−3:0] and WL[0:−3] > GL[0:3]) revealed that only the striatum showed overlapping activation in both contrasts (Fig. 3a,b, Table 3).

**ROI analysis.** Repeated measures ANOVA revealed a significant main effect of ROIs ($F(1,2.17) = 8.7$, $p < 0.001$, $\eta^2 = 0.06$) and a ROIs*Contrast interaction ($F(1,2.17) = 11.39$, $p < 0.001$, $\eta^2 = 0.077$). Bonferroni-corrected post-hoc comparisons demonstrated significantly higher activation for the GW[3:0] > LL[−3:0] contrast then for the WL[0:−3] > LG[0:3] contrast in VMPFC ($0.99 \pm 0.2; 0.32 \pm 0.22$, respectively; $p = 0.038$), but significantly lower activation in the rTPJ and the rPPC (rTPJ : $-0.16 \pm 0.12; 0.39 \pm 0.12$, $p = 0.002$; rPPC: $-0.06 \pm 0.11; 0.37 \pm 0.11$, $p = 0.008$). However there was no significant difference in the rNAcc ($0.34 \pm 0.15; 0.19 \pm 0.15$, $p = 0.46$) between the contrasts (Fig. 3c).

**Discussion**

The current study investigated brain activation in a strictly competitive game, in which the participant's performance had direct consequences for the outcome of the other player in the game. We particularly targeted two different types of winning in such game: Winning with monetary gain and winning without a gain, but incurring a monetary loss to the opponent. Winning trials with monetary gain of the participant were associated with increased activity in the bilateral striatum, VMPFC and middle/posterior insula. Winning which avoided a monetary loss to the participant, but was also associated with a
monetary loss of the opponent, also engaged the bilateral striatum. In addition, it activated the inferior frontal gyrus (IFG), inferior parietal lobe (IPL), and precuneus. The behavioral data demonstrated that participants were faster in reaction time to monetary cues comparing to non-monetary ones, which is in line with other studies which used similar task 20,21. Before we interpret these findings in more detail, we will discuss the main effects and interaction results of our design.

Main effect and interactions. The main effect of *wins* revealed, as expected, activation in regions like bilateral striatum and VMPFC, which is in line with many studies associating these areas with positive valence, in particular in the context of economic decision making (see 12 for recent meta-analysis). The interaction contrasts with self-related monetary winning (in gain frame trials) and self-related non-monetary winning (in loss frame trials) revealed activation in distinct areas. The former showed activation in bilateral striatum, VMPFC, and bilateral middle insulae; d) avoidance of monetary loss/opponent punishment versus missed/not acquiring the monetary gain (WL[0:−3] > LG [0:3]) revealed activation in bilateral striatum, thalamus, TPJ and temporo-parietal lobe. The threshold is $P < 0.05$ FWE corrected, at voxel level. Note: L/R = left/right side of the brain.

Figure 2. Whole brain activation of all participants for: a) winning in gain frame trials (WG[3:0] > LG[0:3]) revealed activation in bilateral striatum, VMPFC, MCC and PCC; b) winning in loss frame trials (WL[0:−3] > LL[−3:0]) revealed activation in bilateral striatum, bilateral temporo-parietal lobe, thalamus, and occipital (visual) areas; c) monetary gain versus monetary loss (WG[3:0] > LL[−3:0]) revealed activation in bilateral striatum, VMPFC, and bilateral middle insulae; d) avoidance of monetary loss/opponent punishment versus missed/not acquiring the monetary gain (WL[0:−3] > LG [0:3]) revealed activation in bilateral striatum, thalamus, TPJ and temporo-parietal lobe. The threshold is $P < 0.05$ FWE corrected, at voxel level. Note: L/R = left/right side of the brain.
Notably, previous studies have also identified MPFC to play a role in mentalizing, while this area was not activated in our study. However, a recent meta-analysis of mentalizing/theory of mind studies suggests that mPFC is predominantly related to trait and false belief statements, which might explain the lack of activation in the present setting which required state inferences 24.

Since the focus of this work was also to investigate responses to different types of wins and losses, we will therefore now discuss the specific results of the corresponding contrasts in detail.

**Monetary gain WG[3:0] > LL[−3:0].** The analysis of different types of winning showed that own monetary gains revealed, as expected brain activation in VS, VMPFC and PCC. This confirms the results

| Region               | L/R | Cluster size | T   | x    | y    | z    |
|----------------------|-----|--------------|-----|------|------|------|
| Putamen              | L   | 423          | 6.9 | −30  | −14  | 0    |
| Caudate              | L   | s.c          | 6.6 | −20  | −3   | 24   |
| Putamen              | L   | s.c          | 6.4 | −35  | 2    | 5    |
| Caudate              | R   | 127          | 6.5 | 21   | 14   | 14   |
| Putamen              | R   | s.c          | 5.3 | 27   | 11   | 19   |
| Caudate              | R   | s.c          | 5.3 | 18   | 26   | 10   |
| Caudate              | R   | 49           | 6.4 | 21   | −9   | 29   |
| Insula               | R   | 89           | 6.4 | 38   | 3    | 5    |
| Caudate              | R   | 42           | 6.4 | 12   | 11   | −10  |
| Putamen              | R   | s.c          | 5.8 | 21   | 11   | −10  |
| Putamen              | R   | 113          | 6.4 | 30   | −8   | 5    |
| Putamen              | R   | s.c          | 6.2 | 33   | −14  | 0    |
| Pallidum             | R   | s.c          | 5.3 | 23   | −6   | 0    |
| Parietal Lobe        | L   | 48           | 6.1 | −27  | −39  | 24   |
| Fusiform Gyrus       | R   | 33           | 5.8 | 27   | −78  | −5   |
| Fusiform Gyrus       | L   | 15           | 5.8 | −35  | −48  | −10  |
| STG                  | R   | 20           | 5.8 | 45   | −33  | 19   |
| MCC                  | L   | 13           | 5.7 | 9    | −24  | 43   |
| STG                  | L   | 13           | 5.6 | −59  | −11  | 5    |
| Parietal Lobe        | L   | 20           | 5.6 | −60  | −20  | 43   |
| Occipital            |     | 11           | 5.6 | 24   | −93  | 14   |
| MCC                  | L   | 45           | 5.6 | −3   | −9   | 38   |
| MCC                  | R   | s.c          | 5.0 | 5    | −15  | 38   |
| Fusiform Gyrus       | R   | 11           | 5.5 | 33   | −65  | −10  |
| VMPFC                |     | 51           | 5.5 | −8   | 51   | 0    |
| VMPFC                | s.c | 5.4          | −6  | 39   | −5   |
| SMA                  |     | 6            | 5.4 | 8    | −14  | 58   |
| MCC                  | L   | 24           | 5.4 | −6   | −35  | 48   |
| Lateral OFC          | L   | 6            | 5.4 | −35  | 54   | −10  |
| Supramarginal Gyrus  | R   | 44           | 5.3 | 54   | −29  | 29   |
| Supramarginal Gyrus  | s.c | 5.1          | 57  | −24  | 19   |
| Lingual Gyrus        | R   | 6            | 5.3 | 23   | −66  | −5   |
| ACC                  |     | 11           | 5.3 | −2   | 17   | 29   |
| Precentral Gyrus     | R   | 7            | 5.2 | 39   | −14  | 43   |
| Temporal Pole        |     | 7            | 5.1 | 51   | −11  | 14   |
| Temporal Pole        |     | 6            | 5.1 | 54   | 2    | 0    |

Table 1. Cluster list of activation for contrast WG[3:0] > LL[−3:0] (threshold p < 0.05 FWE corrected at voxel level). Note: L/R = left/right side of the brain; s.c. = sub-cluster; VMPFC = ventromedial prefrontal cortex, ACC = anterior cingulate cortex, PCC = posterior cingulate cortex, SMA = sensorymotor area, MCC = middle cingulate cortex, STG = superior temporal gyrus.
of numerous studies investigating the processing of primary and secondary rewards in both social and non-social contexts (for reviews see 12,25–27).

Additionally, mPFC and ACC also showed activation when a monetary gain was received. It has been suggested that these areas represent self-perception or self-knowledge in social contexts, as well as the ability to differentiate the self from other objects, and to recognize attributes and preferences related to oneself15,28,29.

Contrary to our hypothesis, we did not observe activation for the contrast LL[−3:0] > WG[3:0] in the insula and in the ACC for self-related monetary loss. Only after reducing the threshold to 0.001 uncorrected we observed activation in bilateral IFG, TPJ and precuneus. A similar situation was given with another losing contrast LG[0:3] > WL[0:−3], where we observed activation in bilateral insulae and left hippocampus only after reducing the threshold to 0.001 uncorrected. One explanation for a lack of significant activity for these contrasts is that the numbers of loss trials was lower than the win trials, to make the task settings believable and let the subjects get more profit. This might however have reduced the statistical power of analyses targeting higher activation in the loss trials.

**Avoidance of monetary loss /opponent’s punishment WL[0:−3] > LG[0:3].** This contrast aimed to compare a situation in which participants achieved a zero payoff, but avoided a monetary loss which instead was incurred to the opponent, with an equivalent situation in terms of payoff, which however carried a monetary gain for the opponent. Interestingly, this revealed rather distinct neural networks. Additionally to activation in VS and PPC, we observed activation in temporo-parietal areas

| Region                  | L/R | Cluster size | T   | x  | y  | z  |
|------------------------|-----|--------------|-----|----|----|----|
| Putamen                | R   | 608          | 8.96| 26 | 8  | 5  |
| Putamen                | R   | 7.48         | 26  | −5 | 5  |    |
| Putamen                | R   | 5.90         | 27  | 18 | −10|    |
| Putamen                | L   | 642          | 8.26| −23| 3  | 5  |
| Putamen                | L   | 8.15         | −24 | 6  | −5 |    |
| Globus Pallidus        | L   | 7.55         | −27 | −14| 5  |    |
| Thalamus               | R   | 163          | 6.41| 8  | −14| 0  |
| Caudate                | R   | 6.09         | 12  | −12| 10 |    |
| Hipothalamus           | L.  | 6.05         | 8   | −5 | −5 |    |
| Thalamus               | L.  | 6.25         | −8  | −14| −5 |    |
| Midbrain               | L.  | 5.00         | −8  | −23| −5 |    |
| Occipital              | L.  | 6.12         | −35 | −77| −10|    |
| IFG                    | R   | 5.85         | −44 | −66| −5 |    |
| Superior Occipital Gyr | L.  | 5.61         | −41 | −57| −10|    |
| Inferior Parietal Gyr  | L.  | 6.04         | −29 | −57| 43 |    |
| Inferior Parietal Gyr  | R   | 5.82         | 38  | −41| 38 |    |
| Middle Occipital Gyr   | L.  | 5.02         | 32  | −45| 43 |    |
| Precuneus              | L.  | 5.60         | −26 | −74| 29 |    |
| IFG                    | L.  | 5.37         | −18 | −66| 34 |    |
| Temporal Lobe          | L.  | 5.50         | −44 | 2  | 53 |    |
| IFG                    | L.  | 5.41         | −48 | −44| 5  |    |
| PCC                    | L.  | 5.28         | −44 | 2  | 34 |    |
| IFG                    | L.  | 5.19         | −38 | 17 | 53 |    |
| Thalamus               | 5   | 5.16         | −12 | −18| 10 |    |
| Supra Marginal Gyr     | 9   | 5.13         | −44 | −53| 29 |    |
| Occipital              | 5   | 5.09         | −24 | −95| 0  |    |
| VMPFC                  | 4   | 5.40         | 5   | −33| −10|    |

**Table 2.** Cluster list of activation for contrast WL[0:−3] > LG[0:3] (threshold p < 0.05 FWE corrected at voxel level). Note: L/R = left/right side of the brain; s.c. = sub-cluster; IFG = inferior frontal gyrus, IPL = inferior parietal lobule.
like bilateral inferior parietal lobule, TPJ, TP, precuneus, and the IFG. The temporo-parietal areas are often described as empathy- and mentalizing-related areas that are recruited when individuals need to understand and predict other people’s intentions and beliefs\(^{14,30–32}\). This is particularly important in social contexts like competition, where we need to observe or are directly made aware of how our own actions and their outcomes affect others.

Neuroimaging studies which used other types of competition tasks also confirmed an engagement of these areas. For example, competition was associated with activation in the right IFG, bilateral temporal lobe, bilateral fusiform and bilateral precuneus during an adapted Stroop Task\(^{33}\). Competition was also associated with activation in the inferior, parietal and medial prefrontal cortices\(^{2}\). Two more studies observed competition-related brain activation in TPJ and TP during a competitive ultimatum game\(^{3}\) and a competitive domino game\(^{4}\). A recent study by Radke et al. also demonstrated activation in parietal cortices and TP when the action of a participant in the game had negative consequences for their opponents\(^{5}\).

In addition to temporo-parietal activation during other’s-related monetary loss, we observed lateral prefrontal (LPFC) and bilateral IFG activation. Earlier accounts had associated these areas with distinguishing self from other\(^{30}\). More recently, several neuroimaging studies observed activation of IFG during loss aversion\(^{34,35}\), safe reward\(^{36}\) and risk aversion\(^{37}\). Hence, activation in IFG during observing someone else’s misfortune might represent a general mechanism of processing losses.

**ROI results.** Our exploratory ROI analysis demonstrated that VMPFC was activated significantly higher during Monetary gain contrast than during Avoidance of monetary loss/opponent’s punishment contrast, while activation for right PCC and right TPJ showed the opposite pattern of activation. These findings also support our hypothesis about that different brain networks involved depend on the type

| Region   | L/R | Cluster size | T   | x   | y   | z   |
|----------|-----|--------------|-----|-----|-----|-----|
| Putamen  | L   | 117          | 6.70| −30 | −14 | 0   |
|          | L   | s.c          | 5.72| −32 | −2  | 0   |
|          | L   |              | 5.27| −27 | −3  | 10  |
|          | R   | 68           | 5.98| 29  | −8  | 5   |
|          | R   | 22           | 5.83| 21  | 11  | −10 |
|          | L   | 5            | 5.12| −24 | 11  | 0   |

*Table 3.* Cluster list of activation for conjunction analysis of the contrasts WG\(^{3:0}\) > LL\(^{−3:0}\) and WL\(^{0:−3}\) > LG\(^{0:3}\) (threshold p < 0.05 FWE corrected at cluster level). Note: L/R = left/right side of the brain; s.c. = sub-cluster.

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**Figure 3.** Analysis of the contrasts, which represent two types of winning (WG\(^{3:0}\) > LL\(^{−3:0}\)) and (WL\(^{0:−3}\) > LG\(^{0:3}\)). a) Overlap of activation for both contrasts in striatum, where red color is activation for WG\(^{3:0}\) > LL\(^{−3:0}\), green color is activation for WL\(^{0:−3}\) > LG\(^{0:3}\) and yellow color is overlap of activation from both contrasts; b) Conjunction analysis of both contrasts revealed activation only in striatum. The threshold is P < 0.05 FWE corrected, at voxel level; c) BOLD signal (Parameter estimates ± SEM) from rNAcc, rPCC, rTPJ and VMPFC. Contrast GW\(^{3:0}\) > LL\(^{−3:0}\) demonstrated significantly higher activation in VMPFC, but significantly lower in rTPJ and rPCC then WL\(^{0:−3}\) > LG\(^{0:3}\) contrast.
of winning. The coordinates for rTPJ and rPCC were taken from the peak of activation of the contrast “Mentalizing about Others versus Mentalizing about Yourself” from the study of 38 and we observed higher activation in these regions for the contrast where the participant had the stronger negative impact on the payoff for the opponent.

**Shared activation for own monetary gain and avoidance/other monetary loss.** One explanation for shared activation in the ventral striatum when participants won a trial and received a monetary gain, and when winning in loss frame trials (which incurred a loss to the opponent) is that this activation is associated with general reward processing39. According to a recent concept it may indicate an enhanced motivational value in the form of incentive salience attribution to stimuli perceived at that moment40. In addition, in our ROI analysis there was no difference in activation in right nucleus accumbens for different types of winning. This also suggests that activation in VS is associated with generalized aspects of winning.

It might be argued that our results can also be explained in a prediction error framework, as areas such as the striatum have been associated in the coding of prediction errors41. However, the present design was not tailored to analyze or interpret our results within such a framework. This is so because the outcome of each trial was very ambiguous and hard to predict for the player, which likely resulted in a complex, subjective and individually varied mixture of positive and negative expectations and expectation violations which could not be modeled.

A different explanation is that a competitive situation may elicit different types of emotional reactions. Participants may experience empathy while observing failure of a group member, but failure of a rival may cause Schadenfreude, i.e. pleasure about someone else’s misfortune. One possible condition when Schadenfreude may arise is when people can gain from another’s misfortune42. Takahashi et al. (2009) demonstrated a stronger correlation between activation in ventral striatum and self-reported Schadenfreude in a situation when misfortunes happened to envied persons43, and a different study concluded that the striatum plays a role in mediating the emotional consequences of social comparison during competition44. Furthermore, in a social group competition an increase of VS activation was observed during success of the favored team or failure of the rival team, even against a third team45. Similarly, the VS was activated during watching a negatively evaluated out-group member receiving pain44, and observing others making errors13.

Although we did not explicitly measure the level of Schadenfreude, pleasantness and motivation in this study, we speculate that activation in the striatum partially is related to these aspects. This interpretation is further supported by a recent study which showed that participants’ self-evaluations of pleasantness were associated with activation in the VS when winning in a competitive game45. Additional research is needed to directly examine the link between VS with Schadenfreude and motivation during competitive interactions.

However, we need to take into account that humans are not exclusively motivated by material self-interests, but that people often also care for the well-being of others46. Moreover it was found that individual differences in prosocial value orientation are important for the allocation of resources between self and others, and that amygdala, striatum and VMPFC play a critical role mediating this effect47–49. Our task design provided no choice but to punish the opponent in the loss condition, and this certainly has affected subjects with differences in prosocial orientations in a different way. Since we however did not collect data on individual differences in prosocial orientation, the question how the neural networks identified in our study are related to such differences needs to be clarified by future studies.

Taken together, this study demonstrates that two distinct brain networks are engaged when people process of two types of winning in the game, i.e., own monetary gain and others-monetary loss. A medial-frontal network demonstrated activation for own monetary gain, while a tempo-parietal network was more involved in response to others’ monetary losses. Both types of winning in the game shared activation in the VS which may represent the “joy of winning” for outperforming someone else during competition. Alternatively, this may suggest that the misfortunes of opponents were treated as reward and elicited Schadenfreude.

In conclusion, the present study demonstrated that, depending on the type of winning in the competitive game, distinct brain areas are engaged in the processing. Our results provide new insights for understanding brain function during competitive contexts and fundamental features of human social interactions.

**Methods**

**Participants.** Sixty nine healthy volunteers (38 females and 31 males) participated in the experiment. The average age was (mean ± SD) 23.8 ± 5.4 years old. All volunteers had no history of psychiatric or neurological disorders or contraindications for high-field MRI scanning. All were right-handed as assessed by the Edinburgh Handedness Inventory. All participants signed informed consent before the study and the study protocol was approved by the ethics committee of the Medical University of Vienna. The methods were carried out in accordance with approved guidelines.

**Competitive Task design.** We employed a Competitive Incentive Delay (CID) task, which was a modification of the Monetary Incentive Delay (MID) task introduced by Knutson and colleagues31. The
CID differed from the MID only by the fact that participants played against another person, rather than trying to stay within a pre-set reaction time as in the original MID.

More specifically, participants were told that they were competing with another participant, to whom they were connected via the computer network. In reality, though, they were playing “against” a pre-programmed computer algorithm. To make the task more believable, all participants had taken part in practice trials, together with the experimenter and before entering the scanner. In these practice trials, experimenter and participant played the CID against each other in real time and while sitting next to each other, in front of a computer. The practice trials also served to familiarize the participants with the task and to minimize learning effects during the experiment. After entering the scanner and before the task started, the abstract silhouette of an opponent and a message that the connection with the opponent’s computer had been initiated was shown on the screen. Participants did not get any personal information about their adversary. In reality, they played against a pre-set computer algorithm, and were debriefed after completion of the experiment.

The CID consisted of one scanning run lasting about 9 min, in which 72 trials were played. At the onset of each trial, participants saw one of three geometrical cues for 250 ms. Next, they anticipated the appearance of a target square, to which they had to respond with a button press as fast as possible. During target anticipation, a fixation crosshair was shown, and the anticipation period was varied randomly between 2000–2500 ms. Immediately after disappearance of the target, feedback was presented for 1650 ms. Feedback informed participants about whether they had won or lost money during that trial, their total score, and the opponent’s total score (Fig. 4a). “Monetary Gain” cues signaled the possibility of winning € 3 (a circle with three horizontal lines; 32 trials), “Monetary Loss” cues signaled the possibility of losing € −3 (a square with three horizontal lines; 24 trials), and cues representing “no monetary outcome” (€ 0; 12 trials) were denoted by a triangle. The rationale for a larger number of gain trials was that we wanted participants to have the chance to finish the game with a net monetary gain.

To increase the competitiveness of the task, and in line with the strictly competitive task setup we intended to implement, the possible outcomes were arranged in a way that participant and “opponent” were always directly linked to each other’s monetary score. I.e., if participants pressed the button in time before the go cue would disappear from the screen, they would win money, while the (alleged) opponent’s payoff was zero. If they failed to respond fast enough, the opponent received the monetary gain and the participant nothing. If participants pressed the button on time after a loss cue, the opponent would lose money, but not the participant. If they missed, the opposite payoff was the case (Fig. 4b). The main overall goal of the task communicated to participants was to maximize their monetary outcome, and to receive more money than the opponent. Thus, participants were paid the final monetary revenue they had achieved after completing the task. Trial types were pseudorandomly ordered within each run. The display duration of the target cue was adapted to the participant’s performance (within 80–370 ms) to ensure that all participants won in approximately 2/3 of all trial types.

Reaction times were analyzed in SPSS 20.0 (SPSS Inc., Armonk, USA) using a repeated-measures ANOVA with 3 levels for the factor outcome (“Monetary Gain”, “Monetary Loss” and “Non-Monetary Outcome”). Significance was evaluated at P < 0.05. Post-hoc tests with Bonferroni correction for multiple comparisons were applied. Data are reported as means ± SD.

**MRI scanning.** MRI scanning was conducted on a 3 Tesla TIM Trio whole body scanner (Siemens, Germany). Participants were scanned using the manufacturer’s 32-channel head coil. Functional images were obtained with a single-shot echo planar imaging (EPI) sequence. The image acquisition parameters were as follows: repetition time (TR) = 1.8 s, echo time (TE) = 38 ms, flip angle (FA) = 90°, 294 whole-brain volumes (matrix size 128 × 128, FoV = 190 × 190 mm², 3 mm slice thickness). For anatomical registration, we obtained high-resolution 3D T1 anatomical images after the fMRI runs (magnetization prepared rapid gradient echo sequence, TR = 2.3 s, TE = 4.21 ms, 1.1 mm slice thickness, 900 ms inversion time, 9° flip angle).

Image analysis was performed using the SPM8 software package (www.filion.ucl.ac.uk/spm) implemented in MATLAB (Mathworks Inc., Natick, USA). Preprocessing included correction for slice timing differences, realignment to the first image to adjust for movement, segmentation, normalization to standard MNI space (at isotropic voxel size), and smoothing with a Gaussian filter (8 mm). The first level (individual subject) analyses were set up using the general linear model approach, with events of interest being modeled by regressors. The fixation cross interval between trials were modeled as an implicit baseline.

The four types of feedback WG[3:0], WL[0:−3], LG[0:3] and LL[−3:0] (two types of wins and losses, in a potential gain or loss framework, respectively) were modeled (Fig. 5).

The anticipation-related responses for all cues were also modeled. Contrast images of these regressors from the first level were then entered into second level random-effects analyses. We used the flexible factorial design option implemented in SPM8 to compare brain activations in response to the different types of feedback.

The contrasts we assessed focused on neural activation differences during the feedback conditions. First, we calculated the contrasts (WG[3:0] + WL[0:−3]) > (GL[0:3] + LL[−3:0]) and (GL[0:3] + LL[−3:0]) > (WG[3:0] + WL[0:−3]) in order to identify the main effect of wins and losses in the game. Secondly, we calculated the interaction (WG[3:0] − LG[0:3]) > (WL[0:−3] − LL[−3:0]) and (WL[0:−3] − LL[−3:0] > (WG[3:0] − LG[0:3]) in order to identify the main effect of wins and losses in the game.
(WG[3:0] > LG[0:3]) in order to see the difference between winning during gain frame trials and winning during loss frame trials. Additionally, we checked separately the contrasts (WG[3:0] > LG[0:3]), (WL[0:−3] > LL[−3:0]) and vice versa, to identify regions specifically involved in winning and losing in gain and loss frame trials.

However, our main interest was to check the contrasts WG[3:0] > WL[−3:0] and WL[0:−3] > LG[0:3] contrasts. The idea behind targeting these specific contrasts was to unveil the neural networks related to self-related or to other-related changes in the monetary scores. For example, the contrast WG[3:0] > LL[−3:0] would inform us about activation related to monetary changes for participants (monetary gain versus monetary loss), while keeping the opponent’s payoff constant (which in both contrasts is zero). Conversely, the contrast WL[0:−3] > LG[0:3] would represent a rather different winning situation, in which while the participant’s monetary payoff was zero, the payoff for the opponent was negative. This contrast WL[0:−3] > LG[0:3] therefore represents a comparison of winning and losing, where we compare the condition “avoidance of monetary loss” (and opponent punishment) versus the condition “missed/not acquiring the monetary gain”.

For all analysis, we used a family-wise error (FWE) correction at the voxel level, at a threshold of $P < 0.05$ and a cluster extent threshold of 5 voxels, for identifying statistically significantly activated voxels. In some cases where we had strong prior hypotheses, data were also explored at more liberal thresholds (see Results). All results are reported in accordance with recommendations from$^{50,51}$.
Figure 5. Schematic illustration of the four types of feedback (two types of winning and losing trials, respectively). The red color represents the two conditions of winning, either with Monetary Gain (WG[3:0]) or Avoidance of monetary loss/opponent punishment (WL[0:−3]), while the blue color represents the two types of losing: either with Monetary Loss (LL[−3:0]), or with missed/not acquiring the monetary gain (LG[0:3]). First number in the brackets represents outcomes for participant and second one for the opponent.

Exploratory ROI analysis. For the exploratory analysis of brain activation in regions associated with reward processing and mentalizing, we prepared four regions of interests. Two regions, the right PCC and the right TPJ, were defined as spheres of 8 mm radius, with the ROI center being taken from the peak of activation of the contrast “Mentalizing about Others” versus “Mentalizing about Yourself” from the study of Lombardo et al. (8−58 28 and 60−60 14, respectively)38. Two other ROIs, VMPFC and right nucleus accumbens, were defined in the same way from a meta-analysis26. The spheres were based on the peak coordinates found for the analysis of monetary outcome (240−3 and 8 14−4, respectively).

Mean parameter estimates within four ROI masks were extracted for the contrasts (WG[3:0] > LL[−3:0]) and (WL[0:−3] > LG[0:−3]) from each individual, and entered into statistical analysis. Group differences for each contrast were analyzed in SPSS 20.0 (SPSS Inc., Armonk, USA) using a repeated-measures ANOVA with ROIs as within-subjects factors and Contrast as between-subjects factor. If the sphericity assumption was violated (significant results in Mauchly’s test of sphericity), degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity. Significance was evaluated at P < 0.05. Post-hoc tests with Bonferroni correction for multiple comparisons were applied.

References
1. Von Neumann, J. & Morgenstern, O. Theory of games and economic behavior (commemorative edition). (Princeton university press, 2007).
2. Decety, J., Jackson, P. L., Sommerville, J. a., Chaminade, T. & Meltzoff, A. N. The neural bases of cooperation and competition: an fMRI investigation. NeuroImage 23, 744–751, doi:10.1016/j.neuroimage.2004.05.025 (2004).
3. Halloy, M.-L., Hlushchuk, Y., Hari, R. & Schürmann, M. Competing with peers: Mentalizing-related brain activity reflects what is at stake. NeuroImage 46, 542–548, doi:10.1016/j.neuroimage.2009.01.063 (2009).
4. Assaf, M. et al. Brain Activity Dissociates Mentalization from Motivation During an Interpersonal Competitive Game. Brain Imaging and Behavior 3, 24–37, doi:10.1007/s11682-008-9047-y (2009).
5. Radke, S., de Lange, F. P., Ullsperger, M. & de Bruijn, E. R. Mistakes that affect others: an fMRI study on processing of own errors in a social context. Exp Brain Res 211, 405–413, doi:10.1007/s00221-011-2677-0 (2011).
6. Cikara, M., Botvinick, M. M. & Fiske, S. T. Us versus them: social identity shapes neural responses to intergroup competition and harm. Psychological science 22, 306–313, doi:10.1177/0956797610397667 (2011).
7. Flessbach, K. et al. Social Comparison Affects Reward-Related Brain Activity in the Human Ventral Striatum. Science 318, 1303–1308 (2007).
8. Dvash, I., Gilam, G., Ben-Zéev, A., Hendler, T. & Shamay-Tsoory, S. G. The envious brain: The neural basis of social comparison. Human Brain Mapping 31, 1741–1750, doi:10.1002/hbm.20972 (2010).
9. Yamada, M., Lamm, C. & Decety, J. Pleasing frowns, disappointing smiles: an ERP investigation of counterempathy. Emotion 11, 1336–1345, doi:10.1037/a0023854 (2011).
10. Lanzetta, J. T. & Englis, B. S. Expectations of cooperation and competition and their effects on observers' vicarious emotional responses. J Pers Soc Psychol 56, 543–554 (1989).
11. Knutson, B., Westdorp, a., Kaiser, E. & Hommer, D. FMRI visualization of brain activity during a monetary incentive delay task. NeuroImage 12, 20–27, doi:10.1006/nimg.2000.0593 (2000).
12. Sescousse, G., Caldu, X., Segura, B. & Dreher, J. C. Processing of primary and secondary rewards: a quantitative meta-analysis and review of human functional neuroimaging studies. Neurosci Biobehav Rev 37, 681–696, doi:10.1016/j.neubiorev.2013.02.002 (2013).
13. de Bruijn, E. R. A., de Lange, F. P., van Cramon, D. Y. & Ullsperger, M. When Errors Are Rewarding. The Journal of Neuroscience 29, 12183–12186 (2009).
14. Lieberman, M. D. Social Cognitive Neuroscience: A Review of Core Processes. Annual Review of Psychology 58, 259–289, doi:10.1146/annurev.psych.58.110405.085604 (2006).
15. Frith, C. D. The social brain? Philosophical Transactions of the Royal Society B: Biological Sciences 362, 671–678 (2007).
16. Knutson, B. & Bossaerts, P. Neural Antecedents of Financial Decisions. The Journal of Neuroscience 27, 8174–8177 (2007).
17. Shigenome, Y., Tsukiura, T., Kambara, T. & Kawashima, R. Remembering with gains and losses: effects of monetary reward and punishment on successful encoding activation of source memories. Cereb Cortex 24, 1319–1331, doi:10.1093/cercor/bha415 (2014).
18. Kringlebach, M. L. & Rolls, E. T. The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. Prog. Neurobiol. 72, 341–372 (2004).
19. Eisenberger, N. I. & Lieberman, M. D. Why rejection hurts: a common neural alarm system for physical and social pain. Trends Cogn. Sci. 8, 294–300 (2004).
20. Votinov, M. et al. A genetic polymorphism of the endogenous opioid dynorphin modulates monetary reward anticipation in the corticostriatal loop. PLoS one 9, e89954, doi:10.1371/journal.pone.0089954 (2014).
21. Spreckelmeyer, K. N. et al. Anticipation of monetary and social reward differently activates mesolimbic brain structures in men and women. Social Cognitve and Affective Neuroscience 4, 158–165 (2009).
22. Cavanna, A. E. & Trimble, M. R. The prefrontal: a review of its functional anatomy and behavioural correlates. Brain: a journal of neuroscience 129, 564–583, doi:10.1093/brain/awl004 (2006).
23. Decety, J. & Lamm, C. The role of the right temporoparietal junction in social interaction: how low-level computational processes contribute to meta-cognition. Neurosciencet 13, 580–593, doi:10.1017/S1073858407034654 (2007).
24. Schurz, M., Radua, J., Aichhorn, M., Richlan, F. & Perner, J. Fractionating theory of mind: a meta-analysis of functional brain imaging studies. Neurosci Biobehav Rev 42, 9–34, doi:10.1016/j.neubiorev.2014.01.009 (2014).
25. Berridge, K. C., Robinson, T. E. & Aldridge, J. W. Dissecting components of reward: ‘liking’, ‘wanting’, and learning.

26. Clithero, J. A. & Rangel, A. Informatic parcellation of the network involved in the computation of subjective value.

27. Diekhof, E. K., Kaps, L., Falkai, P. & Gruber, O. The role of the human ventral striatum and the medial orbitofrontal cortex in the representation of reward magnitude - an activation likelihood estimation meta-analysis of neuroimaging studies of passive reward expectancy and outcome processing. Neuropsychologia 50b, 1252–1266, doi:10.1016/j.neuropsychologia.2012.02.007 (2012).
28. Ochsner, K. N. Reflecting upon feelings: an fMRI study of neural systems supporting the attribution of emotion to self and other. J. Cogn. Neurosci. 16, 1746–1772 (2004).
29. Amodio, D. M. & Frith, C. D. Meeting of minds: the medial frontal cortex and social cognition. Nat Rev Neurosci 7, 288–277 (2006).
30. Decety, J. & Sommerville, J. A. Shared representations between self and other: a social cognitive neuroscience view. Trends Cogn Sci 7, 527–533 (2003).
31. Singer, T. & Lamm, C. The Social Neuroscience of Empathy. Ann N Y Acad Sci 1156, 81–96, doi:10.1111/j.1749-6632.2009.04418.x (2009).
32. Denny, B. T., Kobner, H., Wager, T. D. & Ochsner, K. N. A meta-analysis of functional neuroimaging studies of self- and other judgments reveals a spatial gradient for mentalizing in medial prefrontal cortex. J Cogn Neurosci 24, 1742–1752, doi:10.1162/jocn_a_00233 (2012).
33. Polosan, M. et al. An fMRI study of the social competition in healthy subjects. Brain and cognition 77, 401–411, doi:10.1016/j.bandc.2011.08.018 (2011).
34. Votinov, M. et al. The neural correlates of endowment effect without economic transaction. Neuroscience Research 68, 59–65 (2010).
35. Fukunaga, R., Brown, J. & Bogg, T. Decision making in the Balloon Analogue Risk Task (BART): Anterior cingulate cortex signals loss aversion but not the infrequency of risky choices. Cognitive, Affective, & Behavioral Neuroscience 12, 479–490, doi:10.3758/s13415-012-0102-1 (2012).
36. Tobler, P. N., Christopoulos, G. I., O’Doherty, J. P., Dolan, R. J. & Schultz, W. Risk-dependent reward value signal in human reward processing. PLoS One 7, e35169, doi:10.1371/journal.pone.0035169 (2012).
37. Lombardo, M. V. et al. Shared neural circuits for mentalizing about the self and others. J Cogn Neurosci 22, 1623–1635, doi:10.1162/jocn_a_00233 (2010).
38. Liu, X., Hairston, J., Schrier, M. & Fan, J. Common and distinct networks underlying reward valence and processing stages: a meta-analysis of functional neuroimaging studies. Neurosci Biobehav Reviews 35, 1219–1236, doi:10.1016/j.neubiorev.2010.12.012 (2011).
39. Bertrix, K. C., Robinson, T. E. & Aldridge, J. W. Dissecting components of reward: ‘liking’, ‘wanting’, and learning. Current opinion in pharmacology 9, 65–73, doi:10.1016/j.chop.2008.12.014 (2009).
40. Schultz, W., Dayan, P. & Montague, P. R. A neural substrate of prediction and reward. Science (New York, N.Y.) 275, 1593–1599 (1997).
41. Smith, R. H., Powell, C. A. J., Combs, D. J. Y. & Schultz, D. R. Exploring the When and Why of Schadenfreude. Social and Personality Psychology Compass 3, 530–546, doi:10.1111/j.1748-9988.2009.00181.x (2009).
42. Takahashi, H. et al. When Your Gain Is My Pain and Your Pain Is My Gain: Neural Correlates of Envy and Schadenfreude. Science 323, 937–939 (2009).
43. Hein, G., Silani, G., Preuschhof, K., Batson, C. D. & Singer, T. Neural responses to ingroup and outgroup members’ suffering predict individual differences in costly helping. Neuro 68, 149–160, doi:10.1016/j.neuro.2010.09.003 (2010).
44. Kätysry, J., Hari, R., Ravaja, N. & Nummenmaa, L. The Opponent Matters: Elevated fMRI Reward Responses to Winning Against an Outgroup Member During a Computer Opponent During Video Game Playing. Cerebral Cortex 23, 2829–2839 (2013).
45. Fehr, E. & Fischbacher, U. Why Social Preferences Matter – The Impact Of Non-Selfish Motives On Cooperation, Competition And Incentives. The Economic Journal 112, C1–C33, doi:10.1111/1468-0297.00027 (2002).
46. Haruno, M. & Frith, C. D. Activity in the amygdala elicited by unfair divisions predicts social value orientation. Nat Neurosci 13, 160–161, doi:10.1038/nn.2468mm.2468 (2010).
47. Christopoulos, G. I. & King-Casas, B. With you or against you: social orientation dependent learning signals guide actions made for others. Neuroimage 104, 326–335, doi:10.1016/j.neuroimage.2014.09.015.035.1181(13)00753-8 (2015).
48. Van Lange, P. A. M. & Kuhlman, D. M. Social value orientations and impressions of partner's honesty and intelligence: A test of the might versus morality effect. Journal of Personality and Social Psychology 67, 126 (1994).
49. Poldrack, R. A. et al. Guidelines for reporting an fMRI study. Neuroimage 40, 409–414, doi:10.1016/j.neuroimage.2007.11.048 (2008).
50. Woo, C. W., Krishnan, A. & Wager, T. D. Cluster-extent based thresholding in fMRI analyses: pitfalls and recommendations. Neuroimage 91, 412–419, doi:10.1016/j.neuroimage.2013.12.058 (2014).
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Author Contributions
M.V., J.P., U.S. and C.L. were involved in designing the study, as well as in writing and editing the manuscript. M.V., J.P. and C.W. collected and analyzed the data. All authors reviewed the manuscript.

Additional Information
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