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A common neural code for social and monetary rewards in the human striatum

Stephanie J. Wake and Keise Izuma

Department of Psychology, University of York, Heslington, York YO10 5DD, UK

Correspondence should be addressed to Keise Izuma, Department of Psychology, University of York, Heslington, York YO10 5DD, UK.
E-mail: keise.izuma@york.ac.uk

Abstract

Although managing social information and decision making on the basis of reward is critical for survival, it remains uncertain whether differing reward type is processed in a uniform manner. Previously, we demonstrated that monetary reward and the social reward of good reputation activated the same striatal regions including the caudate nucleus and putamen. However, it remains unclear whether overlapping activations reflect activities of identical neuronal populations or two overlapping but functionally independent neuronal populations. Here, we re-analyzed the original data and addressed this question using multivariate-pattern-analysis and found evidence that in the left caudate nucleus and bilateral nucleus accumbens, social *vs* monetary reward were represented similarly. The findings suggest that social and monetary rewards are processed by the same population of neurons within these regions of the striatum. Additional findings demonstrated similar neural patterns when participants experience high social reward compared to viewing others receiving low social reward (potentially inducing schadenfreude). This is possibly an early indication that the same population of neurons may be responsible for processing two different types of social reward (good reputation and schadenfreude). These findings provide a supplementary perspective to previous research, helping to further elucidate the mechanisms behind social *vs* non-social reward processing.

Key words: social reward; monetary reward; schadenfreude; fMRI; striatum; MVPA

Introduction

Consider this; (i) people think you are wonderful and regard you as a great person, (ii) you win a £100 prize in a raffle. Both feel good, but it remains uncertain whether social reward and non-social tangible reward share the same neural mechanisms. Making important decisions that dictate survival based on both social and non-social information is a part of everyday life, yet we know relatively little about the comparative reward types that we seek on a daily basis.

An abundance of neuroscience studies has found various social and non-social rewards activate the striatum (Fehr and Camerer, 2007; Izuma, 2015). It is well established in non-human neurophysiological studies that striatal neurons respond to reward (Schultz *et al.*, 2000), and this basic finding has been later replicated by human neuroimaging studies (Delgado, 2007). More recently, social neuroscience and neuroeconomics studies demonstrated that the striatum is activated by a variety of socially rewarding stimuli or behavior, such as mutually cooperating with other individuals (Rilling *et al.*, 2002, 2004), punishing unfair behavior (De Quervain *et al.*, 2004; Singer *et al.*, 2006), giving charitable donations (Moll *et al.*, 2006; Harbaugh *et al.*, 2007) and receiving a good reputation from others (Izuma *et al.*, 2008; Korn *et al.*, 2012).

An important question, which remains unanswered in the field, is whether social and non-social rewards share a common neural mechanism. Importantly, activation overlaps between social and non-social rewards reported previously (Fehr and

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Camerer, 2007; Izuma, 2015) cannot be taken as strong evidence for a shared neural mechanism. It may indeed reflect the same population of neurons responding to both types of rewards (i.e. a shared neural mechanism) or it could in fact signify largely distinct populations of neurons specialized for each reward, which are located in close proximity within the same brain region (e.g. striatum). Ruff and Fehr (2014) proposed two schematic processes for dealing with social *vs* non-social stimuli. The first being the 'extended common currency schema', which argues identical neural processes assign motivational relevance to social/non-social information, predicting similar populations of neurons that encode reward values of both social and non-social stimuli. Secondly, the 'social valuation specific schema' assumes an evolved and dedicated neural circuitry which specifically encode reward values associated with interactions and decisions that involve others. This predicts that there are distinct populations of neurons that process social and non-social rewards.

In this study, we aim to provide an insight into this question by applying multivariate-pattern-analysis (MVPA) (Norman *et al.*, 2006) to the data reported previously (Izuma *et al.*, 2008). In the original study (Izuma *et al.*, 2008), the same participants were asked to perform tasks involving non-social reward (money) and social reward (good reputation from others), and the study found that the striatum (see Figure 1; especially the left putamen and left caudate nucleus) were significantly activated for both monetary and social rewards. Using MVPA, the present study further investigates whether the pattern of activity across multiple voxels within the striatum is similar between social and monetary rewards (i.e. that social and monetary rewards share common neural networks).

How to interpret activation overlaps has been a recurring question in cognitive neuroscience, and MVPA is a useful tool that allows us to infer activities of underlying neuronal populations from fMRI signals, helping us interpret the overlaps (Peelen and Dawning, 2007; Kaplan *et al.*, 2015). For example, Woo *et al.*, (2014) found physical pain and social pain, previously known to activate the same regions within the dorsal anterior cingulate cortex (dACC) and insula (Kross *et al.*, 2011), actually showed distinct activation patterns under MVPA, providing important evidence against a popular notion that physical and social pain share the same neural representation (Eisenberger, 2012). Similarly, using MVPA, Krishnan *et al.* (2016) found that felt and seen pain, also known to activate the same dACC region (Singer *et al.*, 2004), in fact demonstrate distinct activation patterns. Thus, as these overlaps that were once thought to indicate a similar neural mechanism under conventional univariate analysis are actually found to be discriminate under MVPA, it seems fundamental that fMRI research utilize this technique to further assess whether underlying neuronal populations are similar.

Materials and methods

Participants

Data from 19 participants (9 male; mean age $= 21.6 \pm 1.5$ years) were included in the reanalysis using the existing dataset (Izuma *et al.*, 2008). All participants gave written informed consent for participation, and the study was approved by the Ethical Committee of the National Institute for Physiological Sciences, Japan.

Procedure

Full details for procedures used in the study have been published previously (Izuma *et al.*, 2008). Briefly, each participant completed two different fMRI experiments (involving monetary and social rewards, respectively) on two separate days.

In the first monetary reward experiment, participants took part in a simple gambling task. In each trial, they were asked to choose one of three cards and were given 0, 30 or 60 yen depending upon the card chosen. However, the amount that they could earn in each block of eight trials was predetermined; thus, the monetary reward each participant received during each block was systematically manipulated. There were three reward levels (i.e. conditions); (i) High, (ii) Low and (iii) No reward (control). After the monetary reward experiment, participants were asked to respond to several personality questionnaires and to introduce themselves in front of a video camera. Participants were specifically told that others would evaluate them based on their responses to these questionnaires and the video-taped self-introduction, and that they would be shown the results in the next fMRI experiment.

In the second social reward experiment, the same 19 participants were presented with a picture of themselves and a word or phrase indicating the impression of them formed by others. In reality, the items presented were predetermined, such that all participants had the same social reward experience. By systematically grouping six items (into one block) based on desirability ratings provided by another group of participants ($n = 33$), the level of social reward experienced by participants in each block was also manipulated. To exclude the possibility that seeing a positive word per se might be rewarding, as was suggested by a previous study (Hamann and Mao, 2002), the impressions of other people were also presented. Thus, there were six conditions in the second experiment [a 2 (Target; Self or Others) $\times$ 3 (Reward level; High, Low or No reward) within-subject design].

Data analysis

fMRI data was reanalyzed using SPM8 as implemented in Matlab 8.1. Head motion was corrected using the realignment program, and the volumes were normalized to the Montreal Neurological Institute space using the EPI template (resampled voxel size $2 \times 2 \times 2$ mm). Spatial smoothing was not applied in order to preserve fine grained activation patterns for multivariate analyses.

Correlation-based MVPA. As done in the original correlation-based MVPA study (Haxby *et al.*, 2001), the data for each participant was split into odd *vs* even runs. This is mainly intended to check the within-condition correlation as well as to get an insight into whether the same population of neurons process social and monetary rewards. For example, if a striatal region processes information related to monetary or social reward, the same condition (e.g. High Monetary Reward condition) should evoke similar activation patterns across different runs (i.e. significant within-condition correlation). Similarly, if the same population of neurons encodes social and monetary rewards, the two conditions should evoke similar activations patterns (i.e. significant between-condition correlation). It should be noted that using the average absolute values of the difference in each realignment parameter between one scan and its successive scan as a motion index (e.g. Yoo *et al.*, 2005), we confirmed that there was no significant difference in head motion (in each of the six motion parameters) between odd *vs* even runs in both monetary and social experiments (all $Ps > 0.103$).

Since each of the monetary and social reward experiments had four fMRI runs, we conducted the same first level analysis

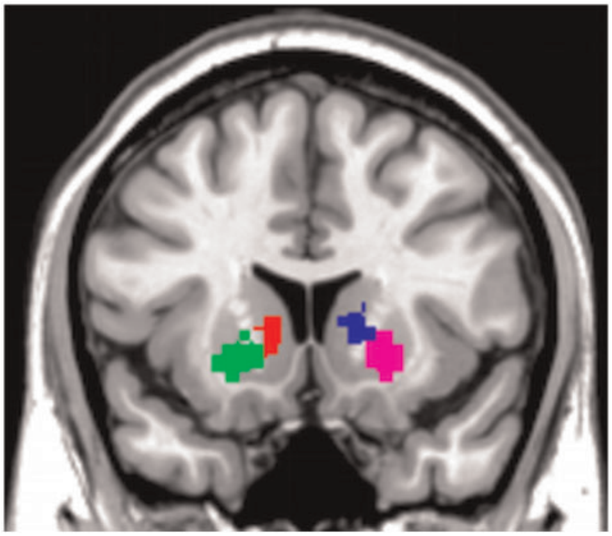

Fig. 1. Axial slice ($y = 14$) showing four ROIs used in the MVPA. These four regions were commonly activated during social *vs* monetary rewards in the original study (Izuma *et al.*, 2008).

using a general linear model as our original study (Izuma *et al.*, 2008), and contrast images were generated separately for odd and even runs, yielding a total of 18 contrast images for each participant; 6 contrast images from the monetary reward experiment [2 (fMRI Run; odd or even) × 3 (Reward level; High, Low or No reward)], and 12 contrast images from the social reward experiment [2 (fMRI Run; odd or even) × 2 (Target; Self or Others) × 3 (Reward level; High, Low or No reward)]. These 18 contrast images were used in the correlation-based MVPA.

Using the data from each of the four regions of interest (ROIs; see below), correlation-based MVPA computes a voxel-by-voxel correlation between one condition in odd runs and the same (within-condition correlation) or different (between-condition correlation) conditions in even runs within each participant. The resulting correlation values are Fisher z transformed and submitted to group level analyses (i.e. one-sample *t*-test [one-tailed]).

Classifier-based MVPA. To check the robustness of our results (especially in the left caudate nucleus), we also ran classifier-based MVPA (a linear support vector machine), which was performed by using custom-made MATLAB scripts in combination with LIBSVM (http://www.csie.ntu.edu.tw/~cjlin/libsvm/). For this analysis, contrast images for each of the four fMRI runs were created separately, and classification performances were evaluated by a leave-one-run-out cross-validation procedure. We first trained and tested a classifier that discriminates the High Monetary Reward condition from the No Monetary Reward condition (i.e. monetary reward classifier). Similarly, we next trained and tested a classifier that discriminates the High Social Reward-Self condition from the No Social Reward-Self condition (i.e. social reward classifier). Finally, we tested whether the monetary reward classifier can discriminate the High Social Reward-Self condition from the No Social Reward-Self condition, and similarly whether the social reward classifier can discriminate the High Monetary Reward condition from the No Monetary Reward condition, an approach known as Multivariate Cross-Classification (Kaplan *et al.*, 2015).

Regions of interest. Striatal areas commonly activated by both monetary and social rewards, which were reported in the original study (Izuma *et al.*, 2008), included the caudate nucleus and putamen bilaterally (see Figure 1). Thus, in order to limit each MVPA to the same anatomical region, we applied anatomical masks (the WFU PickAtlas toolbox for SPM; Maldjian *et al.*, 2003) to the original activation map and created four ROIs (Figure 1); (i) right caudate nucleus (125 voxels), (ii) left caudate nucleus (87 voxels), (iii) right putamen (110 voxels) and (iv) left putamen (99 voxels).

Exploratory searchlight analysis. In addition to the ROI based MVPA mentioned earlier, we conducted a searchlight MVPA to explore whether any other regions within the striatum represent social and monetary rewards in a similar manner. We applied a striatum mask (caudate nucleus and putamen taken from the AAL masks implemented in the WFU pickatlas toolbox; Maldjian *et al.*, 2003) and performed the correlation-based MVPA within each searchlight with a radius of three voxels (maximum of 123 voxels, and less at the boundaries of the striatum). To claim that a striatal region processes values of social and monetary rewards in a similar manner, within each searchlight, we computed the three following voxel-by-voxel correlations; (i) High Monetary Reward within-condition correlation (i.e. odd *vs* even runs), (ii) High Social Reward-Self within-condition correlation, and (iii) High Monetary Reward *vs* High Social Reward-Self between-condition correlation (we took the average of two between-condition correlations). Each correlation was Fisher z transformed and submitted to group level analysis [i.e. one-sample *t*-test (one-tailed)]. We looked for regions within the striatum where all three average Fisher-transformed correlations are simultaneously significantly positive at $P < 0.05$ level [note that the probability of finding such results by chance is 0.0125% (i.e. $0.05^3 = 0.000125$)] with an extent threshold of 50 contiguous voxels.

Results

Correlation- and classifier-based MVPA in the left putamen and left caudate nucleus ROIs

Since the original univariate GLM analysis identified common activations especially in the left putamen and left caudate nucleus (Izuma *et al.*, 2008), we first focused on these two regions. First, we confirmed the reliability of activation patterns in the two main conditions (High Monetary Reward condition and High Social Reward-Self condition). Each of the two conditions showed a significant within-condition correlation in both the left putamen (both $Ps < 0.007$, Figure 2A) and left caudate nucleus (both $Ps < 0.010$; Figure 2B), indicating that each of these two conditions consistently evoked similar activation patterns across odd and even runs within each of the two ROIs. Interestingly, the average correlation between High Monetary Reward and High Social Reward-Self conditions was significantly positive in the left caudate nucleus [average $r = 0.069$, $t(18) = 2.23$, $P = 0.019$; Figure 2B], while it was not significant in the left putamen ($P = 0.43$). To check whether the significant between-condition correlation found in the left caudate nucleus ROI was not due to outliers, we further computed the same correlations after removing outliers (0.23% of the data) based on a Grubbs' test (Grubbs, 1950). The average correlation between High Monetary Reward and High Social Reward-Self conditions was slightly attenuated after removing outliers (average $r = 0.064$), but remained significant [$t(18) = 2.05$, $P = 0.028$].

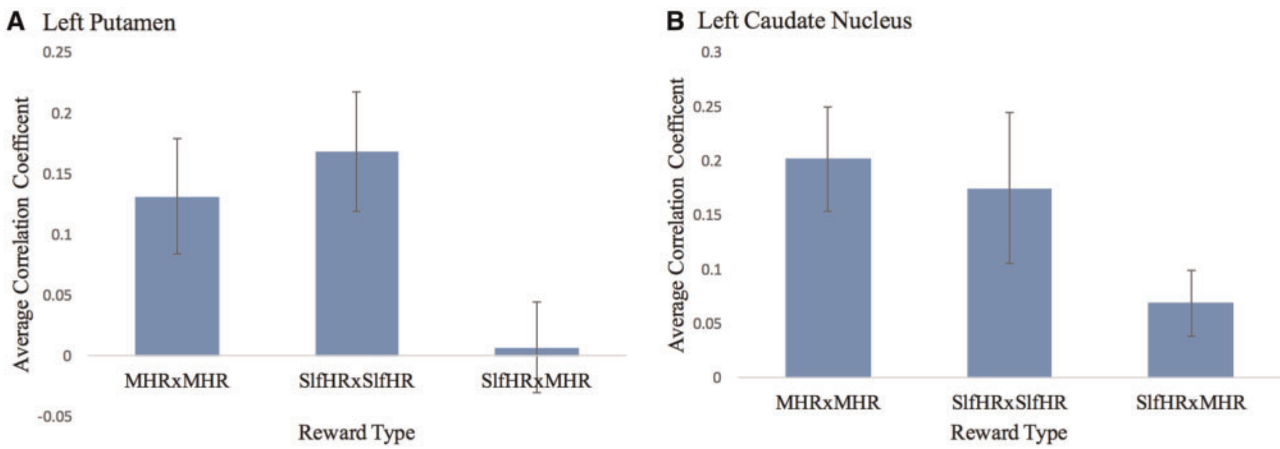

Fig. 2. Correlation-based MVPA results in left putamen (A) and left caudate nucleus (B). MHR: High Monetary Reward, SlfHR: High Social Reward-Self. Error bars denote SEM.

To check the robustness of the findings in the left caudate nucleus ROI, we further conducted a classifier-based MVPA to test whether a monetary reward classifier can classify social reward and *vice versa*. The result first showed that the monetary reward classifier could distinguish High Monetary Reward *vs* No Monetary Reward conditions significantly above the chance level of 50% [average performance = 59.9%, $t(18) = 2.46$, $P = 0.012$]. Similarly, the social reward-self classifier could distinguish High Social Reward-Self and No Social Reward-Self conditions significantly above the chance level [average performance = 56.6%, $t(18) = 2.04$, $P = 0.028$]. Importantly, each classifier was generalizable to a different reward type. The monetary reward classifier could distinguish High Social Reward-Self and No Social Reward-Self conditions significantly above the chance level [average performance = 59.9%, $t(18) = 3.75$, $P < 0.001$]. Likewise, the social reward classifier could distinguish High Monetary Reward and No Monetary Reward conditions significantly above the chance level [average performance = 55.3%, $t(18) = 3.02$, $P = 0.004$]. Furthermore, weight values of the monetary and social reward classifiers were significantly correlated with each other within the left caudate nucleus ROI [average $r = 0.10$, $t(18) = 1.94$, $P = 0.034$]. This result indicates that each voxel within the left caudate nucleus similarly contributed to the classification of monetary and social rewards, suggesting shared neural representations between monetary and social rewards within this area.

Exploratory correlation-based MVPA in the four ROIs

We further investigated all possible correlations across nine conditions (three conditions form the monetary reward experiment and six conditions form the social reward experiment) in the putamen and caudate nucleus in both hemispheres (Figure 1) to explore detailed representational similarity across all conditions (Figure 3A–D). Across all of the four ROIs, for each of the Monetary Reward and Social Reward-Self conditions, the average within-condition correlations were significantly positive (Figure 3E). It should be noted, however, that the average correlations between High Monetary Reward and High Social Reward-Self were significantly positive only in the left caudate nucleus.

Interestingly, we found that the average correlations between High Social Reward-Self and Low Social Reward-Other were all significantly positive across the four ROIs (Figure 3E). As schadenfreude (positive emotion derived from the misfortunate of another individual) is also known to activate the striatum (Takahashi *et al.*, 2009; Cikara *et al.*, 2011), these results may suggest an interesting possibility that two different types of social reward (good reputation toward the self and schadenfreude) share the same neural representations within the human striatum.

Exploratory searchlight analysis within the striatum

The searchlight analysis revealed that only in the bilateral ventral striatum (nucleus accumbens; Figure 4) the average correlation between High Monetary Reward and High Social Reward-Self conditions as well as two average within-condition correlations (i.e. odd *vs* even runs in the High Monetary Reward condition and odd *vs* even runs in the High Social Reward-Self condition) were all significantly positive, suggesting a common neural code for monetary and social rewards in nucleus accumbens.

Discussion

Using the correlation and classifier-based MVPA, this study extends the original study (Izuma *et al.*, 2008) that employed conventional univariate analysis and demonstrated that the left caudate nucleus similarly represents social and monetary rewards. Together with the original finding (Izuma *et al.*, 2008), the left caudate nucleus showed; (i) linear increase in activation according to reward values of both social and monetary rewards (Izuma *et al.*, 2008), (ii) significant voxel-by-voxel correlation between High Monetary Reward and High Social Reward-Self conditions, (iii) the Monetary Reward classifier was generalizable to distinguish Social Reward *vs* No Social Reward (and *vice versa*) and (iv) weight values of Monetary Reward and Social Reward classifiers were significantly correlated with each other, indicating that there is a common neural code for social and monetary rewards in the human striatum. Furthermore, although the left caudate nucleus was the only region that showed a similar representation between two types of reward across the four ROIs (Figure 1), the searchlight analysis revealed that the bilateral nucleus accumbens, one of the brain areas most heavily implicated in reward processing (Haber and Knutson, 2010), also represents social and monetary rewards in a similar manner. The results suggest that the same population of neurons within

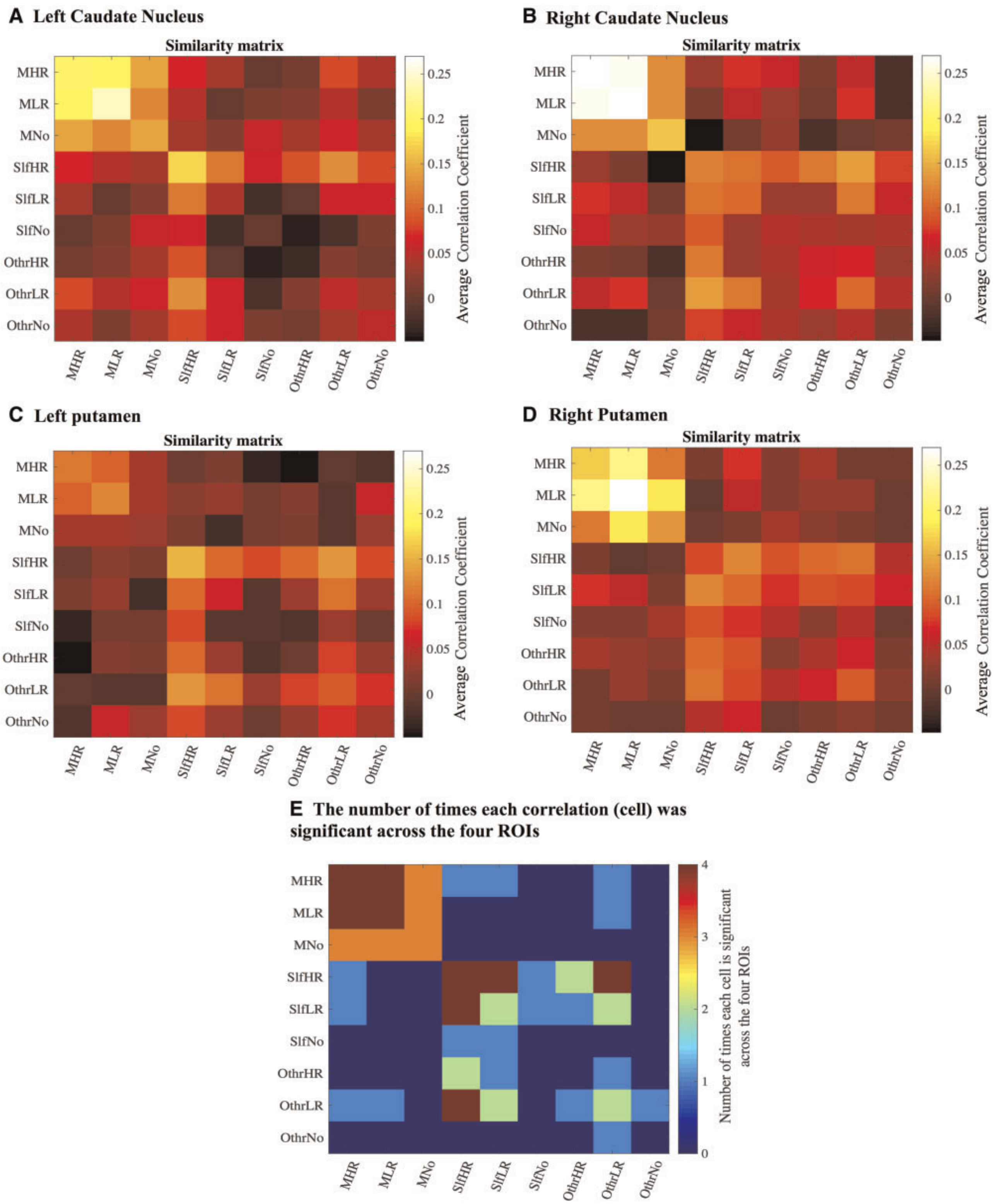

Fig. 3. Average-correlation similarity matrix in the left caudate nucleus (A), the right caudate nucleus (B), the left putamen (C) and the right putamen (D). Each cell represents the group-average voxel-by-voxel correlation coefficient between two conditions across 19 subjects. (E) The number of times each average correlation (cell) was significant (based on one-sample *t*-test, testing if the average Fisher z transformed within-subject correlation is significantly greater than zero) across the four ROIs. MHR, High Monetary Reward condition; MLR, Low Monetary Reward condition; MNo, No Monetary Reward condition; SlfHR, High Social Reward-Self condition; SlfLR, Low Social Reward-Self Condition; SlfNo, No Social Reward-Self condition; OthrHR, High Social Reward-Other condition; OthrLR, Low Social Reward-Other condition; OthrNo, No Social Reward-Other condition.

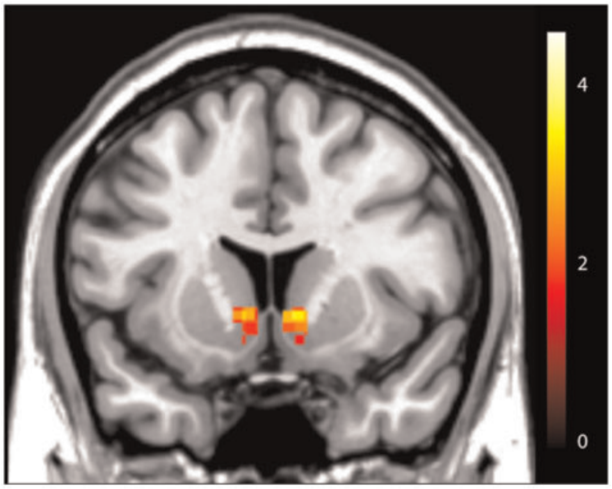

Fig. 4. Axial slice (y = 12) showing the result of the searchlight analysis. Peak coordinates; left nucleus accumbens (x = −8, y = 16, z = 0, 55 voxels, average *r* at the peak = 0.089) and right nucleus accumbens (x = 8, y = 16, z = −6, 63 voxels, average *r* at the peak = 0.109). Colors represent *t* values based on one-sample *t*-test testing the strength of the correlation between High Monetary Reward and High Social Reward-Self conditions. Note that the left nucleus accumbens area slightly overlaps (i.e. 9 voxels) with the left caudate ROI (Figure 1).

each of these areas encode both abstract social reward as well as physical tangible reward and thus provide support for the 'extended common currency schema' (Ruff and Fehr, 2014).

Although significant, the size of the correlations between social and monetary rewards we found in the left caudate ROI and bilateral nucleus accumbens was fairly small (average $r = 0.069$–0.109; Figures 2B and 4), suggesting that only a small subset of neurons in these areas encodes both social and monetary rewards. This is largely consistent with previous neurophysiological studies. For example, Carelli and Wondolowski (2003) found on a single cell level only 8% of neurons in nucleus accumbens responded to both juice and drug rewards in rats, and Robinson and Carelli (2008) found that only 15% of nucleus accumbens neurons responded to both juice and ethanol (alcohol) in rats, whereas Bowman *et al.* (1996) found no neurons (0%) in the ventral striatum responded to both juice and drug rewards in monkeys. More recently, Klein and Platt (2013) presented social images (e.g. hindquarters of female monkeys) as reward to monkeys and found that only 6% of striatal neurons encoded information about both juice reward and social images. Thus, although largely distinct populations of neurons encode different types of reward, there exists a small population of neurons that commonly encode different types of rewards in the striatum. This study further suggests that in the human striatum, there may be the same population of neurons that encode tangible reward and highly abstract social reward of good reputation formed by other people.

Additionally, it may also be noteworthy that we observed that receiving high social reward (i.e., the High Social Reward-Self condition) as well as viewing others receiving low social reward (i.e., the Low Social Reward-Other condition) evoked similar activation patterns across the four striatal ROIs (Figure 3). One speculation at this point may suggest similar neural processes occur for social reward and also for the concept of schadenfreude. This falls in line with previous works that reported striatal activation in response to schadenfreude (Takahashi *et al.*, 2009; Cikara *et al.*, 2011) and may suggest a shared neural representation between experiences of schadenfreude and good reputation. Schadenfreude in this sense could suggest a form of reputation management. As social beings flourishing in groups we always have to ensure our place is secure, therefore heightening our own social reputation induces reward, but it may also be that having another more 'highly ranked' individual's reputation lowered would still give us the rewarding feeling of amplifying our own group status (in relativity). Aside from this explanation being speculative at this stage, it should also be noted that for Low Social Reward-Other, the result was only significant in two out of four ROIs for the within-condition analysis indicating that activation patterns evoked in this condition are not very consistent. Thus, future research should aim to further dissect this fascinating relationship.

Conclusion

In summary, though there have been somewhat discrepant results regarding the encoding of different types of reward in neuroimaging, our results via MVPA suggest that there exists a small population of neurons that commonly encode different types of rewards in the striatum, and this study further suggests that in the human striatum, there may be the same population of neurons that encode tangible reward and highly abstract social reward of good reputation formed by other people. This suggests that the brain processes social *vs* non-social information similarly. Additionally, finding similar neural patterns when participants experience high social reward compared to viewing others receiving low social reward also suggests a potential for similar populations of neurons responsible for processing two different types of social reward (good reputation and schadenfreude). These findings provide an important perspective to some previous research, and help to further illuminate the mechanisms behind social *vs* non-social cognition.

Conflict of interest. None declared.

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