Reward Enhances Connectivity between the Ventral Striatum and the Default Mode Network

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Acknowledgments

This work was supported, in part, by National Institutes of Health grants R21-MH113917 (DVS), R03-DA046733 (DVS), RF1-AG067011 (DVS). We note that DVS was a Research Fellow of the Public Policy Lab at Temple University during the preparation of this manuscript (2019-2020 academic year).

Conflict of interest statement

The authors have no conflicts to disclose.

Data and code availability

Statistical maps can be found on NeuroVault. Analysis code can be found on https://github.com/DVS-Lab/dmn-reward.

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Abstract

One of the central topics in cognitive neuroscience revolves around understanding how responses in the default mode network (DMN) relate to cognitive process and disease states. While there has been many investigations of the intrinsic patterns of activation and connectivity of the DMN with other networks at rest, i.e. when an individual is not engaged in any particular behavior, to truly understand the influence and significance of the DMN activation and connectivity, we must study it in association with a particular process. Reward processing is an integral part of goal-directed behavior that has been shown to rely on the striatum, a subcortical brain region that is connected to multiple regions of the prefrontal cortex (PFC) that belong to the DMN. Yet, it remains unclear how the DMN interacts with the striatum during reward processing. To investigate this issue, we analyzed card-guessing task data of 453 subjects from the Human Connectome Project and applied a novel network-based psychophysiological interaction analysis (nPPI) that quantified reward-dependent connectivity of the DMN. We show that only the DMN exhibits increased connectivity with the ventral striatum (VS) during the receipt of reward. This result was specific to the DMN and the strength of connectivity was associated with the personality characteristic of openness. These findings point to a novel role of the DMN during reward processing, and to the nPPI approach being able to capture a unique contribution of a collection of regions to task performance.

Significance

The default mode network (DMN) has been theorized to participate in a range of social, cognitive, and affective functions. Yet, previous accounts do not consider how the DMN contributes to other brain regions depending on psychological context, thus rendering our understanding of DMN function incomplete. We addressed this gap by applying a novel network-based psychophysiological interaction analysis to the reward task within the Human Connectome Project. We found that the experience of reward enhances task-dependent connectivity between the DMN and the ventral striatum. Surprisingly, the strength of connectivity was correlated with personality characteristics relating to openness. These results advance models of DMN by demonstrating how it contributes to other brain systems and how those contributions relate to individual differences.

Introduction

A cardinal goal of neuroscience relates to characterizing how functional integration organizes discrete brain regions into cohesive networks that shape behavior (Park & Friston, 2013). Several distinct networks have been identified in both resting and task states (Smith et al., 2009). Of these networks, the default mode network (DMN)—including the posterior medial cortex, medial prefrontal cortex, and lateral temporal-parietal regions—may be unique in its elevated baseline energy consumption (Buckner et al., 2008; Buckner & DiNicola, 2019; Raichle et al., 2001). Activation of the DMN appears to be highest when participants are engaged in inward-directed thought and lowest when participants are engaged in externally-directed tasks requiring focused attention (Hasenkamp et al., 2012; Hayden et al., 2009; Scheibner et al., 2017). In addition, the degree of task-related deactivation has been linked to performance (Anticevic et al., 2010; Vatansever et al., 2015), suggesting a key role for the DMN in shaping behavior. Despite these advances, we still know very little about how task-related changes in DMN are linked to changes in effective connectivity with other brain regions.

Many studies have investigated the function of DMN through the lens of individual differences. These studies have helped establish that the DMN is linked to disease and psychopathology (Anticevic et al., 2012; Dobryakova et al., 2018). For instance, individuals at risk for developing Alzheimer's Disease exhibit elevated intrinsic correlations within the DMN (Filippini et al., 2009). Elevated intrinsic activity within the DMN has also been shown in schizophrenia and depression (Whitfield-Gabrieli & Ford, 2012). These psychopathologies have also been linked to aberrant patterns of resting-state functional connectivity within the DMN. For example, individuals with schizophrenia show reduced resting-state functional connectivity between the DMN and the striatum (Wang et al., 2015). Similar effects have also been observed in individuals at risk for psychosis (Hua et al., 2019). Although altered DMN-striatal connectivity has also been observed in depression, the results are more mixed, with some studies suggesting hypoconnectivity (Bluhm et al., 2009), while other studies suggesting hyperconnectivity during resting state (Hwang et al., 2016).

Building on these findings, other studies have begun to point to a key link between the DMN and the striatum. For example, one study using physio-physiological interaction analyses

demonstrated that the striatum interacts with the salience network and DMN (Di & Biswal, 2014). Other studies have shown that striatal dopamine levels are linked to the magnitude of DMN deactivation during visuospatial attention (Tomasi et al., 2009) and tasks requiring cognitive flexibility (Dang et al., 2012). In addition, DMN responses have also been associated with gamma oscillations in the striatum, which may serve to facilitate switching between externally-driven and internally-driven brain states (Nair et al., 2018). While these observations illustrate some indirect relationships between the DMN and the striatum, it remains unclear whether there are direct contributions from the DMN to the striatum during a task. Observing this type of functional coupling would lend support to the emerging idea that a key function of the DMN resides with guiding goal-directed behavior and value-based decision making (Dohmatob et al., 2020).

To further investigate this possibility, we examined connectivity with the DMN during a reward processing task. We hypothesized that the psychological context of reward consumption would alter effective connectivity between the DMN and the striatum. We used data from the Human Connectome Project and applied a network-based psychophysiological interaction (nPPI) analysis (Fareri et al., 2020; Utevsky et al., 2017). This analytical approach merges canonical PPI analyses (Friston et al., 1997; McLaren et al., 2012; Smith et al., 2016) with dual-regression analysis (Filippini et al., 2009; Nickerson et al., 2017; Smith et al., 2014) to assess how networks interact with other regions as a function of task context. Our analyses focused on two key questions. First, does the receipt of reward drive connectivity between the DMN and striatum? Second, if there is reward-dependent connectivity between the DMN and striatum, is it associated with behavior and personality characteristics that are functionally relevant to reward processing?

Methods

Participants

We obtained behavioral and neuroimaging data of 495 subjects from the Human Connectome Project (HCP; www.humanconnectome.org), an open-access database aimed at collecting

healthy participant data from over 1,200 people. Although recent work has shown that effect sizes for reward-related striatal activation in the HCP is modest with a median d = 0.40 (Poldrack et al., 2017), we anticipated effect sizes associated with connectivity would be much smaller. Yet, even with a smaller expected effect size, we reasoned that a subsample of at least 376 participants would be sufficient for detecting small effects (d = 0.20) with 90% power and a two-sided paired t-test with alpha = 0.01. While less is known about the effect sizes for individual differences in brain-behavior relationships, there is good reason to believe such effects are generally small. For example, a recent examination of 87 meta-analyses on individual differences revealed a median r = 0.19 (Gignac & Szodorai, 2016). Detecting this effect with 90% power and alpha = 0.01 would require at least 405 participants. Within our subsample of 495 participants, ages ranged from 22 to 35 years old (Barch et al., 2013).

Because of technical difficulties and excessive head motion, 457 out of the 495 downloaded subjects were used in the final analysis (see below for details). Within this sample, familial relationships were unknown for 4 individuals (including on participant without NEO scores); these participants were excluded from our analysis since it was impossible to account for family structure (Winkler et al., 2014). After all exclusions, our final sample consisted of 453 participants (females = 270).

Behavioral Paradigm

Participants completed a card-guessing task adapted from previous work (Delgado et al., 2000) where they had to guess whether the number on a facedown card was higher or lower than 5. Following their response, participants were presented with one of three feedback options: 1) a green up arrow indicating a correct guess resulting in a gain of $1.00; 2) a red down arrow indicating an incorrect guess resulting in a loss of $0.50; or 3) a gray double-headed arrow for neutral trials. Stimuli were presented in blocks of eight trials. Trial blocks were either mostly reward or mostly loss, including six of the main conditions and two randomized trials from the remaining conditions. Each condition lasted 28 sec. Two runs were completed, composed of 2 mostly reward, 2 mostly loss, and 4 randomly placed fixation blocks. The facedown card with a

"?" was presented for up to 1.5 sec, with 1 sec allotted for feedback and a 1 sec ITI for the presentation of a fixation cross. All participants received standardized monetary compensations after completing the task. See Barch et al., (2013) for more details.

fMRI preprocessing

Our data preprocessing and analysis was carried out using FMRIB Software Library tools (v6.00; www.fmrib.ox.ac.uk/fsl). For the analyses in the current paper, we used the minimally preprocessed data, the end product of the volume-based fMRI pipeline, which were motion corrected and normalized to the MNI template (Glasser et al., 2013). We excluded 31 subjects whose average relative volume-to-volume motion qualified as an outlier relative to other subject; we identified outlier subject using a standard boxplot threshold (i.e., the 75th percentile plus 1.5*Interquartile Range (IQR); IQR for right-to-left phase encoding scan: 0.154; IQR for left-to-right phase encoding scan: 0.174). We excluded an additional 7 subjects due to technical difficulties (e.g., corrupt downloads).

Further we removed the first 15 volumes to achieve steady state magnetization; and applied spatial smoothing with a 4 mm full-width at half-maximum (FWHM) Gaussian kernel. The output of the preprocessing was further processed with ICA-AROMA (Pruim et al., 2015), which removed motion components from the dataset and output a de-noised dataset that was further temporally filtered (high-pass temporal filtering 90 sec).

fMRI analysis

Statistical analysis was carried out using FILM pre-whitening with local autocorrelation correction (Woolrich et al., 2001). We constructed five models to evaluate reward processing and to evaluate reward-dependent connectivity of the 4 RSNs (corresponding to the DMN and 3 other RSNs whose regions are structurally connected to the striatum: ECN, lFPN, rFPN). All networks were taken from prior work (Smith et al., 2009). The reward and punishment blocks that lasted for 28 sec were used as regressors and were convolved with the double-gamma hemodynamic response function (HRF). We constructed four generalized network PPI (nPPI) models (McLaren et al., 2012) with 14 regressors in each model. In addition to the reward and

punishment regressors, following regressors of interest were included in nPPI model: RSN time course, reward x RSN time course interaction, and punishment x RSN time course interaction. For the PPI regressors, we set the minimum value of the psychological regressor to zero, and de-meaned the physiological regressor (RSN time course). To control for the influence of other networks, we included the time courses of all the other 9 RSNs as regressors of no interest. To average contrast estimates over runs within each subject, we carried out a fixed effects analysis by forcing the random effects variance to zero in FLAME (FMRIB's Local Analysis of Mixed Effects) (Beckmann et al., 2003; Woolrich et al., 2004).

We assessed statistical significance of group results using PALM (permutation analysis of linear models), a nonparametric permutation-based cluster-extent thresholding method, with 5000 random permutations and with cluster-forming threshold set to $z > 2.3$ (Eklund et al., 2016; Winkler et al., 2014). We specifically used PALM because it allowed us to control for family structure, account for the effects of heritability that would make data points from related individuals non-independent, and restricts the number of time data can be permuted.

Network Identification and Extraction

To obtain an independent estimate of RSN connectivity during reward processing, we used the RSN maps from Smith et al. (2009) and ran spatial regression to extract whole-brain time courses associated with each RSN. Spatial regression was performed as part of dual-regression analysis (e.g. (Filippini et al., 2009; Gordon et al., 2012; Smith et al., 2015; Smith et al., 2014). The first step of the dual-regression analysis regresses the group spatial maps (RSNs in our case) on the functional data of each participant, and produces a time point by network matrix, which describes temporal behavior of each subject and network. The RSNs time course output from spatial regression was used to set up the PPI models (Figure 1).

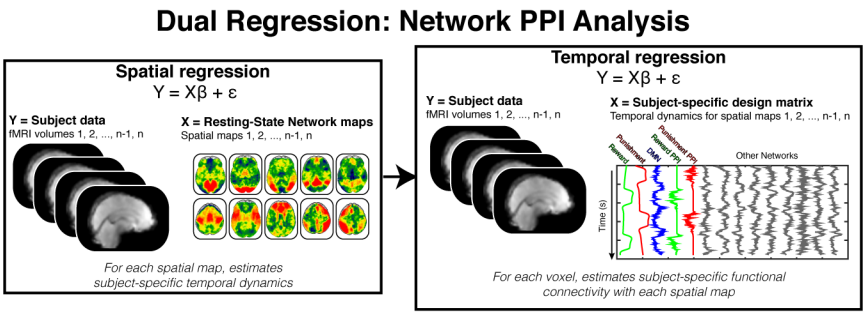

Figure 1: Analysis Schematic. *Our network psychophysiological interaction analysis (nPPI) approach builds off of the dual-regression approach in that in consists of two key stages. In the first stage, the functional data from each participant is regressed onto a set of spatial maps reflecting common networks found in both resting-state and task-based data. This spatial regression results in a set of subject-specific temporal dynamics for each network. In the second stage, the temporal dynamics for each network are included in standard general linear model along with the task regressors (temporal regression). Regressors corresponding to psychophysiological interaction terms are created by multiplying each task regressor by the network of interest (i.e., default mode network).*

Behavioral data

HCP provides rich behavioral data related to personality factors and cognition. However, we decided to focus on data related to impulsivity and personality as these constructs have been previously shown to be associated with PFC areas belonging to RSNs and striatal functioning (e.g. (Kunisato et al., 2011; Mitchell, 2011)) as well as with RSNs. To examine whether RSN connectivity during reward processing would show an association with cognitive and personality constructs we performed multiple regression analysis between behavioral measures obtained outside of the scanner and connectivity results. Specifically, we examined impulsivity as assessed by delayed discounting task and personality as assessed by Neuroticism/Extroversion/Openness Five Factor Inventory (NEO-FFI). We used area-under-the-curve discounting measure from the delayed discounting task as it provides a summary measure about the degree one discounts delayed rewards. From the NEO-FFI, a validated

personality inventory (Costa & McCrae, 2008), we used subscales that that assesses individual's degree of agreeableness, openness, conscientiousness, neuroticism, and extraversion. The regression included mean relative motion, NEO-FFI (agreeableness, openness, conscientiousness, neuroticism, extraversion), and discounting measures.

Results

Reward-Related activation

As a manipulation check, we examined whether there is differential activation in the striatum during reward processing. Consistent with prior studies using the card task (e.g., (Delgado et al., 2000; Tricomi et al., 2006), we observed that the receipt of reward in comparison to punishment, evoked greater activation in the striatum and other regions ($p>0.001$, $z > 3.1$, corrected for multiple comparisons; Table 1). This finding also furthers previously reported results from the HCP data (Barch et al., 2013). No regions survived the threshold during the punishment vs. reward comparison.

Table 1. Brain regions showing greater activation to reward vs. punishment.

Region	Number of Voxels	Hemisphere	Peak Z	Peak X	Peak Y	Peak Z
Occipital Pole	23088	R	16.1	14	-96	18
Ventral Striatum	4560	R	9.58	6	14	-2
Dorsomedial Prefrontal Cortex	2266	L	7.35	-44	8	32
Supramarginal gyrus	157	L	4.66	-50	-48	16
Amygdala/parahippocampal gyrus	114	L	4.75	-30	-10	-14
Supplementary Motor Area	107	L	5.1	-6	6	56

Posterior Lobe, Cerebellum	83	R	6.14	20	-42	-46
Paracingulate gyrus	65	L	4.34	-8	24	44
Putamen	48	R	4.96	28	-12	10
Parahippocampal Gyrus	48	L	5.19	-16	-30	-6
Parahippocampal Gyrus	39	R	4.94	8	-32	-4
Middle Temporal Gyrus	39	R	4.39	48	-10	-14
Caudate Tail	33	R	4.49	22	-18	24
Putamen	32	R	4.77	32	-10	-10

We also examined how reward and punishment modulated responses of the DMN. To do this, we extracted the network responses using the spatial regression component of dual regression analysis (Fareri et al., 2020; Nickerson et al., 2017; Smith et al., 2015). These network responses were then regressed onto a model containing the predicted hemodynamic responses for reward and punishment blocks. Consistent with prior work, we found that the DMN was strongly deactivated during the task (Figure 2; $t(453) = -75.31$, $p < 0.0001$), but the magnitude of deactivation did not significantly differ between reward and punishment blocks ($t(453) = 1.35$, $p = 0.1792$). For completeness, we also assessed task-related responses in other networks that have been theorized to play and antagonist role with the DMN (Fox et al., 2005; Uddin et al., 2009). These networks included the executive control network (ECN) and the left and right frontoparietal networks (lFPN and rFPN). Each of these networks exhibited a positive response to the task (ECN: $t(453) = 2.37$, $p = 0.0184$; lFPN: $t(453) = 24.11$, $p < 0.0001$; rFPN: $t(453) = 37.57$, $p < 0.0001$). Although the response to reward relative to punishment was larger in the ECN ($t(453) = 3.52$, $p = 4.7838e-04$) and the lFPN ($t(453) = 4.71$, $p = 3.3716e-06$), we found that the rFPN exhibited a larger response to punishment compared to reward ($t(453) = -2.55$, $p = 0.0110$). While some reward-related processes have been shown to be lateralized in some contexts (Palminteri et al., 2009), such differences are beyond the scope of our paper, as they could be driven by the single-handed button-press response procedure in the HCP.

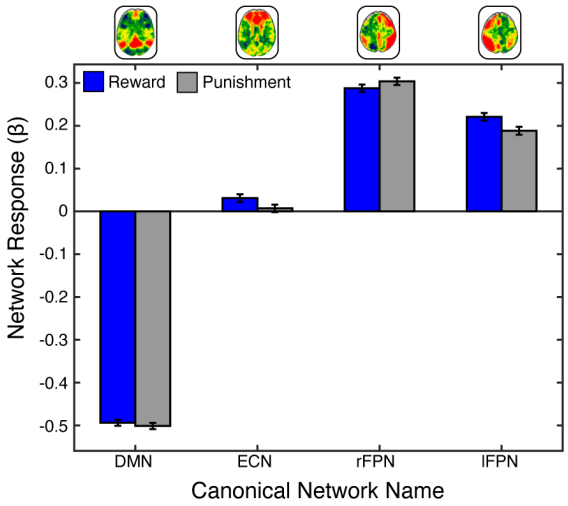

Figure 2. Network Responses to Reward and Punishment. We examined task-related responses for each network by regressing its activity onto a general linear model containing regressors for reward and punishment. We found that networks exhibited positive response to the task. As expected, we also found that the default mode network (DMN) was strongly deactivated during both reward and punishment. Abbreviations: DMN = default mode network; ECN = executive control network; rFPN = right fronto-parietal network; lFPN = left fronto-parietal network.

Reward Enhances Coupling Between the DMN and Ventral Striatum

Using the nPPI analysis, we examined reward-dependent connectivity of the DMN and the DMN showed increased connectivity with the left ventral striatum (VS) during the receipt of reward (relative to punishment) (Figure 3). Additionally, the DMN showed significant connectivity with the occipital pole and occipital fusiform gyrus. This result might suggest that the DMN is not simply a task-negative network but also has functional significance beyond self-referential processing and interacts with other brain regions engaged in task performance (the striatum during reward processing in the current analysis).

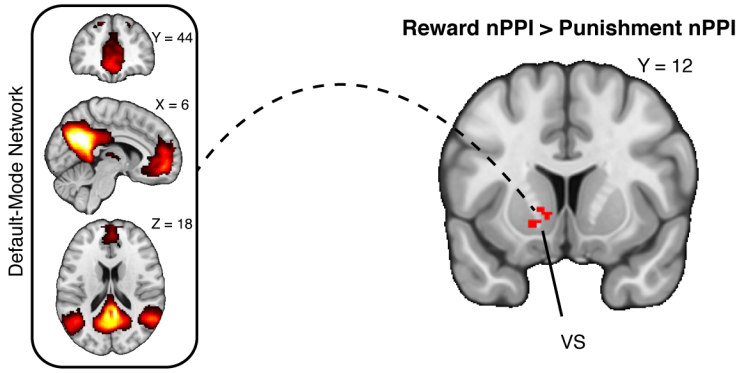

Figure 3: Enhanced Coupling between DMN and Ventral Striatum During Reward. We examined task-dependent changes with the DMN using a variant of psychophysiological interaction analyses. We found that an area of ventral striatum that exhibited increased connectivity with the DMN during reward relative to punishment.

Since the DMN has been shown to contribute to a spectrum of behaviors and psychological processes, we attempted to evaluate functional significance of DMN-VS connectivity by assessing whether discounting and personality measures are significant predictors of DMN-VS connectivity (Table 2). Results of the linear regression indicated that delayed discounting was not a significant predictor of DMN-VS connectivity. However, the constructs of openness (β=.138, p=.004) and agreeableness (β=-.124, p=.02) from NEO-FFI were significant predictors of DMN-VS connectivity. The NEO-FFI factor of openness has been shown to be related to sensation seeking and to reflect openness to experience, with low and high openness being characteristic of psychiatric disorders (Piedmont et al., 2009; Whiteside & Lynam, 2001). While there has been substantial research into the relationship of impulsivity (as measured by delayed discounting) with brain activity and connectivity (Chen et al., 2017) (Hobkirk et al., 2019; Li et al., 2013), investigations of the relationship between personality characteristics and brain activity/connectivity are in its early stages.

Table 2. Multiple regression analysis results

Predictors	Beta	t	p
NEO-FFI Agreeableness	**-0.124**	**-2.404**	**0.017**
NEO-FFI Openness to Experience	**0.138**	**2.881**	**0.004**

NEO-FFI Conscientiousness	0.043	0.803	0.422
NEO-FFI Neuroticism	-0.045	-0.841	0.401
NEO-FFI Extraversion	0.036	0.676	0.499
Delay Discounting Area Under the Curve for $200	0.031	0.48	0.631
Delay Discounting Area Under the Curve for $40,000	-0.035	-0.548	0.584
Pos > Neg activation	0.022	0.468	0.64
Mean Relative Motion	-0.03	-0.626	0.532

We conducted additional analyses to evaluating the specificity of DMN findings by examining the connectivity between the VS other networks. Repeated measures ANOVA on connectivity parameters from each network showed the DMN to have the strongest connectivity with the VS ($F(453,1)=17,122$, $p < 0.0001$). Post-hoc paired t-tests revealed that the DMN-VS connectivity was significantly greater than ECN-VS connectivity ($t=3.3$, $p<.005$), rFPN-VS connectivity ($t=5.8$, $p<.0001$), and lFPN-VS connectivity ($t=5.8$, $p<.0001$), pointing to the specificity of DMN-VS coupling during reward processing in comparison to other RSNs.

Discussion

With decision making and processing of action-outcome associations being vital in everyday life, it is imperative to understand the involvement of RSNs in these core processes, since they are purported to play an integral part in neural organization. Here, we examined the functional relationship between the DMN and processing of rewarding outcomes in a large sample of healthy individuals. Our findings demonstrate that the receipt of reward enhances connectivity between the DMN and the VS. This is consistent with a recent coordinate-based meta-analyses that documents an overlap between DMN and subjective value network regions that includes the VS (Acikalin et al., 2017). Further, increased DMN-VS connectivity is consistent with the nature of the card-guessing task. This task is not cognitively demanding, compared to a task that requires learning from rewards. Indeed, DMN has been shown to be engaged more during

effortless/automatic decision-making (Vatansever et al., 2017). We might see greater connectivity between the ECN and the VS during a more effortful and cognitively demanding task, such as a learning task, where rewards reflect performance feedback (Denkova et al., 2019). The goal of the card-guessing task is to win monetary rewards for oneself. Thus, our results can be interpreted in light of the DMN being shown to be engaged in self-referential processing (Acikalin et al., 2017; Gusnard et al., 2001). Reward processing during the card-guessing task can fall under the umbrella of self-referential processing as subjects are winning monetary rewards for themselves. Thus, our findings point to a novel role for the DMN in reward processing and communication with the striatum, extending previous research about DMN connectivity and its role in behavior.

Our analysis also revealed that the strength to the DMN-VS connectivity during reward processing is positively associated with the personality factor of openness and agreeableness. While we did not have any *a priori* hypothesis about the directionality of the association between connectivity and personality, we speculate that this result contributes to the growing body of literature that investigates brain correlates of various personality types in both healthy (Beaty et al., 2018; Sampaio et al., 2014; Wei et al., 2014) and clinical populations (Takahashi et al., 2013). Further, recently openness has been shown to be associated with increased functional connectivity and dopamine release from the substantia nigra (Passamonti et al., 2014; Suridjan et al., 2012), a subcortical brain area that is heavily involved in reward processing and projects to the striatum (Haber & Knutson, 2010).

Nevertheless, our results are also accompanied by limitations that merit further discussion. First, although our results may reflect a context-specific (reward receipt) modulation of effective connectivity from the DMN to the VS, such findings could also be explained by a modulation of stimulus-specific responses in the VS (Friston et al., 1997). Specifically, responses in the DMN may enhance the striatal response to reward without a change in connectivity. Future studies may be able to disambiguate these alternative explanations using dynamic causal modeling (Friston et al., 2003) or noninvasive brain stimulation (Polania et al., 2018). Second, it is not clear how our reported links between DMN-VS connectivity and openness would generalize to more diversified samples. Indeed, the HCP consists of healthy young adults,

which may contribute to the limited range in openness scores and relatively small effect size in the brain-behavior correlations (Yarkoni, 2009). Third, our results are limited to the narrow construct of reward consumption. Examining other domains of reward processing—including anticipation (Knutson et al., 2000), learning (Daw et al., 2011), and valuation (Arulpragasam et al., 2018)—may reveal other patterns of DMN-VS connectivity or connectivity with other networks (Hallquist et al., 2018). In a similar vein, it will be important for future work to examine how DMN-VS connectivity during reward processing is modulated by contextual factors, such as perceived control (Wang & Delgado, 2019), effort (Dobryakova et al., 2017), and social context (Fareri & Delgado, 2014).

Despite these caveats, our results support the conclusion that DMN plays an active role in shaping responses in the VS during the execution of a reward processing task. These results broaden our conceptualization of DMN function by going beyond simplistic activation/deactivation schemes and show how responses in other brain regions are influenced by the engagement of DMN. More efforts to understand the dynamic interplay between the DMN and other brain regions could lead to a more integrative and parsimonious view of its function (Dohmatob et al., 2020). Such efforts could also help understand how the DMN contributes to clinical syndromes such as schizophrenia (Hu et al., 2017), depression (Posner et al., 2016), and substance abuse (Zhang & Volkow, 2019), potentially providing new avenues for treatment and interventions.

Figure Captions

Figure 1: Analysis Schematic

Our network psychophysiological interaction analysis (nPPI) approach builds off of the dual-regression approach in that in consists of two key stages. In the first stage, the functional data from each participant is regressed onto a set of spatial maps reflecting common networks found in both resting-state and task-based data. This *spatial regression* results in a set of subject-specific temporal dynamics for each network. In the second stage, the temporal dynamics for each network are included in standard general linear model along with the task regressors (*temporal regression*). Regressors corresponding to psychophysiological interaction terms are created by multiplying each task regressor by the network of interest (i.e., default mode network).

Figure 2: Network Responses to Reward and Punishment

We examined task-related responses for each network by regressing its activity onto a general linear model containing regressors for reward and punishment. We found that networks exhibited positive response to the task. As expected, we also found that the default mode network (DMN) was strongly deactivated during both reward and punishment. Abbreviations: DMN = default mode network; ECN = executive control network; rFPN = right fronto-parietal network; lFPN = left fronto-parietal network.

Figure 3: Enhanced Coupling between DMN and Ventral Striatum During Reward

We examined task-dependent changes with the DMN using a variant of psychophysiological interaction analyses. We found that an area of ventral striatum that exhibited increased connectivity with the DMN during reward relative to punishment.

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