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Greater preference consistency during the Willingness-to-Pay task is related to higher resting state connectivity between the ventromedial prefrontal cortex and the ventral striatum

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Abstract

The significance of why a similar set of brain regions are associated with the default mode network and value-related neural processes remains to be clarified. Here, we examined i) whether brain regions exhibiting willingness-to-pay (WTP) task-related activity are intrinsically connected when the brain is at rest, ii) whether these regions overlap spatially with the default mode network, and iii) whether individual differences in choice behavior during the WTP task are reflected in functional brain connectivity at rest. Blood-oxygen-level dependent (BOLD) signal was measured by functional magnetic resonance imaging while subjects performed the WTP task and at rest with eyes open. Brain regions that tracked the value of bids during the WTP task were used as seed regions in an analysis of functional connectivity in the resting state data. The seed in the ventromedial prefrontal cortex was functionally connected to core regions of the WTP task-related network. Brain regions within the WTP task-related network, namely the ventral precuneus, ventromedial prefrontal and posterior cingulate cortex overlapped spatially with publically available maps of the default mode network. Also, those individuals with higher functional connectivity during rest between the ventromedial prefrontal cortex and the ventral striatum showed greater preference consistency during the WTP task. Thus, WTP task-related regions are an intrinsic network of the brain that corresponds spatially with the default mode network, and individual differences in functional connectivity within the WTP network at rest may reveal *a priori* biases in choice behavior.

Keywords

fMRI; value; preference; default mode network; ventromedial prefrontal cortex; ventral striatum

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Introduction

Assessing the expected value of a behavioral outcome is a critical aspect of goal-directed decision-making. The neural representation of this evaluative process can be identified with functional magnetic resonance imaging (fMRI) during performance of the willingness-to-pay (WTP) task, an auction paradigm which identifies the maximum expected value of individual consumer products (Becker et al., 1964). In the original food version of the WTP task, subjects bid for the opportunity to eat or to avoid eating a range of appetitive and aversive food items (Plassmann et al., 2007, Plassmann et al., 2010, Hare et al., 2011). It has consistently been shown using a range of different products and services that the value of bids in the WTP task is linearly related to the level of neural activity in a network of brain regions including the ventromedial prefrontal cortex (vmPFC) and ventral striatum (vStr) (Chib et al., 2009, Hare et al., 2010, Kang et al., 2011, Janowski et al., 2013). The localization of valuation related neural processes in the vmPFC and ventral striatum is supported by a broad body of evidence including human lesion (e.g. (Fellows and Farah, 2007), neuroimaging (e.g. (Erk et al., 2002, Paulus and Frank, 2003, McClure et al., 2004) and animal studies (e.g. (Berridge et al., 2009, Bouret and Richmond, 2010). However, other brain areas that are also reliably recruited during the WTP task, including cortex in the posterior cingulate (PCC), ventral precuneus (vPrC) and the inferior parietal lobule (IPL), have received less attention with regard to their potential contribution to value judgments (Clithero and Rangel, 2012).

There are many anatomical similarities between the WTP task-related network and the default mode network. The default mode network is defined as the set of brain regions that exhibit high metabolic activity relative to the rest of the brain when the subject is not engaged in an externally oriented task (Gusnard and Raichle, 2001). The default network is also an intrinsic network of the brain that is functionally connected at rest (Greicius et al., 2003). While the function of the default network has not been definitively established, it has been hypothesized that it may be the neural substrate of spontaneous cognition (“daydreaming”) as conceptualized by Singer and colleagues (Singer and Antrobus, 1963, Antrobus et al., 1966, Mason et al., 2007) or the mental simulation of self-relevant events which facilitates the anticipation and evaluation of future outcomes (Buckner et al., 2008). The brain regions typically associated with the default network, namely the vmPFC, the PCC and retrosplenial cortex, the vPrC, and the IPL (Greicius et al., 2003, Fox et al., 2005, Fransson, 2006, Uddin et al., 2009, Zhang and Li, 2012), resemble the WTP task-related network. Despite intensive research directed at understanding these neuroimaging phenomena separately, no study to date has sought to establish the anatomical comparability of the two networks and explore the functional significance of this relationship.

Here, we ask i) whether the brain regions that exhibit neural activity related to expected value during the WTP task are functionally connected at rest in the same subjects, ii) whether the identified valuation regions overlap spatially with the default mode network, and iii), since it has been hypothesized that intrinsic resting state networks may represent individual *a priori* cognitive biases (Harmelech and Malach, 2013), we also asked whether

intrinsic connectivity strength within the WTP valuation network might predict individual differences in behavior during the WTP task.

Materials and Methods

Subjects

Nineteen right-handed subjects (9 males and 10 females) participated in the experiment (mean age and standard deviation 31.5 ± 11 years). All aspects of the study were performed in accordance with the Declaration of Helsinki. Resting state data were not usable in one subject and task-related data were unusable in two other subjects due to technical issues during data acquisition.

Willingness-to-pay (WTP) Task

The WTP task is a modified Becker-DeGroot-Marshack auction which is designed to identify the subjective threshold between an option's anticipated value and its cost, i.e. the maximum amount an individual is willing to pay for an expected outcome (Becker et al., 1964, Plassmann et al., 2007). Subjects are provided with three 1 dollar bills that may be used to purchase the opportunity to eat or to avoid eating a series of visually presented food items (Figure 1). Response options range between positive three and negative three dollars in increments of one dollar (i.e. 3\$, 2\$, 1\$, 0, -1\$, -2\$, or -3\$). Positive and negative bids are made for appetitive (e.g. potato chips) and aversive foods (e.g. baby food), respectively. The subject is instructed that one trial will be selected for implementation at the end of the experiment and that their bid on that trial will compete with a random computer generated bid. For positive (appetitive) bids, if the subject bids more than the computer, he/she receives the purchased item and must pay the experimenter the amount of the bid. Otherwise the subject keeps the three dollars. For negative (aversive) bids, if the subject bids more than the computer (e.g. subject bids -3\$ and the computer bids -2\$), then the subject must pay the amount bid but is not required to eat the unwanted food item. Otherwise, the subject keeps the three dollars and must eat the food item. The optimal strategy for the subject is to treat each trial as if it were the one selected for implementation at the end of the experiment and to make the bid that most closely matches the maximum amount that they would be willing to pay to eat or to avoid eating the food.

The task was programmed and performed with Adobe Flash Professional CS5 (Adobe, Washington). Subjects bid on sixty unique items which were presented serially for four seconds each. There was a variable intertrial delay of 0–15 seconds (mean 8 seconds) during which a fixation cross was displayed. Once the subjects had entered bids on all sixty items, the trials were repeated in a different randomized order (i.e. total number of trials = 120). Images were displayed to subjects in the bore of the magnet by a back-projection system and responses were made on an MRI-compatible button box.

Several measures of behavior during the WTP task were calculated for each subject, namely the mean, standard deviation, skewness, and kurtosis of all bids (Table 1). Also, since each item was presented in two separate trials, a measure of *preference consistency* was

calculated as the correlation in value between the first and second presentation of the same item.

Data Acquisition

fMRI data sensitive to blood oxygenation level-dependent (BOLD) contrast were collected with a Discovery MR750 3 Tesla scanner (GE Healthcare, Milwaukee, Wisconsin) equipped with a 32-channel head-coil. Randomized fast-event related T2*-weighted echo planar imaging (EPI) scans [TR=2000 ms, TE=32 ms, FOV=230 mm², 64x64 matrix, 40 2.6mm axial slices with 1.4 mm gap, flip angle=90°] were obtained while subjects performed the WTP task. A high-resolution T1-weighted image [spoiled gradient recalled (SPGR), TR=8 ms, TE=3 ms, FOV=25 cm, ~1 mm³ voxels] was also obtained for anatomical reference. Resting-state data were acquired in the sagittal plane using a multi-echo simultaneous multi-slice (MESMS) data acquisition (Olafsson et al., 2012), where three slices are simultaneously excited for each of the three echoes collected to control for head motion (FOV 200mm²; matrix: 100x40; no gap between slices; TR=2000ms; TE1=15.5ms, TE2=36.7ms, TE3=57.9ms, flip angle=30; in-plane sensitivity encoded (SENSE) acceleration factor of 2.5). During the resting state scans subjects were instructed to focus on a visually presented fixation cross displayed on a black background and were told: “Try not to think about anything in particular.” Resting state data were acquired before subjects performed the WTP task.

Image Preprocessing

Functional and structural neuroimaging data were preprocessed with the Analysis of Functional Neuroimages (AFNI) software library (Cox, 1996). GE DICOM slices were reconstructed into AFNI BRIK format. EPI images were co-registered using a 3D-coregistration algorithm developed to minimize the amount of image translation and rotation relative to all other images. Voxels with abnormally large amplitudes were replaced by linear interpolation. Six motion parameters were obtained across the time series for each subject and subsequently used as nuisance regressors to accommodate EPI intensity changes due to motion artifacts. The functional echoplanar dataset was co-registered to the anatomical images and an outlier file was generated to determine if additional time points should be censored based on whether a given time point greatly exceeded the mean number of voxel outliers for the time series.

Statistical analysis

Analysis of the data was performed in two steps: 1) regions of interest (ROI) were identified by the WTP task; 2) these ROIs served as seeds to explore networks of intrinsic functional connectivity in the resting state data.

Step 1 Localization of WTP task-related ROIs

The preprocessed images were analyzed using a multiple regression model. Three regressors of interest (i.e. positive, negative and neutral bids during the WTP task) were generated by convolving the time series of the events with a modified hemodynamic response function. Baseline and motion regressors representing small head movements and linear drift were

also included in the model. A linear contrast was produced by subtracting percent signal change from baseline during negative bids from percent signal change during positive bids. To account for individual anatomical differences, the contrast image was spatially blurred with a Gaussian blur (4mm FWHM) before automated transformation to MNI-space. Voxelwise one sample t-tests on the positive minus negative contrast images were used to produce a 3-dimensional statistical parametric map. Voxels were thresholded at $t_{16} = 2.92$, $p=0.01$. To control for multiple comparisons, an additional cluster-size threshold of 7 contiguous voxels (448 μ L) as determined by a Monte Carlo simulation (AFNI, AlphaSim) was used so that brain regions meeting these two criteria had an *a posteriori* probability of $p < 0.05$. Nine ROIs, which represent value during the WTP task and correspond to brain areas expected on the basis of a meta-analysis of subjective value (Clithero and Rangel, 2013), were identified (i.e. clusters 2–7 & 9–11 in Table 1).

Step 2 Functional connectivity analysis of resting state data

To determine whether the WTP task-related network is intrinsically connected at rest, the nine ROIs identified by the WTP task in step 1 were used as seeds in separate resting state functional connectivity analyses. The remainder of this article focuses on the functional connectivity of the vmPFC seed, although the results of analyses using the other seeds are reported in Supplemental Materials. In the resting state data, Pearson correlations were calculated between the whole brain four-dimensional residuals and the average time-series for each seed (Jo et al., 2010). The resulting correlation coefficients were transformed to Fisher's Z-scores and blurred with a Gaussian blur (4mm FWHM) to accommodate individual anatomical variability. Since we were interested specifically by network coherence and the spatial overlap with the WTP task-related network, only positive correlations are reported here. Parametric statistical maps were generated by voxelwise one-sample t-tests on the Z-scores. Significance was determined as described in step 1 (i.e. clusters of 7 or more significant voxels ($t_{16} = 2.92$ $p=0.01$) had an *a posteriori* probability of $p < 0.05$).

In addition to this whole-brain analysis, the average Z-score was extracted in each of the 9 ROIs identified by the WTP task in step 1 to examine directly whether the WTP task-related ROIs are intrinsically connected at rest with the vmPFC seed. The average Z-score for each ROI was assessed for significance by one sample t-test (SPSS v.20, IBM).

Overlap with the Default Mode Network

The amount of overlap was determined between i) the WTP task-related regions or ii) the network of regions intrinsically connected to the vmPFC seed and publically available templates <http://fsl.fmrib.ox.ac.uk/analysis/brainmap+rsns/> identifying the default mode network with independent components analysis (ICA) (see cluster 4₂₀ in Smith *et al.*, 2009) in i) resting state data and ii) a large database of fMRI and PET studies (BrainMap) containing data from 29,761 subjects. The resting state and BrainMap ICA maps corresponding to the default mode network, were thresholded at $z=3$ as reported in the original publication (Smith et al., 2009).

Exploration of Behavioral Correlations

Behavioral correlations were also examined to determine whether WTP task-related activity or resting state intrinsic connectivity predict individual differences in behavior during the WTP task. Since several of the behavioral measures calculated on the basis of subjects' responses to the WTP task were highly collinear (i.e. the mean value of all bids correlated strongly with skewness while preference consistency correlated strongly with standard deviation and kurtosis), only individual differences in the mean value of bids and preference consistency were examined in relation to the neuroimaging data. The average percent signal change within each of the nine identified ROIs, namely clusters 2–7 & 9–11 in Table 1, was extracted from the linear contrast image (i.e. positive minus negative bids) created in step 1. Spearman rank-order correlations between the average value within the nine WTP task-related ROIs and the two behavioral measures (i.e. mean value and preference consistency) were examined. A Bonferroni correction for multiple comparisons was applied to the significance threshold, $p = 0.05/10 = 0.005$. Significant correlations between WTP task-related activity and preference consistency provided *a priori* hypotheses to be tested on the average z-scores extracted from the brain regions whose activity significantly correlated with the vmPFC seed in the independently sampled resting state data.

Results

Behavior

The percentage of responses at each level of bidding (−\$3 to +\$3) was relatively uniform, ranging from 8% to 22% of trials (Figure 1). Participants did not endorse more positive than negative bids (paired $t_{16} = 0.1$, $p = 0.9$). The reaction time during all positive bids was slightly longer than during all negative bids (paired $t_{16} = -2.5$, $p = 0.02$). The mean overall bid value was −\$0.2 (s.d. ± 0.7) and the mean overall preference consistency was $r = 0.86$ (s.d. ± 0.14). The average difference between bids on identical items across all subjects was \$0.47 (s.d. ± 0.28).

Step 1. What brain regions track the value of bids during the WTP task?

The statistical contrast between percent signal change associated with positive and negative bids identified several brain regions that track the value of bids during the WTP task (Table 1) (Figure 2). The nine brain regions including vStr, vmPFC, PCC, and vPrC that are typically observed in neuroimaging studies of subjective value (Clithero and Rangel, 2013) are marked with an arrow in Table 1.

Step 2. Is the WTP task-related network also intrinsically connected at rest?

The nine ROIs identified by the WTP task in step 1 were used as individual seeds in separate functional connectivity analyses. Clusters of significant positive functional connectivity are displayed in Table 2 for the vmPFC seed and in Supplemental Materials Tables 3–10 for all other seeds. Figure 3 illustrates the location of voxels that track value during the WTP task and are intrinsically connected with the vmPFC seed at rest. These voxels were found in the vmPFC, PCC, and medial frontal polar (mFP) region. With the IPL, the vmPFC seed is intrinsically connected at rest with cortex on the angular gyrus (cluster 3, Table 2) just

posterior to the region on the supramarginal gyrus that represents value during the WTP task (cluster 9, Table 1). The connectivity of the vmPFC seed at rest specifically with each of the ROIs identified in step 1 is plotted in Figure 3. One-way t-tests indicated that expected positive functional connectivity was significantly greater than zero in the right vStr, left mFP, right PCC, left vStr, left dorsomedial prefrontal cortex, and right PCC ROIs, $p < 0.05$.

Overlap with the Default Mode Network

Several WTP task related regions overlapped spatially with the default mode network as identified by ICA (Smith et al., 2009) in an independent sample of resting state data (Table 3) and a large database of functional neuroimaging studies (BrainMap) (supplemental Table 12). Similarly, several regions intrinsically connected to the vmPFC seed in resting state data overlapped spatially with the default mode network as identified by ICA in an independent sample of resting state data (Table 3) and a large database of functional neuroimaging studies (BrainMap) (supplemental Table 12). Regions of overlap include the vmPFC, mFP, PCC and vPrC.

Behavioral Correlations. Does WTP task-related activity or resting state intrinsic connectivity predict individual differences in behavior?

Due to the high collinearity between several behavioral variables only two were examined with respect to the neuroimaging data: mean bid value and preference consistency (see Methods). An outlier on the preference consistency measure identified graphically and confirmed by Dixon's Q-test was removed. Preference consistency was negatively correlated with mean percent signal change within the right and left vStr and right PCC ROIs identified by the WTP task ($\rho = -0.51$, $\rho = -0.56$, and $\rho = -0.60$, respectively, $p < 0.05$) i.e. neural activity in the left vStr and right PCC tracked the value of bids more closely in individuals that were the least consistent in their valuation of the same items on different trials. Based on this correlation in the task-related data, it was predicted in the independently obtained resting state data that vStr and PCC ROIs identified by the vmPFC seed would also be correlated with preference consistency. Indeed, the connectivity between the vmPFC seed and the right vStr ($\rho = 0.65$) but not the left vStr or PCC ROIs in the resting state data was significantly correlated with preference consistency, $p < 0.01$.

Discussion

The WTP task recruits a circumscribed neural network which includes the vmPFC, mFP, PCC, and vPrC. It has been shown here that this valuation related network is i) intrinsically connected at rest (Figure 2) and ii) overlaps spatially with the default mode network (Table 3). An interesting exception to this is found within the IPL: the region representing the value of bids during the WTP task (supramarginal gyrus) is located just anterior to the IPL region that is connected to the vmPFC seed at rest (angular gyrus). Importantly, those individuals with higher resting state connectivity between the vmPFC and vStr exhibited greater preference consistency (Figure 5) which indicates that functional connectivity may be used to predict individual differences in choice behavior.

Preference consistency reflected in brain activity at rest

It has been hypothesized that the structure of spontaneous brain activity at rest represents the reactivation of neuronal networks formed by prior mental experience (Harmelech and Malach, 2013). As a consequence, functional activity at rest might provide a measurable marker of the *a priori* cognitive and emotional biases that collectively shape an individual's unique set of personality characteristics and cognitive traits. Several studies have demonstrated the existence of this relationship between resting state connectivity and behavior (e.g. (Coste et al., 2011, Koyama et al., 2011, Baldassarre et al., 2012). The present study is also consistent with the network reactivation hypothesis in finding that individual differences in connectivity of the vStr with the vmPFC are related to preference consistency. Those individuals with greater functional connectivity between the vmPFC seed and the right vStr exhibited greater consistency in their valuation of the same objects on separate trials. Temporally stable representations of preference may depend upon the functional integration of the vStr and vmPFC.

It is possible that variation in the preference consistency measure might not represent fluctuations in subjective value over time but rather could be due to difficulties in expressing a continuous range of subjective value in terms of discrete dollar increments, i.e. the range of subjective value is more nuanced than the scale used to express it. Indeed, the small average difference between bids across all subjects, \$0.47 (s.d. $\pm$ 0.28), is consistent with both possibilities. Using an alternate measure of preference consistency e.g. violations of transitivity in a binary forced choice task (Lee *et al.*, 2009), would not necessarily resolve this issue. If differences in the subjective value of the paired items in the forced choice task were small or negligible a similar confound could arise between the expression of value and actual fluctuations in subjective value over time. Interestingly, manipulations that emphasize emotional processing of stimuli in a forced choice task result in fewer violations of transitivity (Lee *et al.*, 2009). Since the VS and vmPFC have been implicated in the both valuation processes (Clithero and Rangel, 2012) and the regulation of emotion (Ochsner and Gross, 2005), the present findings may offer insight on the neural mechanisms mediating the role of emotion in preference consistency. This hypothesis could be addressed in a future study that also included a measure of trait or state differences in the awareness of emotions during decision-making.

From a psychiatric research perspective, the possibility that *a priori* valuation biases could be determined from resting state data would be useful in the study and treatment of psychiatric diseases that are known to involve abnormal valuation processing related to goal-directed behavior, such as substance use disorders and depression (Paulus et al., 2009, Dillon et al., 2014), both of which have been associated with vmPFC dysfunction (Mayberg et al., 2005, Verdejo-Garcia and Bechara, 2009, Mackey and Paulus, 2013). As a potential diagnostic tool in psychiatry, resting state connectivity has a significant advantage over behavioral tasks because there are no task-related learning effect across multiple scan points that could interfere with the interpretation of results. Future research will be needed to examine group differences (e.g. depressed or substance dependent patients vs. healthy controls) in the relationship of preference structure to resting state connectivity in brain regions associated with valuation such as the WTP task-related network.

Inferior parietal cortex

Although there was substantial overlap between the WTP task-related network and the default mode network as defined by an ICA of resting state data and a large database of functional neuroimaging studies (BrainMap), it was also shown here that the IPL region (angular gyrus) connected at rest to the vmPFC seed is not the same IPL region (supramarginal gyrus) that represents value during the WTP task. It is unlikely that this finding is the result of individual anatomical variability since the resting state and task-related data were collected in the same individuals. Diffusion tractography and resting state functional connectivity indicate that differential connectivity patterns distinguish these two parts of the human IPL and resemble the connectivity of comparable regions of the macaque brain as established by physiological tract tracing studies (Mars et al., 2011). Several studies have linked the posterior IPL with attentional control and salience in visual tasks (Mevorach et al., 2006, Leathers and Olson, 2012). Liljeholm and colleagues have suggested that cortex within the anterior IPL on the supramarginal gyrus may be involved in the control of strategic switching between habit-based and goal-directed decision-making dependent on their differential outcome probabilities (Liljeholm et al., 2013).

Study Limitations

Several factors limit the interpretation of the current findings. The sample size was relatively small which may impact the representativeness of the sample and replicability of the findings. Negative correlations in the functional connectivity data were not explored because the study focused on the positive relationship between the WTP task-related network and the default mode network. A tentative explanation for the correlation within individuals of preference consistency with the functional connectivity between the vmPFC and the vSTr was proposed here, however, the significance of intrinsic connectivity and the default mode network are still intensely debated (Buckner et al., 2008, Uddin, 2013). Although the correspondence is not identical, resting state functional connectivity is similar to structural connectivity established by physiological tracer studies in the macaque monkey and diffusion tensor imaging in humans suggesting that the default network partially reflects the underlying anatomy (Vincent et al., 2007, Damoiseaux and Greicius, 2009, Margulies et al., 2009).

Conclusion

The valuation related network identified by the WTP task is an intrinsic network of the brain active during periods of rest and corresponds spatially with the default mode network. Individual differences in functional connectivity within the WTP network at rest reveal *a priori* biases in choice behavior that may ultimately be a useful as biomarker in psychiatric diseases of valuation.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Abbreviations

IPL	inferior parietal lobe
mFP	medial frontal polar
PCC	posterior cingulate cortex
vmPFC	ventromedial prefrontal cortex
vPrC	ventral precuneus
vStr	ventral striatum
WTP	willingness-to-pay

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Figure 1. Schematic diagram (left) of one trial of the WTP task and bar graphs (right) representing the percentage of trials each bid level was selected (top) and the average reaction time for each bid level (bottom). The reaction time for the zero bid is not represented in the lower graph because subjects were not required to make a response for the zero option.

Figure 2.

Red circles indicate several regions that track linearly the value of bids during the WTP task: (from left to right) ventral striatum, ventromedial prefrontal cortex, posterior cingulate cortex and ventral precuneus. Graphs represent percent signal change in BOLD signal during positive (+) and negative (-) bids.

Figure 3.

Conjunction mask (left) showing voxels in the vmPFC, mFP and PCC that exhibit WTP task-related activity AND are intrinsically connected to the vmPFC seed at rest in whole brain analyses. Bar graph (right) showing functional connectivity at rest of the vmPFC seed specifically with the WTP task-related ROIs. ROIs were identified in Step 1. Asterisks signify $p < 0.05$.

Figure 4.

Coronal brain section (left) to show the location of task related ROI in the left vStr ROI circled in red. Scatterplot (right) illustrating that individuals with higher intrinsic connectivity between the vmPFC seed and the right vStr also exhibit greater preference consistency (Spearman $\rho = 0.65$).

Table 1

WTP task-related regions (Step 1)

Brain Region		Coordinates			Size (voxels)
		X	Y	Z	
1	R. Lingual Gyrus	6	-74	-14	12
→ 2	R. Ventral Striatum/Anterior Caudate and Posterior Ventromedial Frontal Cortex (Area 25)	6	15	-4	11
→ 3	L. Medial Frontal Polar Cortex (Area 10)	-1	58	12	11
→ 4	L. Posterior Cingulate Gyrus	-3	-35	38	11
→ 5	L. Ventromedial Prefrontal Cortex (Area 14m)	-8	43	1	9
→ 6	L. Gyrus Rectus (Area 14r)	-14	27	-14	7
→ 7	L. Anterior Caudate and Subgenual Cingulate Gyrus (Area 24)	-6	18	5	7
8	L. Dorsomedial Frontal Cortex	0	48	19	7
→ 9	R. Supramarginal Gyrus	62	-34	32	7
→ 10	R. Posterior Cingulate Gyrus	1	-45	39	7
→ 11	L. Precuneus	-2	-66	39	7

Regions expected on the basis of a meta-analysis of subjective value (Clithero and Rangel, 2013) are indicated with an arrow. Arrowed regions were used as the seed regions in step 2. Coordinates represent the location of the peak value in MNI-space. Architectonic area labels for regions within the ventral frontal cortex are based on Mackey and Petrides (2010).

Table 2

vmPFC seed (step 2)

	Brain Region	Coordinates			Size (voxels)
		X	Y	Z	
★1	L. Ventromedial & Polar Frontal Cortex	-6	40	6	248
2	L. Angular Gyrus	-42	-73	31	56
3	R. Angular Gyrus	46	-69	31	46
★4	L. Posterior Cingulate Cortex	-2	-32	38	34
5	R. Posterior Cingulate Cortex & Ventral Precuneus	6	-52	36	25
6	R. Dorsomedial Frontal Cortex	6	39	33	12
7	L. Superior Frontal Gyrus	-14	37	59	12
8	L. Posterior Cingulate Cortex & Ventral Precuneus	-14	-64	14	11
9	L. Superior Temporal Gyrus/Posterior Insula	63	-22	3	9
10	L. Middle Frontal Gyrus	-30	21	62	9
11	L. Middle Frontal Gyrus	-42	17	53	8

Brain regions that are intrinsically connected with the vmPFC seed at rest. Those regions that also spatially overlap the WTP task-related ROIs (reported in Table 1) are marked with a ★. Coordinates represent the location of the peak value in MNI-space.

Table 3

Spatial overlap of default mode network identified by ICA in a resting state functional connectivity database (cluster 4₂₀ in Smith *et al.* 2009)

Brain Region	Coordinates			Size (voxels)
	X	Y	Z	
With WTP task-related ROIs				
1 L. & R. Medial Frontal Polar Cortex	0	56	12	9
2 L. & R. Posterior Cingulate Cortex	−1	−34	36	7
3 R. Posterior Cingulate Cortex	1	−45	39	7
4 L. & R. Ventral Precuneus	−2	−66	39	7
5 L. Ventromedial Prefrontal Cortex	−7	45	2	6
6 L. & R. Dorsomedial Prefrontal Cortex	0	50	20	4
7 L. Ventromedial Prefrontal Cortex	−10	40	−5	2
8 L. & R. Dorsomedial Prefrontal Cortex	0	44	15	2
With vmPFC seed network at rest				
1 L. & R. Ventromedial Prefrontal Cortex	−1	48	6	122
2 L. Angular Gyrus	−41	−73	35	54
3 R. Angular Gyrus	46	−70	35	34
4 R. Posterior Cingulate Cortex	1	−37	34	30
5 R. Ventral Precuneus	9	−58	26	25
6 L. Ventral Precuneus	−14	−63	13	11

Coordinates represent the location of the center of mass in MNI-space.