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The neuroanatomical correlates of individual differences in delay discounting: A voxel-based morphometry study

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Abstract

Delay discounting refers to the reduction in the present value of a future reward as the delay to that reward increases, which is related to various problematic behaviors, such as substance abuse. In this study, we explored the neuroanatomical correlates of delay discounting by employing voxel-based morphometry and the individual difference approach. We found that participants' delay discounting, measured by the Monetary Choice Questionnaire, was correlated with the gray matter volume (GMV) of two cortical regions. On the one hand, individuals with a larger GMV of the orbitofrontal cortex (OFC) were likely to discount future values less steeply and choose large but delayed rewards. On the other hand, individuals with a larger GMV of the anterior cingulate cortex (ACC) are likely to discount the future value more steeply and prefer small but immediate rewards. Our study revealed the neuroanatomical correlates of delay discounting across the whole brain, and may help to understand the delay discounting in the frame of the hot versus cool system, which demonstrates the dynamics of resisting present temptation for future rewards.

In our daily life, we frequently face conflicts in decision making between a small but immediate reward (SIR), such as eating high-cholesterol cheesecake, and a large but delayed reward (LDR), such as having a healthy body shape. The rational choice is simple, which is to choose LDR over SIR. However, in reality we find it difficult to resist SIR, because in our mind the present value of LDR is significantly reduced because of the delay in time. Kirby and Marakovic (1995) coined this phenomenon as "delay discounting", which refers to the reduction in the present value of a future reward as a function of the delay to that reward. The consequence of the lack of delay discounting can be devastating, as individuals who prefer SIR are more likely to perform worse in scholastic tests (Mischel, Shoda, & Rodriguez, 1989), have more impulsive behaviors (Richards, Zhang, Mitchell, & Wit, 1999), and suffer misconducts such as gambling (Alessi & Petry, 2003), cigarette smoking (Bickel, Odum, & Madden, 1999), alcohol consumption (Vuchinich & Simpson, 1998), substance abuse (Bickel & Marsch, 2001; Madden, Petry, Badger, & Bickel, 1997; Petry, 2002, 2003; Petry & Casarella, 1999), and mental illness (Allen, Moeller, Rhoades, & Cherek, 1998; Crean, de Wit, & Richards, 2000). Here in this study, we examined the neuroanatomical correlates of delay discounting, which may shed light on its underlying mechanism.

A great number of studies have been conducted to study the neural correlates of delay discounting from neurophysiological (Kalenscher, Windmann, Diekamp, Rose, & Colombo, 2005; Montague & Berns, 2002), neuropsychological (Cardinal, Pennicott, Lakmali, Robbins, & Everitt, 2001; Sellitto, Ciaramelli, & di Pellegrino, 2010), and neuroimaging perspectives (brain structure: Bjork, Momenan, & Hommer, 2009; Yu, 2012; brain function: Casey et al., 2011; Shamosh et al., 2008; brain connectivity: Christakou, Brammer, & Rubia, 2011; Peters & Büchel, 2010). These studies have identified that multiple regions are involved in delay discounting, such as the hippocampus (Bar, 2009; van der Meer, Johnson, Schmitzer-Torbert, & Redish, 2010), the medial prefrontal cortex (Kable & Glimcher, 2007; Luhmann, Chun, Yi, Lee, & Wang, 2008; McClure, Ericson, Laibson, Loewenstein, & Cohen, 2007; McClure, Laibson, Loewenstein, & Cohen, 2004; Peters & Büchel, 2009; Weber & Huettel, 2008), the orbitofrontal cortex (OFC; Myerson, Green, Scott Hanson, Holt, & Estle, 2003; Roesch, Taylor, & Schoenbaum, 2006), the anterior cingulate cortex (ACC; Hoffman et al., 2008; Marco-Pallarés, Mohammadi, Samii, & Münte, 2010; McClure et al., 2007; Pine et al., 2009), the posterior cingulate cortex (Ballard & Knutson, 2009; Kable & Glimcher, 2007; Luhmann et al., 2008; McClure et al., 2007; McClure et al., 2004; Peters & Büchel, 2009; Weber & Huettel, 2008), the ventral striatum (Ballard & Knutson, 2009; Kable & Glimcher, 2007; Luhmann et al., 2008; McClure et al., 2007; McClure et al., 2004; Peters & Büchel, 2009; Weber & Huettel, 2008; Wittmann, Leland, & Paulus, 2007), and the dorsolateral prefrontal cortex (Leon & Shadlen, 1999; Roesch & Olson, 2003; Schultz, Tremblay, & Hollerman, 2000; Tanaka et al., 2004;

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Tsujimoto & Sawaguchi, 2005; Wallis & Miller, 2003). Specifically, the ACC and OFC are the two classic brain regions that are involved in delay discounting. The OFC is involved in delay discounting via representing the incentive value of rewards (Peters & Büchel, 2011), whereas the ACC is involved in delay discounting via conflict monitoring and strategy adaptation (Hoffman et al., 2008; Marco-Pallarés et al., 2010; Pine et al., 2009).

Most of these studies have focused on the functionality of these regions in delay discounting, and only three studies have explored the neuroanatomy (Bjork et al., 2009; Cho et al., 2013; Yu, 2012) that is the basis of the functionality. However, the findings from these three studies are not consistent. Bjork et al. (2009) used a region of interest approach and found greater discounting of delayed rewards was correlated with a small cluster of the inferolateral frontal cortex and the dorsolateral frontal cortex, whereas with a whole-brain, voxel-based analysis approach, Yu (2012) and Cho et al. (2013) failed to find any neuroanatomical correlates in the gray matter. The inconsistency possibly resulted from the lack of sufficient power to detect the neuroanatomical correlates. For example, Yu's study (2012) reported several gray matter volumes (GMV) correlated with delay discounting, but the correlation did not reach significance after whole-brain correction. Cho et al. (2013) relied on small volume correction to identify the association between the GMV of the ACC and the OFC and delay discounting. This may explain why Bjork et al. (2009) chose to focus on a small portion of the brain (i.e., the frontal cortex), but this approach provides incomplete information for the relation between neuroanatomy and functionality in delay discounting in the whole brain.

To reveal the neuroanatomical correlates of delay discounting across the whole brain, here we measured the degree of delay discounting of a larger sample of participants ($N = 325$), and then used the individual difference approach to correlate the behavioral performance with GMV across the whole brain to identify the neuroanatomical correlates of delay discounting.

Materials and Methods

Participants

We used G*Power to estimate the sample size needed in the present study (Faul, Erdfelder, Buchner, & Lang, 2009). Assuming small-to-moderate effect sizes (i.e., $r = .1$, $p = .001$), based on the literature (Li et al., 2014), and setting power at 0.8, a sample size of 224 people was suggested. Because multiple corrections are required for a whole-brain analysis in magnetic resonance imaging (MRI) studies, in this study we thus recruited 325 college students from Beijing Normal University, Beijing, China. Participants reported no psychiatric illness, hearing impairment, or neurological disorders (e.g., epilepsy, traumatic brain injury, neurodegenerative disorders, or cerebrovascular disease). This study was approved by the Institutional Review Board of Beijing Normal University. Prior to the experiment, written informed consent was obtained from all participants.

Assessment of delay discounting

The degree of delay discounting was assessed with the Monetary Choice Questionnaire (MCQ; Kirby, Petry, & Bickel, 1999). The MCQ is a self-report measure that consists of a set of 27 choices between pairs of two monetary rewards – one small but immediate reward (SIR) and one large but delayed reward (LDR), such as "Would you prefer ¥55 today or ¥75 in 61 days?", and the participants indicated their preferred reward. In the questionnaire, the SIRs ranged from ¥11 to ¥80, whereas the LDRs ranged from ¥25 to ¥85, with delays ranging from 1 week to 6 months.

Each participant completed his/her own questionnaire separately. To ensure the participants made choices based on their genuine preference, besides the monetary compensation for the experiment, they also received the reward based on their choice randomly selected among 27 choices of the completed questionnaire. There was no time limit for finishing the MCQ.

The degree of delay discounting, also coined as a k value, shows the steepness of the reduction in present value as a function of delay in time (Kirby et al., 1999). The larger the k value, the steeper the reduction, and the more likely that the participants choose SIRs over LDRs. In other words, a larger k value indicates stronger preference for SIR and thus more impulsiveness in decision making.

The k values were calculated with a standardized procedure of the MCQ (Kirby, 2009; Kirby et al., 1999). There are 10 k values in the MCQ, ranging from 0.00016 to 0.25, and each k value is associated with a choice pattern. Each participant's choice pattern was matched to the 10 patterns accordingly, and a k value whose pattern showed the highest consistency to the participant's was the k value indicating this participant's degree of delay discounting. Note that if a participant's highest consistency was lower than 85%, the match was considered not successful, and the participant was then excluded from further analyses. Four participants did not satisfy this criterion. Finally, the k values were log-transformed (Ln(k), natural log transformation) to approximate a normal distribution.

MRI acquisition

Participants were scanned using a Siemens 3T-scanner (MAGENTOM Trio, a Tim system) with a 12-channel phased-array head coil at BNU Imaging Center for Brain Research, Beijing, China. Magnetic resonance (MR) structural images were acquired using a 3D magnetization-prepared rapid gradient-echo (MP-RAGE) T1-weighted sequence (TR/TE/TI = 2530/3.39/1100 ms, flip angle = 7 degrees, FOV = 256 × 256 mm). To cover the whole brain, 128 contiguous sagittal slices were acquired with 1 × 1 mm in-plane resolution and a 1.33-mm slab thickness.

Image processing for VBM

VBM was used to explore the neuroanatomical correlates of delay discounting. VBM provides a quantitative measure of tissue volume for each voxel (Ashburner & Friston, 2000), which was performed using SPM8 (Statistical Parametric Mapping, Wellcome Department of Imaging Neuroscience, London, UK), with an optimized VBM protocol (Good et al., 2001) on T1-weighted structural images. First, the quality of structural images was assessed manually by visual inspection. Six participants were removed from further analyses because of extraordinary scanner artifacts (e.g., head movement during MRI scanning) or abnormal brain structure (e.g., unusually large ventricles). Second, the brain origin for each participant was manually set to the anterior commissure. Third, using a unified segmentation approach, four distinct tissue classes: gray matter (GM), white matter, cerebrospinal fluid, and everything else (e.g., skull and scalp) were segmented from the structural images (Ashburner & Friston, 2005). Fourth, the GM images were spatially normalized to the Montreal Neurological Institute (MNI) 152 space using the Diffeomorphic Anatomical Registration through Exponential Lie algebra (DARTEL) registration method (Ashburner, 2007).

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Table 1. Clusters of voxels correlated with delay discounting

Brain regions	Cluster size (voxels)	Peak *z* score	MNI coordinate			Statistic	Correlation coefficient
			x	y	z		
ACC	388	3.76	46	67	55	$p < .001$, corrected	.21
Left OFC	227	3.98	53	68	23	$p < 0001$, corrected	−.22
Right OFC	100	3.97	36	67	23	uncorrected	−.22

Note: MNI = Montreal Neurological Institute.

Table 2. The variables explained the individual differences in delay discounting

	Standardized coefficients	*t*	*p*
Gender	0.23	3.95	<0.001
ACC	0.26	4.39	<0.001
Left OFC	-0.16	1.98	0.049
Right OFC	-0.21	2.49	0.013

DARTEL registration involves repetitively computing the study-specific template and warping the GM images to the generated template. Fifth, to preserve the original gray matter volume (GMV) for each participant, the normalized individual GM images were modulated by multiplying each voxel's GM value with the voxel-specific Jacobian determinants derived from the spatial normalization. The modulated GM images, depicting a GMV measure for each voxel, were then smoothed using an 8-mm, full-width at half-maximum (FWHM) isotropic Gaussian kernel. Finally, the modulated GM images were masked using an absolute masking with a threshold of 0.2. That is, all voxels with a GMV value less than 0.2 were excluded. The masked-modulated GM images were further examined with a statistical analysis.

Statistical analysis

A whole-brain GMV analysis was performed to explore neuroanatomical correlates of delay discounting. Because four participants were excluded in the behavioral assessment on delay discounting and six participants showed unsatisfied MR image quality, 315 participants (96.9% of the total participant population) were included in this analysis (169 females, 18–25 years of age, mean age = 21.85 years, $SD = 0.99$). Voxel by voxel, a generalized linear model (GLM) was performed using the GMV extracted from the GM images as the dependent variable, with the Ln(k) values as the covariate of interest. Given that the modulated GM images contained variations in brain size, we took the total GMV as a confounding covariate in the statistical model. In addition, gender difference in GMV has been reported (e.g., Luders, Gaser, Narr, & Toga, 2009); therefore, gender was also included as a confounding covariate. The whole-brain correction (WBC) for multiple comparisons was performed by setting the voxel-wise intensity threshold at $p < .001$ and a cluster-level threshold determined by the AlphaSim program in AFNI with Monte Carlo simulations (Ward, 2000).

Results

Participants' Ln(k) values were used as an index for the degree of their delay discounting, with a higher Ln(k) value indicating greater discount of future values and thus stronger preference for SIRs. The kurtosis (-0.07) and skewness (-0.09) of the Ln(k) values indicated the normality of the data (Marcoulides & Hershberger, 1997). The mean of the Ln(k) values is -5.16 and the standard deviation is 1.43, suggesting a significant amount of individual differences.

To explore the neuroanatomical correlates of delay discounting, we correlated the GMV of each voxel across the whole brain with the Ln(k) value of each participant. We found that the Ln(k) value was negatively correlated with the GMV of a cluster in the left orbitofrontal cortex (OFC; MNI coordinate: 53,68,23; cluster size: 227; $p < .001$, WBC; Table 1, Figure 1). Moreover, similar to the left OFC, we also found that the Ln(k) value was negatively correlated with the GMV of a cluster in the right OFC (MNI coordinate: 36,67,23; cluster size: 100; uncorrected; Table 1, Figure 2), but the significance level did not surpass the strict probability levels determined by the WBC for multiple comparisons. One possibility of the trend observed in the right OFC might come from correlation transmissibility because the left OFC's GMV was highly correlated with the right OFC ($r = .74$, $p < .001$). To rule out this possibility, a partial correlation analysis was performed between the right OFC and the Ln(k) value after controlling for the left OFC's GMV. The correlation coefficient at the peak voxel of the right OFC was reduced from -.22 ($p < .001$) to -.12 ($p = .04$), but the correlation was still significant. Therefore, the correlation between the right OFC's GMV and the Ln(k) value was not completely derived from the association observed in the left OFC. In short, participants with a larger OFC's GMV may discount the future value less steeply, and thus prefer to choose LDRs.

In contrast, the Ln(k) value was positively correlated with the GMV of a cluster in the ACC (MNI coordinate: 46, 67, 55; cluster size: 338; $p < .001$, WBC; Table 1, Figure 3). That is, participants with larger ACC's GMV likely discounted the future value more steeply, and therefore may chose SIRs.

In summary, three brain regions have been found to be associated with delay discounting in this study: the ACC, the left OFC and the right OFC (Table 1). Here, we further asked how these three brain regions were related to delay discounting. Did they independently contribute to delay discounting, and how much did individual differences of these three regions explain individual differences of delay discounting? To answer these questions, we performed a stepwise multiple regression analysis, where the Ln(k) value of each participant was an independent variable and five factors as dependent variables. To avoid the bias in signal-to-noise ratio when calculating mean GMVs from different cluster sizes, we used the peak voxel of a cluster to represent this cluster. These five dependent variables were gender, the total GMV, the GMV of the peak voxel of the ACC, and the left and right OFC. The stepwise regression analysis showed that four variables were left in the regression model, $F(4, 310) = 10.80$, 95% CI [0.15, 0.59], $p < .0001$, Cohen's $d = 0.37$: gender and the GMV of the peak voxel of the three clusters (Table 2), suggesting that these three regions contributed to delay discounting relatively independently.

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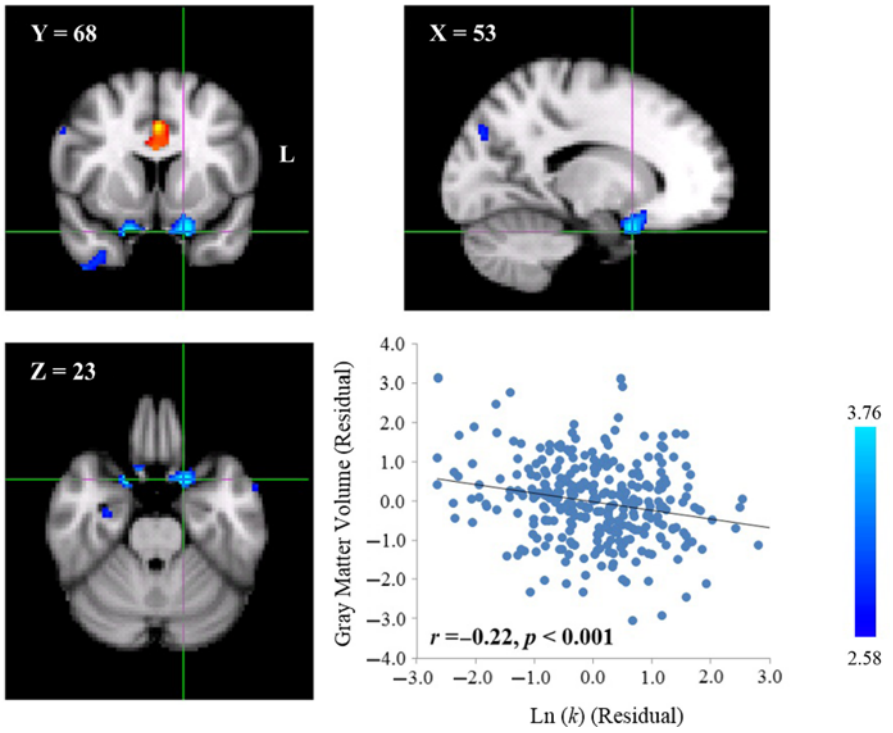


Fig 1. Neuroanatomical correlates of delay discounting in the left OFC. A cluster with a negative correlation between GMV and the Ln(*k*) value was found in the left OFC (MNI coordinate: 53,68,23; cluster size: 227; $p < .001$, WBC) in the MNI space. The scatter plot between the distributions of the Ln(*k*) value and GMV in the peak voxel of the cluster after controlling for gender and total GMV is shown for display purposes. Each dot represents one participant.

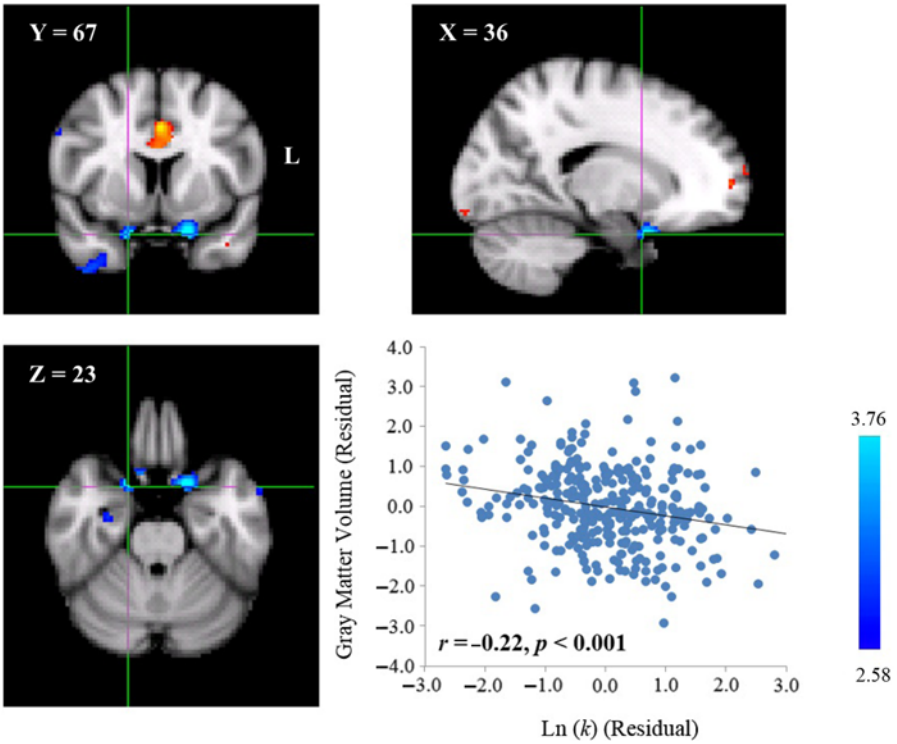


Fig. 2. Neuroanatomical correlates of delay discounting in the right OFC. A cluster with a negative correlation between GMV and the Ln(*k*) value was found in the right OFC (MNI coordinate: 36,67,23; cluster size: 100; uncorrected). The scatter plot is shown for display purpose. Each dot represents one participant.

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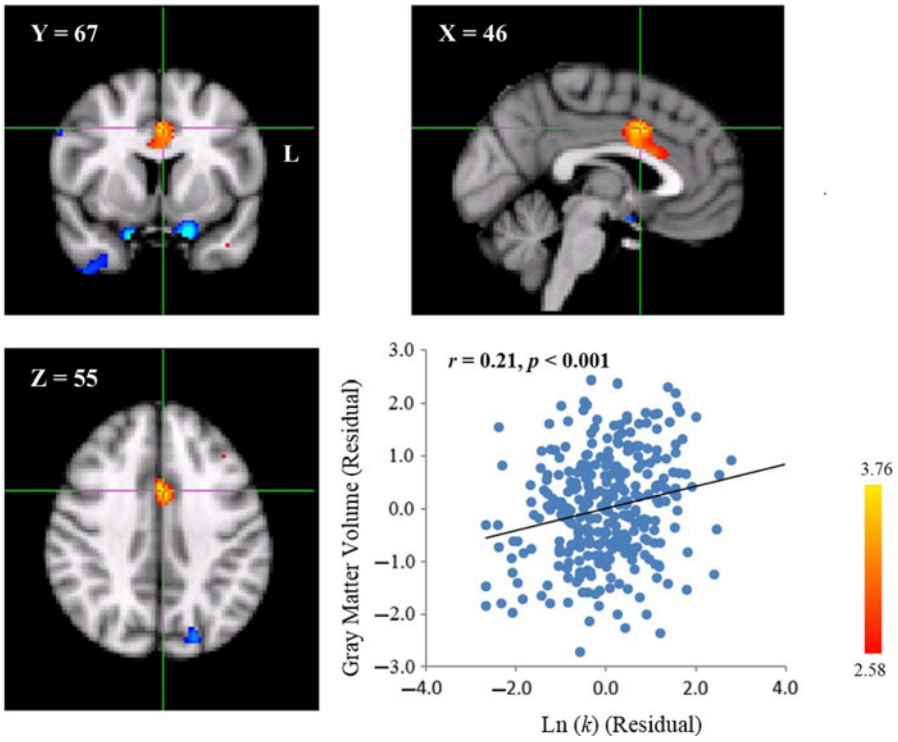


Fig. 3. Neuroanatomical correlates of delay discounting in the ACC. A cluster with a positive correlation between GMV and the Ln(k) value was found in the ACC (MNI coordinate: 46, 67, 55; cluster size: 338; $p < .001$, WBC) in the MNI space. A scatter plot between the distributions of the Ln(k) value and GMV in the peak voxel of the cluster after controlling for gender and total GMV is shown for display purpose. Each dot represents one participant.

In total, these four variables explained 12.2% of the total variation of the Ln(k) value.

Discussion

In the present study, we used the individual difference approach to investigate the neuroanatomical correlates of delay discounting across the whole brain. First, we found negative correlations of the left and right OFC's GMV with the Ln(k) value, suggesting that individuals with larger OFC's GMV discounted the future value less steeply, and are more likely to choose LDR over SIR. Second, we found a significant positive correlation of ACC's GMV with the Ln(k) value, suggesting that individuals with a larger GMV in the ACC discounted the future value more steeply, and may prefer SIR. Third, a stepwise regression analysis showed that these three regions contributed to delay discounting relatively independently, which in total explained 12.2% variance of delay discounting along with gender. A great number of neuroimaging studies have shown that both the ACC and the OFC are activated when participants perform tasks on delay discounting (e.g., Peters & Büchel, 2011). Our study complements these findings by demonstrating that the brain structure of the OFC and the ACC was also related to participants' performance in delay discounting.

The finding that larger OFC's GMV was associated with the preference to LDRs is consistent with previous studies. In neuropsychological studies, the lesion of the OFC in both humans (Berlin, Rolls, & Kischka, 2004; Sellitto et al., 2010) and animals (Mobini et al., 2002; Rudebeck, Walton, Smyth, Bannerman, & Rushworth, 2006) leads to steep discounting of future values and strongly prefers SIRs. In addition, a neuroimaging study reveals that the weaker the activation of the bilateral OFC is, the more likely that individuals choose SIRs (Boettiger et al., 2007). Our finding provides a possible interpretation on these studies because smaller OFC's GMV suggests a smaller number or a smaller body size of neurons in the OFC. As a result, the OFC was unable to generate sufficient neural activation to serve its role properly as a part of the cool system (Metcalfe & Mischel, 1999) that represents the incentive value of rewards (Chib, Rangel, Shimojo, & O'Doherty, 2009; Kable & Glimcher, 2009; Kringelbach & Rolls, 2004; Peters & Büchel, 2010) and engages cognitive control to suppress impulsivity.

In contrast, as a part of the hot system (Metcalfe & Mischel, 1999), the ACC is located in the limbic system. The limbic system, which is a core region in representing rewards (Gregorios-Pippas, Tobler, & Schultz, 2009) and pleasure (Haines & Ard, 2006), has a great preference for instant gratification. Therefore, it is not surprising that individuals with larger ACC's GMV prefer SIRs. Besides, the ACC is thought to be involved in delay discounting through conflict monitoring and strategy adaptation (Peters & Büchel, 2011). Indeed, the degree of decision conflicts is found to be correlated with the neural activation of the ACC, with higher activation for a harder decision (Hoffman et al., 2008; Marco-Pallarés et al., 2010; Pine et al., 2009). That is, for the same conflict between SIR and LDR, individuals with larger ACC's GMV may consider the conflict more severe, which requires more resources to solve the conflict. Therefore, they may choose the SIR that consumes less amount of resources, which finally leads to a steep reduction in future values.

In sum, we demonstrated the neuroanatomical correlates of the OFC and the ACC in delay discounting. This finding relied heavily on a large number of participants because the correlation between the GMV of these two regions and the behavioral performance in delay discounting was moderate. Indeed, previous efforts with a whole-brain analysis in establishing such a relationship apparently

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suffered insufficient statistical power (Cho et al., 2013; Yu, 2012). For example, 112 participants in Yu's (2012) and 36 participants in Cho et al.'s (2013) studies were much smaller than the number of participants suggested by the power analysis. Therefore, future studies in establishing neuroanatomical correlates may need a large number of participants or data gathered from multiple studies. Second, we also suggested the division of labor of these two regions, as their correlation to delay discounting is in the opposite direction. That is, the OFC is in the prefrontal cortex, which belongs to the cool system, whereas the ACC is a part of limbic system, which is the core of the hot system. Therefore, our finding fits nicely with the hot versus cool system, with the ACC competing for SIRs and the OFC suppressing impulsive behaviors with cognitive control (Hirsh, Guindon, Morisano, & Peterson, 2010). Future studies are needed to elucidate the role of the hot versus cool system in delay discounting on how a balanced hot and cool system leads to an optimal choice between presence and the future.

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References

Alessi S. and Petry N. (2003). Pathological gambling severity is associated with impulsivity in a delay discounting procedure. *Behavioural Processes*, **64**, 345–354.

Allen T.J., Moeller F.G., Rhoades H.M. and Cherek D.R. (1998). Impulsivity and history of drug dependence. *Drug and Alcohol Dependence*, **50**, 137–145.

Ashburner J. (2007). A fast diffeomorphic image registration algorithm. *Neuroimage*, **38**, 95–113.

Ashburner J. and Friston K.J. (2000). Voxel-based morphometry — The methods. *Neuroimage*, **11**, 805–821.

Ashburner J. and Friston K.J. (2005). Unified segmentation. *Neuroimage*, **26**, 839–851.

Ballard K. and Knutson B. (2009). Dissociable neural representations of future reward magnitude and delay during temporal discounting. *Neuroimage*, **45**, 143–150.

Bar M. (2009). The proactive brain: Memory for predictions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **364**, 1235–1243.

Berlin H., Rolls E. and Kischka U. (2004). Impulsivity, time perception, emotion and reinforcement sensitivity in patients with orbitofrontal cortex lesions. *Brain*, **127**, 1108–1126.

Bickel W.K. and Marsch L.A. (2001). Toward a behavioral economic understanding of drug dependence: Delay discounting processes. *Addiction*, **96**, 73–86.

Bickel W.K., Odum A.L. and Madden G.J. (1999). Impulsivity and cigarette smoking: Delay discounting in current, never, and ex-smokers. *Psychopharmacology*, **146**, 447–454.

Bjork J.M., Momenan R. and Hommer D.W. (2009). Delay discounting correlates with proportional lateral frontal cortex volumes. *Biological Psychiatry*, **65**, 710–713.

Boettiger C.A., Mitchell J.M., Tavares V.C., Robertson M., Joslyn G., D'Esposito M. and Fields H.L. (2007). Immediate reward bias in humans: Fronto-parietal networks and a role for the catechol-O-methyltransferase 158Val/Val genotype. *The Journal of Neuroscience*, **27**, 14383–14391.

Cardinal R.N., Pennicott D.R., Lakmali C., Robbins T.W. and Everitt B.J. (2001). Impulsive choice induced in rats by lesions of the nucleus accumbens core. *Science*, **292**, 2499–2501.

Casey B., Somerville L.H., Gotlib I.H., Ayduk O., Franklin N.T., Askren M.K. … Teslovich T. (2011). Behavioral and neural correlates of delay of gratification 40 years later. *Proceedings of the National Academy of Sciences*, **108**, 14998–15003.

Chib V.S., Rangel A., Shimojo S. and O'Doherty J.P. (2009). Evidence for a common representation of decision values for dissimilar goods in human ventromedial prefrontal cortex. *The Journal of Neuroscience*, **29**, 12315–12320.

Cho S.S., Pellecchia G., Aminian K., Ray N., Segura B., Obeso I. and Strafella A.P. (2013). Morphometric correlation of impulsivity in medial prefrontal cortex. *Brain Topography*, **26**, 479–487.

Christakou A., Brammer M. and Rubia K. (2011). Maturation of limbic corticostriatal activation and connectivity associated with developmental changes in temporal discounting. *Neuroimage*, **54**, 1344–1354.

Crean J.P., de Wit H. and Richards J.B. (2000). Reward discounting as a measure of impulsive behavior in a psychiatric outpatient population. *Experimental and Clinical Psychopharmacology*, **8**, 155–162.

Faul F., Erdfelder E., Buchner A. and Lang A.-G. (2009). Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, **41**, 1149–1160.

Good C.D., Johnsrude I., Ashburner J., Henson R.N., Friston K.J. and Frackowiak R.S. (2001). Cerebral asymmetry and the effects of sex and handedness on brain structure: A voxel-based morphometric analysis of 465 normal adult human brains. *Neuroimage*, **14**, 685–700.

Gregorios-Pippas L., Tobler P.N. and Schultz W. (2009). Short-term temporal discounting of reward value in human ventral striatum. *Journal of Neurophysiology*, **101**, 1507.

Haines D.E. and Ard M.D. (2006). *Fundamental neuroscience for basic and clinical applications*. Philadelphia, PA: Churchill Livingstone/Elsevier.

Hirsh J.B., Guindon A., Morisano D. and Peterson J.B. (2010). Positive mood effects on delay discounting. *Emotion*, **10**, 717.

Hoffman W.F., Schwartz D.L., Huckans M.S., McFarland B.H., Meiri G., Stevens A.A. and Mitchell S.H. (2008). Cortical activation during delay discounting in abstinent methamphetamine dependent individuals. *Psychopharmacology*, **201**, 183–193.

Kable J.W. and Glimcher P.W. (2007). The neural correlates of subjective value during intertemporal choice. *Nature Neuroscience*, **10**, 1625–1633.

Kable J.W. and Glimcher P.W. (2009). The neurobiology of decision: Consensus and controversy. *Neuron*, **63**, 733–745.

Kalenscher T., Windmann S., Diekamp B., Rose J. and Colombo M. (2005). Single units in the pigeon brain integrate reward amount and time-to-reward in an impulsive choice task. *Current Biology*, **15**, 594–602.

Kirby K.N. (2009). One-year temporal stability of delay-discount rates. *Psychonomic Bulletin & Review*, **16**, 457–462.

Kirby K.N. and Maraković N.N. (1995). Modeling myopic decisions: Evidence for hyperbolic delay-discounting within subjects and amounts. *Organizational Behavior and Human Decision Processes*, **64**, 22–30.

Kirby K.N., Petry N.M. and Bickel W.K. (1999). Heroin addicts have higher discount rates for delayed rewards than non-drug-using controls. *Journal of Experimental Psychology: General*, **128**, 78–87.

Kringelbach M.L. and Rolls E.T. (2004). The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. *Progress in Neurobiology*, **72**, 341–372.

Leon M.I. and Shadlen M.N. (1999). Effect of expected reward magnitude on the response of neurons in the dorsolateral prefrontal cortex of the macaque. *Neuron*, **24**, 415–425.

Li X.T., De Beuckelaer A., Guo J.H., Ma F.L., Xu M. and Liu J. (2014). The gray matter volume of the amygdala is correlated with the perception of melodic intervals: A voxel-based morphometry study. *PloS One*, **9**, e99889.

Luders E., Gaser C., Narr K.L. and Toga A.W. (2009). Why sex matters: Brain size independent differences in gray matter distributions between men and women. *Journal of Neuroscience*, **29**, 14265–14270.

Luhmann C.C., Chun M.M., Yi D.-J., Lee D. and Wang X.-J. (2008). Neural dissociation of delay and uncertainty in intertemporal choice. *The Journal of Neuroscience*, **28**, 14459–14466.

Madden G.J., Petry N.M., Badger G.J. and Bickel W.K. (1997). Impulsive and self-control choices in opioid-dependent patients and non-drug-using control patients: Drug and monetary rewards. *Experimental and Clinical Psychopharmacology*, **5**, 256–262.

Marco-Pallarés J., Mohammadi B., Samii A. and Münte T.F. (2010). Brain activations reflect individual discount rates in intertemporal choice. *Brain Research*, **1320**, 123–129.

Marcoulides G.A. and Hershberger S.L. (1997). *Multivariate statistical methods: A first course*. New York: Psychology Press.

https://doi.org/10.1017/prp.2019.22 Published online by Cambridge University Press

McClure S.M., Ericson K.M., Laibson D.I., Loewenstein G. and Cohen J.D. (2007). Time discounting for primary rewards. *The Journal of Neuroscience*, **27**, 5796–5804.

McClure S.M., Laibson D.I., Loewenstein G. and Cohen J.D. (2004). Separate neural systems value immediate and delayed monetary rewards. *Science*, **306**, 503–507.

Metcalfe J. and Mischel W. (1999). A hot/cool-system analysis of delay of gratification: dynamics of willpower. *Psychological Review*, **106**, 3–19.

Mischel W., Shoda Y. and Rodriguez M.I. (1989). Delay of gratification in children. *Science*, **244**, 933–938.

Mobini S., Body S., Ho M.-Y., Bradshaw C., Szabadi E., Deakin J. and Anderson I. (2002). Effects of lesions of the orbitofrontal cortex on sensitivity to delayed and probabilistic reinforcement. *Psychophar macology*, **160**, 290–298.

Montague P.R. and Berns G.S. (2002). Neural economics and the biological substrates of valuation. *Neuron*, **36**, 265–284.

Myerson J., Green L., Scott Hanson J., Holt D.D. and Estle S.J. (2003). Discounting delayed and probabilistic rewards: Processes and traits. *Journal of Economic Psychology*, **24**, 619–635.

Peters J. and Büchel C. (2009). Overlapping and distinct neural systems code for subjective value during intertemporal and risky decision making. *The Journal of Neuroscience*, **29**, 15727–15734.

Peters J. and Büchel C. (2010). Neural representations of subjective reward value. *Behavioural brain research*, **213**, 135–141.

Peters J. and Büchel C. (2011). The neural mechanisms of inter-temporal decision-making: understanding variability. *Trends in Cognitive Sciences*, **15**, 227–239.

Petry N.M. (2002). Discounting of delayed rewards in substance abusers: relationship to antisocial personality disorder. *Psychopharmacology*, **162**, 425–432.

Petry N.M. (2003). Discounting of money, health, and freedom in substance abusers and controls. *Drug and Alcohol Dependence*, **71**, 133–141.

Petry N.M. and Casarella T. (1999). Excessive discounting of delayed rewards in substance abusers with gambling problems. *Drug and Alcohol Dependence*, **56**, 25–32.

Pine A., Seymour B., Roiser J.P., Bossaerts P., Friston K.J., Curran H.V. and Dolan R.J. (2009). Encoding of marginal utility across time in the human brain. *The Journal of Neuroscience*, **29**, 9575–9581.

Richards J.B., Zhang L., Mitchell S.H. and Wit H. (1999). Delay or probability discounting in a model of impulsive behavior: effect of alcohol. *Journal of the Experimental Analysis of Behavior*, **71**, 121–143.

Roesch M.R. and Olson C.R. (2003). Impact of expected reward on neuronal activity in prefrontal cortex, frontal and supplementary eye fields and premotor cortex. *Journal of Neurophysiology*, **90**, 1766–1789.

Roesch M.R., Taylor A.R. and Schoenbaum G. (2006). Encoding of time-discounted rewards in orbitofrontal cortex is independent of value representation. *Neuron*, **51**, 509–520.

Rudebeck P.H., Walton M.E., Smyth A.N., Bannerman D.M. and Rushworth M.F. (2006). Separate neural pathways process different decision costs. *Nature Neuroscience*, **9**, 1161–1168.

Schultz W., Tremblay L. and Hollerman J.R. (2000). Reward processing in primate orbitofrontal cortex and basal ganglia. *Cerebral Cortex*, **10**, 272–283.

Sellitto M., Ciaramelli E. and di Pellegrino G. (2010). Myopic discounting of future rewards after medial orbitofrontal damage in humans. *The Journal of Neuroscience*, **30**, 16429–16436.

Shamosh N.A., DeYoung C.G., Green A.E., Reis D.L., Johnson M.R., Conway A.R. . . . Gray J.R. (2008). Individual differences in delay discounting relation to intelligence, working memory, and anterior prefrontal cortex. *Psychological Science*, **19**, 904–911.

Tanaka S.C., Doya K., Okada G., Ueda K., Okamoto Y. and Yamawaki S. (2004). Prediction of immediate and future rewards differentially recruits cortico-basal ganglia loops. *Nature Neuroscience*, **7**, 887–893.

Tsujimoto S. and Sawaguchi T. (2005). Neuronal activity representing temporal prediction of reward in the primate prefrontal cortex. *Cortex*, **93**, 3687–3692.

van der Meer M.A., Johnson A., Schmitzer-Torbert N.C. and Redish A.D. (2010). Triple dissociation of information processing in dorsal striatum, ventral striatum, and hippocampus on a learned spatial decision task. *Neuron*, **67**, 25–32.

Vuchinich R.E. and Simpson C.A. (1998). Hyperbolic temporal discounting in social drinkers and problem drinkers. *Experimental and Clinical Psychopharmacology*, **6**, 292.

Wallis J.D. and Miller E.K. (2003). Neuronal activity in primate dorsolateral and orbital prefrontal cortex during performance of a reward preference task. *European Journal of Neuroscience*, **18**, 2069–2081.

Ward B.D. (2000). *Simultaneous inference for fMRI data. AFNI 3dDeconvolve documentation. Medical College of Wisconsin. Retrieved from http://afni.nimh.nih.gov/pub/dist/doc/manual/AlphaSim.pdf.*

Weber B.J. and Huettel S.A. (2008). The neural substrates of probabilistic and intertemporal decision making. *Brain Research*, **1234**, 104–115.

Wittmann M., Leland D.S. and Paulus M.P. (2007). Time and decision making: differential contribution of the posterior insular cortex and the striatum during a delay discounting task. *Experimental Brain Research*, **179**, 643–653.

Yu R. (2012). Regional white matter volumes correlate with delay discounting. *PloS One*, **7**, e32595.

https://doi.org/10.1017/prp.2019.22 Published online by Cambridge University Press