

Research Article

Individual Differences in Delay Discounting

Relation to Intelligence, Working Memory, and Anterior Prefrontal Cortex

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ABSTRACT—Lower delay discounting (better self-control) is linked to higher intelligence, but the basis of this relation is uncertain. To investigate the potential role of working memory (WM) processes, we assessed delay discounting, intelligence (g), WM (span tasks, 3-back task), and WM-related neural activity (using functional magnetic resonance imaging) in 103 healthy adults. Delay discounting was negatively correlated with g and WM. WM explained no variance in delay discounting beyond that explained by g , which suggests that processes through which WM relates to delay discounting are shared by g . WM-related neural activity in left anterior prefrontal cortex (Brodmann's area 10) covaried with g , $r = .26$, and delay discounting, $r = -.40$, and partially mediated the relation between g and delay discounting. Overall, the results suggest that delay discounting is associated with intelligence in part because of processes instantiated in anterior prefrontal cortex, a region known to support the integration of diverse information.

Self-control is a critical human faculty that affects many spheres of life (e.g., Tangney, Baumeister, & Boone, 2004). One way of gauging self-control is by assessing individuals' tendencies to prefer smaller, more immediate rewards to larger, delayed rewards (e.g., Rachlin, Ranieri, & Cross, 1991). These delay-discounting tasks measure self-control in a way that is relevant both to microeconomics, such as personal financial planning (Angeletos, Laibson, Repetto, Tobacman, & Weinberg, 2001),

and to mental health, including substance abuse, attention-deficit/hyperactivity disorder, and problem gambling (for reviews, see Bickel & Marsch, 2001; Critchfield & Kollins, 2001). Nonetheless, the mechanistic bases of individual differences in delay discounting are largely unknown (but see Hariri et al., 2006). Understanding the bases of such differences could potentially lead to interventions for enhancing self-control.

In a recent meta-analysis, we found clear evidence for a negative relation between delay discounting and intelligence (Shamosh & Gray, 2008). Nearly all of the included studies found that preference for immediate rewards was associated with lower intelligence (IQ). The quantitative synthesis across 26 effect sizes revealed a small to moderate effect size (weighted mean $r = -.23$), establishing definitively that delay discounting and intelligence are negatively correlated (cf. Benjamin, Brown, & Shapiro, 2008; Frederick, 2005). However, this review could not address the nature of the mechanisms supporting this relation.

One possibility is that individual differences in working memory (WM) account for the relation between delay discounting and intelligence. WM is the ability to maintain active representations of goal-relevant information despite interference from competing or irrelevant information (cf. WM capacity; Engle, 2002). WM is strongly related to general intelligence (g ; for a review, see Conway, Kane, & Engle, 2003), a latent variable that accounts for the widely observed positive intercorrelations among scores on cognitive tests (e.g., Jensen, 1998). Correlations between WM capacity and g are typically large and robust, although the two constructs are not isomorphic (Ackerman, Beier, & Boyle, 2005; Kane, Hambrick, & Conway, 2005). Furthermore, brain regions involved in WM overlap

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substantially with those that support fluid intelligence, the ability to reason and solve novel problems (Gray & Thompson, 2004; Kane & Engle, 2002).

WM may also be related to delay discounting. Imposing a WM load increases impulsive responding on delay-discounting tasks (Hinson, Jameson, & Whitney, 2003), which suggests that performing these tasks requires WM (e.g., to maintain reward values actively as one manipulates and integrates diverse information in order to choose between the alternatives). Consistent with this interpretation are findings that deficits in the executive functions of WM are associated with high trait impulsiveness (Whitney, Jameson, & Hinson, 2004). Moreover, neural networks supporting WM are activated during performance of delay-discounting tasks (e.g., McClure, Laibson, Loewenstein, & Cohen, 2004), as well as during other decision-making tasks that require incurring short-term losses to achieve long-term gains (e.g., Yarkoni et al., 2005).

The goal of the present research was to identify candidate neural mechanisms that might account for the relation between intelligence and delay discounting, focusing especially on mechanisms involved in WM. We operationalized intelligence by combining two tests of fluid reasoning and two tests of crystallized knowledge to derive a measure of g , because the relation between intelligence and delay discounting holds across a diverse array of measures (Shamosh & Gray, 2008). We operationalized WM as a latent variable based on WM span tasks and as performance on a 3-back task. WM-related brain activity was assessed by functional magnetic resonance imaging (fMRI) during the 3-back task. We replicated the finding that delay discounting is negatively related to intelligence, and also found that it is negatively related to WM, as expected. To identify brain regions responsible for individual differences in WM, we first identified candidate regions by testing for WM-related neural activity that covaried with task performance. We then tested these regions for correlations with both delay discounting and g . Finally, we used mediation analyses to test whether activity in the surviving candidate regions plausibly contributed to the relation between delay discounting and intelligence.

METHOD

Participants and Procedure

Participants were recruited from Washington University in St. Louis and the surrounding community. All participants gave informed consent, and none had a history of neurological or psychiatric disorder. The experimental protocol was approved by the Washington University Medical Center Human Subjects Committee. Only participants with complete delay-discounting data were included in the analyses. In addition, we excluded 1 participant whose accuracy on the 3-back task was not above chance ($d' = 0.31$, 3.51 standard deviations below the mean), as well as the participant with the highest 3-back accuracy ($d' = 3.70$, 3.60 standard deviations above the mean), whose data

unduly influenced analyses (Cook's $d = 0.39$ when delay discounting was regressed on d'). Participants completed the behavioral measures prior to scanning, and returned on a separate day for the fMRI testing session (final $n = 103$; 59 females, 44 males; age range = 18–40 years, $M = 22.9$).

Measures

Delay Discounting

We administered a delay-discounting task (Rachlin et al., 1991) in which participants made a series of hypothetical choices between two monetary rewards, one immediate and one delayed, in two conditions. In one condition, the delayed reward was always \$200, and the amount of the immediate reward ranged from \$10 to \$200 in increments of \$10. In the other condition, the delayed reward was always \$40,000, and the amount of the immediate reward ranged from \$2,000 to \$40,000 in increments of \$2,000. For each delayed-reward condition, participants made one choice for each combination of immediate-reward amount and delay period. Seven delay periods were tested: 1 month, 6 months, 1 year, 2 years, 3 years, 5 years, and 8 years.

Delay discounting was taken as the area under the curve because this measure has good psychometric properties (Myerson, Green, & Warusawitharana, 2001). This method involves determining, for each individual, the present value of the delayed option when paired with each immediate-reward amount (i.e., the estimated indifference point between the immediate and delayed rewards), plotting the resulting function, and calculating the proportion of total area falling under the curve. The scores for the two delayed-reward amounts were averaged, and this average was subtracted from 1.00 so that higher values would correspond to greater discounting. These scores were highly reliable (split-half $r = .98$), and previous research has demonstrated that delay discounting is stable over time (Ohmura, Takahashi, Kitamura, & Wehr, 2006).

Intelligence

All participants completed Raven's Advanced Progressive Matrices, Set II (Raven, Raven, & Court, 1998) and the Cattell Culture Fair Intelligence Test (Cattell, 1973), which are standard measures of abstract reasoning used to assess fluid intelligence. They also completed the Vocabulary subscale of the Wechsler Adult Intelligence Scale–Revised (Wechsler, 1997) and the National Adult Reading Test–Revised (Blair & Spreen, 1989), which measure vocabulary knowledge to assess crystallized intelligence. To assess g , we averaged each participant's standardized scores on these four tasks. Cronbach's alpha for the four tasks was .88. Factor analysis of the four measures (principal axis factoring, unrotated) revealed that a single factor explained 74% of the total variance (the scree plot suggested that a second factor was unlikely) and that all variables loaded strongly and approximately equally on this factor (loadings ranged from .79 to .84). Defining g as the first

principal component (rather than the average) of the scores on the four tasks did not change any of the conclusions, and had the potential disadvantage of capitalizing on sampling variability.

Working Memory

Participants completed four WM span tasks that all required participants to keep information actively in mind in the face of interference (Conway et al., 2003). Two of these tasks were designed to be verbal: Operation span required keeping several words in mind over a short delay while doing math problems, and reading span required keeping several letters in mind while reading sentences out loud and judging their meaningfulness. The other two WM span tasks were spatial: Symmetry span required keeping several positions in mind while making symmetry judgments, and rotation span required keeping the size and direction of several arrows in mind while making unrelated judgments that required mental rotation. For all four WM span tasks, keeping more items in mind resulted in a higher score; all were scored using the same metric (0.00–1.00). Confirmatory factor analysis showed that all four tasks had high loadings on a single factor that accounted for 70% of the total variance (loadings ranged from .81 to .86). WM span was taken as the average score across all four measures.

In the fMRI scanner, participants performed a 3-back version of the N -back task, a standard WM paradigm that requires pressing one key if the item presented is identical to that presented N trials previously ($N = 3$ in our study), and another key if the item is different. Most participants completed the 3-back task over six functional scanning runs; 2 participants completed four runs, and 9 others completed five runs. Each scanning run involved two blocks of 32 trials (i.e., 64 trials per functional run); trials lasted for 2 s each. We discarded the first 3 trials of each block because no match was possible; thus, 58 trials from each functional run were eligible for analysis. Three runs had faces as stimuli, and three had concrete nouns; order was counterbalanced across participants. Every run was preceded by a short video. Four of these videos were intended to induce positive or negative emotion; the order of emotions was counterbalanced. We do not focus on the emotion induction in this report. Our measure of 3-back performance was the signal detection measure of accuracy, d' , averaged across runs. Cronbach's alpha for d' across the six runs was .84.

On the 3-back task, participants did not show a speed-accuracy trade-off, $r(101) = -.004$, and response times for this task did not covary with any effects of interest.

fMRI Data Acquisition

We used a 3-T Allegra System (Siemens, Erlangen, Germany) to collect whole-brain images: T1-weighted magnetization-prepared rapid gradient-echo (MP-RAGE) structural images (field of view = 256 mm; 256 × 256 matrix; axial slices 1.25 mm thick) and T2*-weighted blood-oxygenation-level-dependent

(BOLD) functional images (asymmetric spin-echo echo-planar sequence; whole-brain repetition time, TR = 2,360 ms; echo time = 25 ms; field of view = 256 mm; flip angle = 90°; matrix = 64 × 64; axial slices 4 mm thick). Each functional run comprised 149 sequential whole-brain volumes (32 contiguous slices, 4- × 4-mm in-plane resolution).

During each functional run, the intertrial intervals were jittered across a range from 0 to 4,720 ms (0–2 whole-brain TRs) in steps of 2,360 ms (1 TR). Each task block was preceded and followed by a 35-s resting fixation block. Additionally, each scanning run began with an unanalyzed fixation period equal to 4 TRs, which allowed the scanner to reach steady state.

fMRI Data Analysis

Data were analyzed using SPM2 software (Wellcome Trust Center for Neuroimaging, London; <http://www.fil.ion.ucl.ac.uk/spm>). Each functional run was preprocessed prior to analysis. Data were realigned using INRIAlign (Freire, Roche, & Mangin, 2002) to correct for movement and then coregistered to the participant's anatomical scan. Images were normalized to Montreal Neurological Institute stereotaxic space using a 12-parameter affine transformation followed by nonlinear warping using basis functions, resampled into 3-mm isotropic voxels, and smoothed using an 8-mm full-width at half-maximum Gaussian kernel.

For each participant, we computed a basic contrast, activation greater during the 3-back task than during fixation, across all six functional runs. Each 32-trial block of 3-back performance was modeled as a boxcar function convolved with a canonical hemodynamic response function. The magnitude of neural activity at each voxel was estimated using the general linear model. A contrast comparing task-related activity with fixation-related activity produced a statistical parametric map of the t statistic at each voxel for each subject. These maps were used in all subsequent fMRI analyses.

To identify WM-related neural mechanisms related to both delay discounting and g , we first isolated candidate regions of interest (ROIs) supporting WM-related processes by identifying regions in which WM-related activity covaried with WM performance. We subjected each resulting ROI to three additional criteria to ascertain whether it likely contributed to the relation between g and delay discounting. Specifically, activity in the ROI had to correlate with both g and delay discounting and to statistically mediate the relation between g and delay discounting (a significance threshold of $p < .05$, Bonferroni corrected, was used in each analysis). (We also conducted a similar analysis in which we identified regions with WM-related activity that correlated with delay discounting and then probed those regions using ROI analyses. The findings from this approach agreed with those based on the method reported here.)

Accordingly, we first conducted a group-level random-effects analysis to identify regions in which activity during the 3-back task covaried with 3-back accuracy (i.e., regions of 15 or more

contiguous voxels in which values from the task-fixation contrast correlated significantly with d' , $p < .001$, uncorrected). We defined these as ROIs using the MarsBar toolbox for SPM2 and used t tests to determine the extent to which each ROI was related to delay discounting and g . At a group level, performing the 3-back task was associated with activation or deactivation in some, but not all, of the ROIs. The mean percentage signal change for each individual in each ROI was computed from task-related activity (mean b values across all voxels in the ROI) and global signal (mean across all voxels). These values were used to test for correlations with behavioral measures (d' , g) and to conduct mediation tests using the bootstrap method to test significance of indirect effects (bias-corrected confidence-interval method; bootstrap $N = 2,000$; Shrout & Bolger, 2002). In an imaging context, mediation analyses can be used to test whether a given region can plausibly account for the covariation between two behavioral variables, thereby implicating the region in supporting a complex function (cf. Gray, Chabris, & Braver, 2003). In the present study, a significant mediation effect indicates that WM-related brain activity is likely to be responsible, at least in part, for the observed relation between g and delay discounting.

RESULTS

Behavioral Findings

Table 1 presents descriptive statistics for the behavioral measures, along with the correlations among them. As expected, WM was strongly related to g . The two WM measures (d' , span) were highly correlated, indicating good convergent validity. Also as expected, delay discounting was negatively correlated with g (i.e., greater self-control was associated with higher intelligence). Delay discounting was also negatively correlated with both measures of WM, and to similar degrees.

When delay discounting was regressed on WM span and g simultaneously, the association between WM span and delay dis-

counting was not significant ($\beta = .02$, $p = .87$), whereas the relation between g and delay discounting remained strong ($\beta = -.41$, $p < .001$), $F(2, 100) = 9.55$, $p < .001$, $R^2 = .16$. This R^2 value was effectively identical to that for g alone, which indicates that WM span did not account for variability in delay discounting above and beyond the variability accounted for by g , $\Delta R^2 = .00$.

The same conceptual analysis with d' substituted for WM span yielded virtually identical conclusions. When delay discounting was regressed on d' and g simultaneously, the association between d' and delay discounting was eliminated ($\beta = -.01$, $p = .95$), whereas the relation between g and delay discounting remained robust ($\beta = -.40$, $p < .001$), $F(2, 100) = 9.54$, $p < .001$, $R^2 = .16$. Again, this R^2 value was effectively identical to that for g alone, which indicates that d' did not account for variability in delay discounting above and beyond the variability accounted for by g , $\Delta R^2 = .00$.

The behavioral findings suggest that g is related to delay discounting in part because of processes or mechanisms common to g and WM (in our study, g shared approximately 35% of its variance with WM). There was effectively no unique contribution of WM to delay discounting, so we conclude that WM mechanisms that relate to delay discounting are shared by g . To further clarify the nature of these shared mechanisms, we used WM-related neural activity to identify brain regions that plausibly support the relation between g and delay discounting.

fMRI Findings

Following the rationale elaborated earlier, we first identified candidate neural regions that plausibly supported individual differences in WM performance. Across the whole brain, variation in accuracy on the 3-back task (d') covaried with task-related activity in six ROIs (Table 2); correlations were positive or negative, depending on the region. The relation between g and WM-related neural activity was similar to that for d' and WM-related neural activity in all six regions (Table 2).

TABLE 1
Descriptive Statistics and Correlations Among the Behavioral Measures

Measure	1	2	3	4	5	6	7	8
1. g	—							
2. Raven APM	.88	—						
3. Cattell Culture Fair Intelligence Test	.90	.76	—					
4. WAIS Vocabulary	.70	.59	.62	—				
5. NART-R	.46	.58	.56	.79	—			
6. Working memory (d')	.60	.59	.60	.44	.42	—		
7. Working memory span	.58	.58	.63	.45	.47	.55	—	
8. Delay discounting	-.40	-.37	-.31	-.41	-.28	-.25	-.22	—
Mean	0.00	25.1	29.4	48.6	20.7	1.98	0.70	0.43
Standard deviation	0.51	6.09	5.46	8.83	8.74	0.48	0.13	0.20

Note. $n = 103$. See the Method section for a description of the measures. All correlations were significant, $p < .025$ (two-tailed), $p_{rep} = .92$. APM = Advanced Progressive Matrices; NART-R = National Adult Reading Test-Revised; WAIS = Wechsler Adult Intelligence Scale.

TABLE 2
Regions of Interest and Their Relation to the Behavioral Variables

Region	Coordinates			Cluster extent	Correlation, $r(101)$			3-back vs. fixation activation, $t(102)$	Mediation (β)	
	x	y	z		With WM d'	With g	With DD		WM $d' \rightarrow$ DD	$g \rightarrow$ DD
Left middle frontal gyrus (BA 10; aPFC)	-22	61	8	17	.37*	.26*	-.40*	-2.23	-.13* (.04)	-.08* (.03)
Left anterior cingulate (BA 32)	-3	40	7	145	-.38*	-.37*	.28*	-9.07*	-.08 (.05)	-.06 (.05)
Left inferior parietal lobule (BA 40)	-59	-32	22	24	-.36*	-.30*	.23	-0.64	-.06 (.05)	-.04 (.03)
Right precuneus (BA 7)	10	-70	54	65	.44*	.26*	-.17	13.19*	-.03 (.04)	-.02 (.02)
Right temporal cortex (BA 21)	39	-9	-11	86	-.36*	-.27*	.27*	-2.88*	-.08 (.05)	-.05 (.03)
Left posterior cingulate gyrus (BA 30)	-9	-62	12	17	-.34*	-.29*	.23	-9.88*	-.06 (0.04)	-.04 (.03)

Note. Regions of interest (ROIs) were defined as regions in which neural activity during the 3-back working memory (WM) task was correlated with accuracy (d') on that task, $p < .001$ (uncorrected). The cluster-extent threshold was 15 voxels. The t tests indicate whether, at the group level, activity in the ROI was significantly different during the 3-back task than during fixation periods (positive values mean greater activity during the 3-back task). For each ROI, two mediation analyses are reported, one testing the ROI as a mediator of the relation between WM d' and delay discounting (DD; illustrated in Fig. 1c), and the other testing the ROI as a mediator of the relation between g and DD. The table lists the strength of the indirect effects, with standard errors in parentheses. aPFC = left anterior prefrontal cortex; BA = Brodmann's area.

* $p < .0083$ ($p < .05$, Bonferroni-corrected for six regions of interest), $p_{rep} > .955$.

Three of the six ROIs showed significant associations with delay discounting (Table 2). The strongest association ($r = -.40$) was in a region of left anterior prefrontal cortex (aPFC), lateral frontopolar cortex (Brodmann's area 10). Figure 1a shows the region's location, and Figure 1b illustrates how WM-related neural activity in this region varied with both WM performance and delay discounting. Unlike most of the ROIs, this region did not show group-level WM-related activation or deactivation (despite greater activity being associated with better WM performance; Table 2 also shows the results of analyses testing whether activation was greater during the 3-back task than during fixation in each ROI).

For a final test of whether each candidate region plausibly supported the relation between g and delay discounting, we conducted mediation analyses. Of the six ROIs, left aPFC was the only significant mediator (see Table 2). For left aPFC, the indirect effect of g on delay discounting was significant, and the direct effect of g on delay discounting also remained significant after the indirect path was included in the model, an indication of partial mediation (Fig. 1c). We note that the same left aPFC region also partially mediated the relation between WM accuracy (d') and delay discounting (Table 2), and was again the only region to show significant mediation.

DISCUSSION

To our knowledge, this study is the first to investigate and identify neural mechanisms that account for the relation between intelligence and individual differences in delay discounting. We replicated our meta-analytic finding that delay discounting is negatively related to intelligence (Shamosh &

Gray, 2008), and also found that delay discounting covaried negatively with WM, especially WM processes shared with intelligence. Additionally, individual differences in left aPFC partially explained the tendency of more intelligent individuals to resist smaller, sooner rewards. Across 103 subjects, neural activity in left aPFC during a difficult WM task was positively associated with WM accuracy and intelligence, and negatively associated with delay discounting. A path analysis showed that this neural activity partially mediated the association between g and delay discounting (and between WM and delay discounting). In a neuroimaging context, this mediation indicates that it is plausible that the region supports the covariation between g and delay discounting. This finding is consistent with the overlapping neural substrates of g and WM (Gray & Thompson, 2004; Kane & Engle, 2002) and suggests that these substrates also overlap with those of delay discounting.

Our findings suggest that the link between g and delay discounting is supported in part by aPFC. In our data, aPFC activity was associated with better WM performance, higher intelligence, and reduced delay discounting. Interestingly, activity in left aPFC may improve WM without being essential to it, because group-mean activity in this region was not reliably different from zero despite the significant association between left aPFC activity and better WM performance across individuals. However, this interpretation depends on aPFC activity in the baseline condition, and some meta-analyses have found aPFC to be engaged during N -back tasks (e.g., Owen, McMillan, Laird, & Bullmore, 2005). Our results, in conjunction with previous research, suggest that this region may be flexibly involved in various forms of higher cognition. The left-aPFC ROI falls within a brain region that has been implicated in a

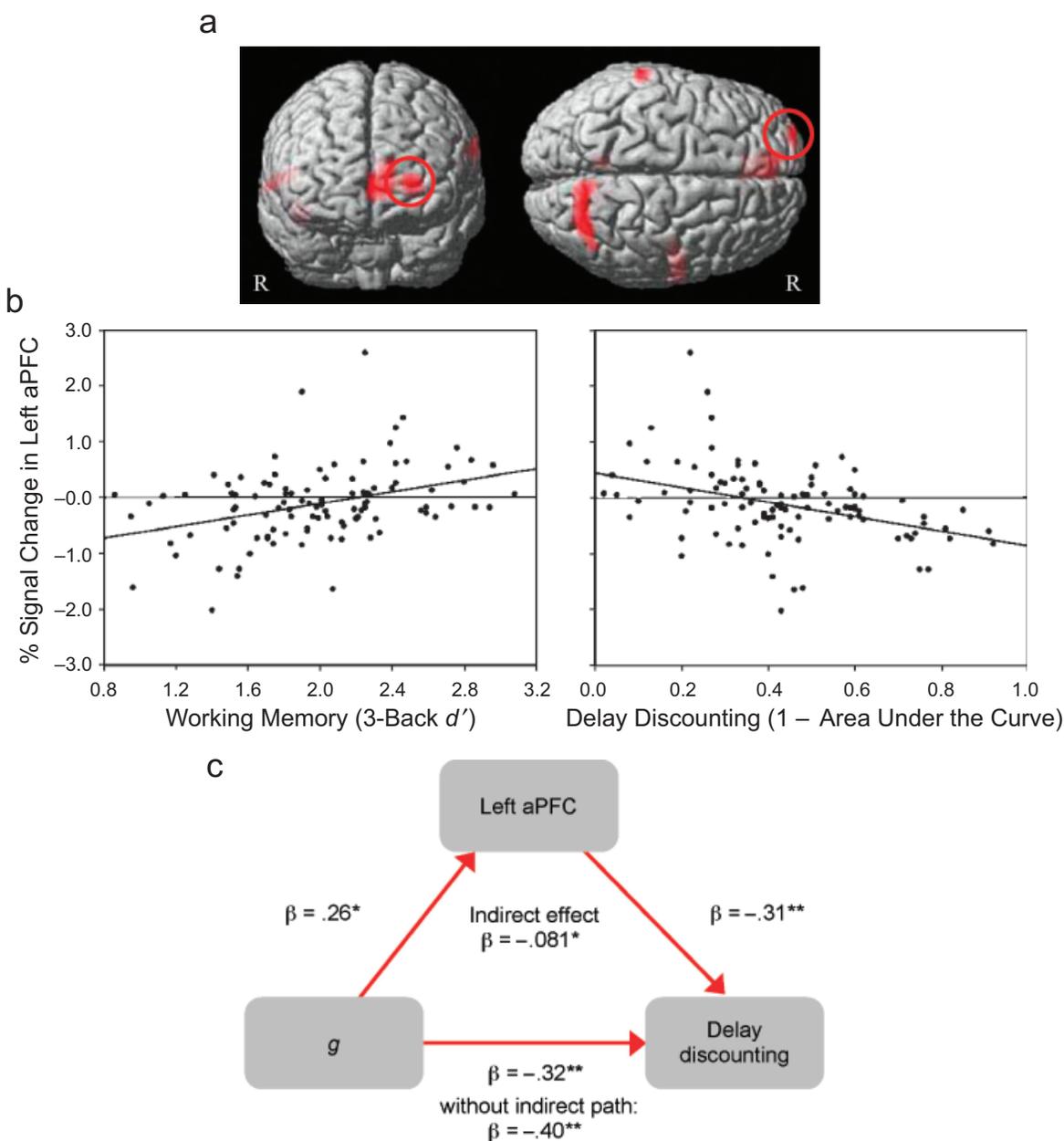


Fig. 1. Empirical results. The images in (a) illustrate the location of brain regions in which neural activity during the 3-back working memory (WM) task correlated significantly with performance on that task (shaded in red), $p < .001$, uncorrected (cluster extent threshold ≥ 15 voxels). The left anterior prefrontal cortex (aPFC) region of interest is circled. The label “R” indicates the right hemisphere. The scatter plots in (b) show the association between WM-related activity in the aPFC region of interest and both WM accuracy (d') and delay discounting. The path diagram in (c) illustrates the indirect relation between g and delay discounting, as mediated by WM-related activity in left aPFC. Values next to the arrows are regression coefficients for the path analysis, in which all three regressions are simultaneous. The zero-order coefficient for the relation between g and delay discounting, labeled “without indirect path,” is provided for comparison. The indirect effect represents the variance that g transmits to delay discounting through left aPFC, controlling for the direct path from g to delay discounting. Asterisks indicate the significance of the coefficients, $*p < .0083$, $p_{\text{rep}} > .955$; $**p < .001$, $p_{\text{rep}} = .99$.

wide range of cognitive processes (for a review, see Gilbert et al., 2006), which is noteworthy in part because, by definition, g refers to the common variance among diverse abilities. It is also notable that this region is among those in which cortical development tracks with maturation of intelligence in children

(Shaw et al., 2006). According to unifying theories of aPFC function that may explain its flexibility (Koechlin & Hyafil, 2007; Ramnani & Owen, 2004), the region’s principal role is to integrate the products of multiple, concurrent subtasks promoting a superordinate behavioral goal, especially when

these products are abstract or complex. Given this interpretation, it is not surprising that, in our study, better performance on the WM task (3-back) tracked with greater recruitment of this region: Ramping up this integrative machinery could facilitate coping with any number of the task's demanding attributes (e.g., integrating decision making about the target with the updating of WM content following presentation of each item).

The association of aPFC activity with delay discounting and intelligence, in addition to WM performance, is consistent with several neuroimaging studies implicating left lateral aPFC in integration as distinct from other processes more specifically associated with WM, such as maintenance and manipulation of information. We recently found, for example, that activity in left lateral aPFC associated with abstract, relational integration varies independently of other WM demands in analogical reasoning (Green, Fugelsang, Kraemer, Shamosh, & Dunbar, 2006). Left lateral aPFC appears to play a similar selective role in integration during mathematical problem solving (De Pisapia, Slomski, & Braver, 2007), matrix reasoning (Christoff et al., 2001), and episodic memory (Reynolds, McDermott, & Braver, 2006). In view of these converging results, the present finding has several implications regarding the nature of delay discounting and individual differences on this measure. It is consistent with the abstract nature of the goals and component arguments (e.g., future selves, reward events, delay periods) represented during the calculation of delay discounting. Moreover, it suggests that some of the variability in delay discounting hinges on individual differences in the ability to successfully integrate these abstract goals and component arguments.

The specific role of integration in delay discounting could play out in a number of ways. Delay-discounting tasks appear to recruit two distinct neural systems, one limbic and one prefrontal (McClure et al., 2004), and differences in aPFC function could affect the way in which signals from these systems are combined. Delay-discounting tasks may also involve the integration of cognitive and affective processes (Gray, Braver, & Raichle, 2002), or yet other processes, such as evaluating abstract and concrete features of the imagined events of receiving the rewards (Trope & Liberman, 2003) and maintaining information about previous options and choices in order to achieve temporally consistent behavior (Yarkoni et al., 2005). Whatever the specific role of integration in delay discounting, more intelligent individuals may discount less in part either because they are better at integration or because they adopt more integration-intensive strategies on delay-discounting tasks (cf. Frederick, 2005).

The present study raises some additional questions for future research. First, mediation of the relation between g and delay discounting by WM-related mechanisms was only partial, which means that other mechanisms also contribute to the association between g and delay discounting. This conclusion is also consistent with our behavioral finding that g accounted for variance in delay discounting independently of WM. Other mechanisms through which intelligence relates to delay discounting remain

to be investigated. Second, other regions besides aPFC demonstrated WM-related activity that was correlated with delay discounting. Although those correlations were substantially weaker and failed to mediate the relation between g and delay discounting, investigating their possible role in delay discounting is worthwhile, especially given that previous studies (e.g., McClure et al., 2004) have implicated some of them directly as being involved during delay-discounting tasks.

In summary, we found that WM-related activity in a region of left lateral frontopolar aPFC partially mediated the relation between g and delay discounting. Because g and WM are closely related behaviorally and neurally (Gray & Thompson, 2004), and because WM did not predict delay discounting independently of g in behavioral analyses, this region likely supports processes through which WM and g jointly relate to delay discounting. In the context of previous work suggesting that aPFC supports abstract, relational integration, our findings suggest that such integration may be critically involved in intertemporal choice and other demanding tasks. Thus, individuals with higher intelligence may prefer larger, later rewards to smaller, sooner ones primarily because they are better at abstract, integrative processes, or because they are more likely to use these processes when making certain types of decisions.

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