Neural mechanisms of general fluid intelligence

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We used an individual-differences approach to test whether general fluid intelligence (gF) is mediated by brain regions that support attentional (executive) control, including subregions of the prefrontal cortex. Forty-eight participants first completed a standard measure of gF (Raven's Advanced Progressive Matrices). They then performed verbal and nonverbal versions of a challenging working-memory task (three-back) while their brain activity was measured using functional magnetic resonance imaging (fMRI). Trials within the three-back task varied greatly in the demand for attentional control because of differences in trial-to-trial interference. On high-interference trials specifically, participants with higher gF were more accurate and had greater event-related neural activity in several brain regions. Multiple regression analyses indicated that lateral prefrontal and parietal regions may mediate the relation between ability (gF) and performance (accuracy despite interference), providing constraints on the neural mechanisms that support gF.

Understanding how and why people differ is a fundamental, if distant, goal of research efforts to bridge psychological and biological levels of analysis[1]. Individual differences are of wide practical importance and provide an opportunity to test theories of mental function at a finer level of detail than group-based studies. General fluid intelligence (gF) is a major dimension of individual differences and refers to reasoning and novel problem–solving ability[2]. A conceptual integration of evidence from cognitive (behavioral) and anatomical studies suggests that gF should covary with both task performance and neural activity in specific brain systems when specific cognitive demands are present, with the neural activity mediating the relation between gF and performance. Direct investigation of this possibility will be a critical step toward a mechanistic model of human intelligence[3–5]. In turn, a mechanistic model might suggest ways to enhance gF through targeted behavioral or neurobiological interventions.

Cognitively, gF is thought to be related to metacognition[6] (knowing about and reflecting upon one's own ongoing mental processes) and to working memory[4,5,7–9] (the active maintenance of domain-specific information plus domain-general attentional or 'executive' control of ongoing processing). One component of attentional control is the ability to overcome interference that would otherwise disrupt performance by compromising task goals or information held active in working memory. Individual differences in gF are most pronounced in behavioral measures when attentional control is required[4,8,10]. For this reason, gF is thought to be related to attentional control specifically[4,10,11]. These considerations imply that there should be a covariation of gF with brain activity in regions that are critical for attentional control. Moreover, the relationship between gF and brain activity should be stronger under high-interference conditions than under low-interference conditions.

Anatomically, the neural substrate of gF is thought to include portions of the prefrontal cortex (PFC)[12–16]. These data suggest a key constraint (localization) on the mechanisms of gF but have not further detailed the cognitive contribution(s) of PFC to intelligent behavior[3,5]. Moreover, previous neuroimaging studies of gF have been at best indirect because, to our knowledge, none has correlated gF with neural function across individuals to identify the neural systems. An attentional control view suggests that gF should be related to brain regions implicated in attentional control, namely lateral PFC[17–22], dorsal anterior cingulate[17,19,22–25] and lateral posterior cerebellum[17,26,27] (but see ref. 28). Investigating individual variability is essential because a lack of gF-related variation in lateral PFC would seriously undermine a major conclusion of group-based studies. Finding gF-related variation outside of lateral PFC would also be of significant interest.

To test whether individual differences in gF are mediated at a neural level by attentional control mechanisms, we first assessed gF in 48 subjects using a standard measure (Raven's Advanced Progressive Matrices) administered outside of the MR scanner. We then used fMRI to measure event-related brain activity as participants performed a challenging computerized task that was intended to activate the relevant neural systems. The three-back is widely used to probe working memory. In the present version (**Fig. 1**), participants viewed a series of stimuli that were either all words or all faces for a given scanning run, with a new stimulus item appearing every 2.36 s. Participants were instructed to indicate as quickly and accurately as possible whether each stimulus matched or did not match the stimulus seen three items previously, using two response buttons. A three-back match requires a 'target response'; in the sequence A–B–C–A, the second A is a target. If the current stimulus does not match the stimulus three-back, the trial requires a 'non-target response'; the D in B–C–A–D is a non-target because it does not match the B.

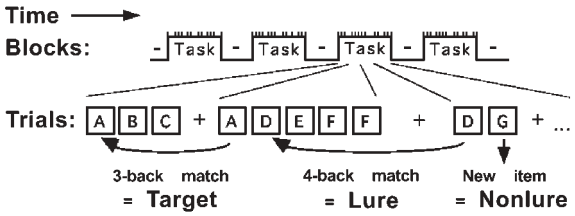


Fig. 1. Behavioral protocol, three-back task. Single capital letters represent task stimuli, which were either all words or all faces for a given scanning run. Blocks of task trials are separated by blocks of fixation (dash).

The task was administered in a standard way, but to assess brain activity during high and low attentional control conditions, we made a critical distinction among the non-target trials (compare with refs. 20,21). On some trials, the stimulus matched a recently seen, but non-target, stimulus: a two-back, four-back or five-back match (for example, the second D in D–E–F–F–D). We classified such non-target trials as 'lures' (higher interference from the recent stimulus and hence higher demand for control). All other non-target trials were classified as non-lures (for example, items never seen previously in the task; thus lower interference, less demand). A lure item can be easily confused with a target because the mere fact that it was seen recently is typically far more salient than its precise position within the temporal sequence of recent stimuli. Lure trials should require additional attentional control to overcome the tendency to make a target response merely on the basis of recency[20,21].

The main focus of the fMRI data analysis was event-related activity on trials for which a correct response was made; these comprised 87% of task trials (9% lures, 48% non-lures, 30% targets). We also examined task-related activity that was sustained across the task blocks (**Fig. 1**). Note that because task blocks are composed of trial events, any sustained (state, task block) activity overlaps in time with all trial-type effects (item, event-related). Variance in the MR signal was decomposed and assigned to sustained and event-related regressors using a general linear model (GLM)[29]. The sustained effect represents activity that was both present during the task blocks (relative to fixation blocks) and not explained by individual events. Each event-related effect represents the phasic deviation on a given trial type from the sustained level of activity.

We predicted and found that individual differences in gF were most evident on lure trials, both in terms of task performance and neural activity in areas that are critical for cognitive control. Moreover, our findings are consistent with the idea that brain activity in lateral PFC and parietal cortex mediates the relation between gF and task performance.

Results

Behavioral data

The demand for attentional control differed strongly by trial type, as revealed in behavioral performance (**Fig. 2a**). Lure trials were far more difficult (accuracy, 75% ± 2.5% correct (mean ± s.e.m.); response time (RT), 1,149 ± 27 ms) than non-lure trials (96% ± 0.4% correct, RT 919 ± 23 ms; $t_{57} > 9.3$, $P < 0.001$ for both accuracy and RT). Lure trials were as difficult as target trials in terms of accuracy (lure, 75% ± 2.5% correct; target, 78% ± 1.7% correct; $t_{57} = 1.58$, $P > 0.10$) but more difficult in terms of RT (lure, 1,149 ± 27 ms; target 992 ± 18 ms; $t_{57} = 7.26$, $P < 0.001$).

Across individuals, higher gF correlated positively with accuracy on lure trials ($r = 0.36$, $P < 0.01$; **Fig. 2b**). Although higher gF was also correlated positively with accuracy on non-lure trials

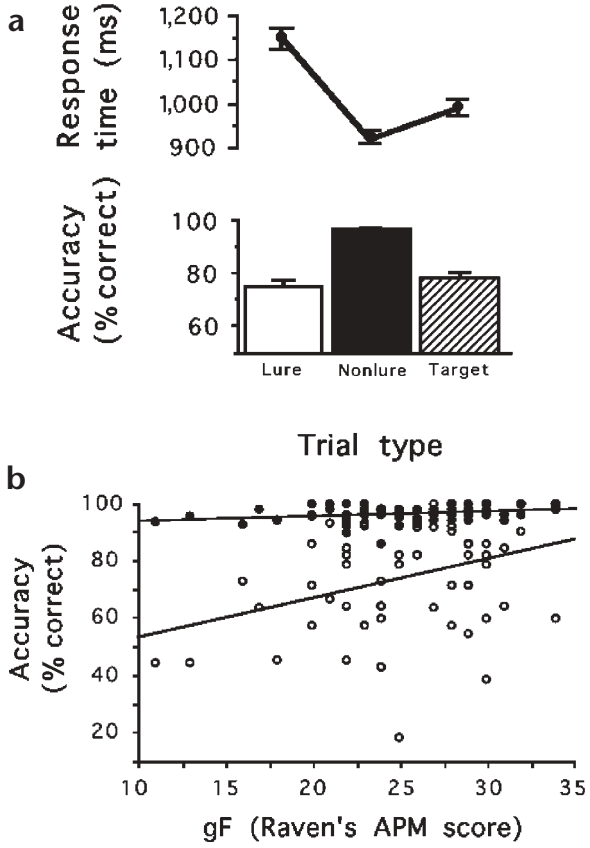


Fig. 2. Three-back task performance (n = 58). (**a**) Accuracy and response time by trial type (mean, error bars represent s.e.m.) (**b**) gF versus accuracy on lure (○) and non-lure (●) trials.

($r = 0.29$, $P < 0.05$) and on target trials ($r = 0.36$, $P < 0.01$), gF explained incremental variance in accuracy on lure trials after controlling statistically for accuracy on non-lure trials (hierarchical regression, $pr = 0.27$, $P < 0.05$) and, in a separate analysis, after controlling for accuracy on target trials ($pr = 0.26$, $P < 0.05$). gF was unrelated to RT ($r = 0.08$ lure, $r = -0.04$ non-lure, $r = -0.003$ target).

Neuroimaging data

On lure trials, gF correlated positively with the magnitude of event-related activity in the *a priori* search space: lateral PFC, dorsal anterior cingulate, and lateral cerebellum (**Fig. 3** and **Table 1**). Across the whole brain (unconstrained search), similar relations held within parietal and temporal cortex as well.

To probe these results, we conducted further analyses at a region level (as illustrated for left lateral PFC, **Fig. 4**). For these analyses, we averaged together the activity estimates from all voxels within a region, and combined the verbal and nonverbal conditions. For each region in **Table 1**, the relation between gF and correct lure-trial activity remained significant in a regression analysis controlling for the following factors: brain activity within that region on both correct non-lure and correct target trials during the same scanning run, accuracy on lure trials and RT on lure trials. These analyses indicate a robust and specific covariation of gF with brain activity on lure trials.

Further, we used multiple regression to formally test whether brain activity in each identified region could mediate

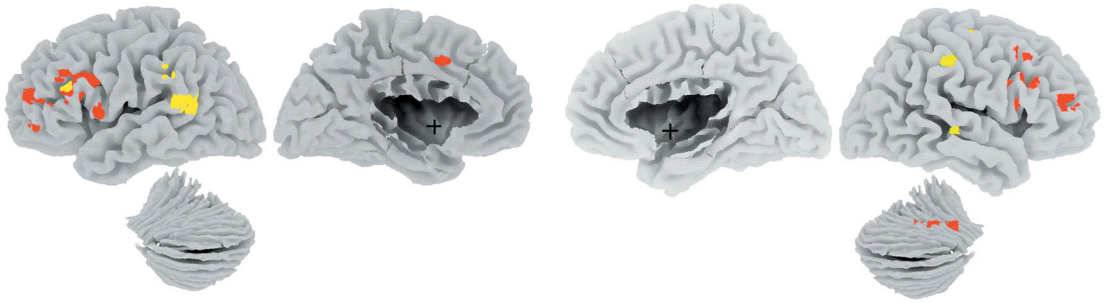


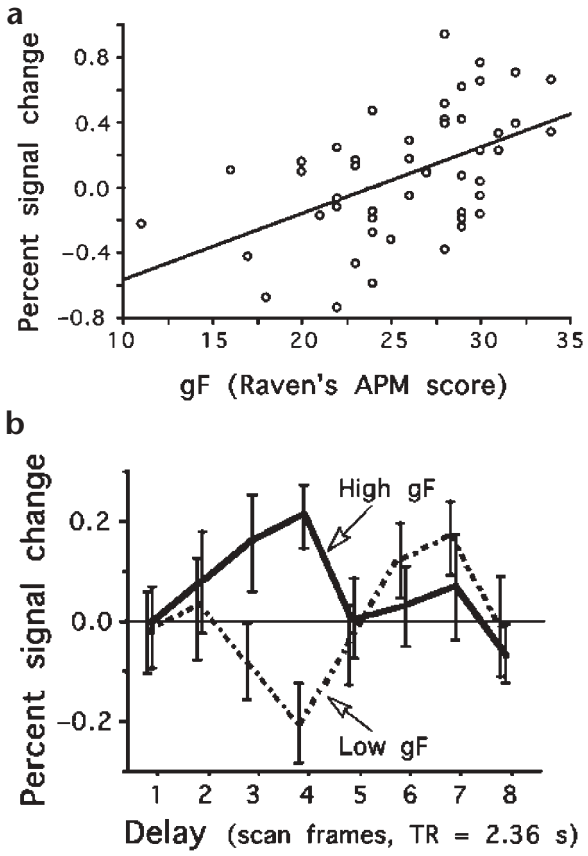
Fig. 3. Regions in which gF predicted lure-trial activity, using *a priori* (red) and whole-brain (yellow) search criteria, shown on the folded surface of a standard brain[48]. From left to right: left lateral, left medial, right medial and right lateral views. The corresponding lateral cerebellar surface is shown below each lateral cortical surface. Voxels meeting the *a priori* threshold outside of the search space are not shown.

the association between gF and behavioral performance on lure trials. For each region, when controlling for lure-trial activity within the region (as a hypothesized mediator variable), the shared variance between gF (ability, predictor variable) and accuracy (performance, dependent variable) decreased by up to 92% (**Table 1**, note c); that is, up to 92% of the gF–lure accuracy relation ($R^2 = 0.09$) could have been mediated by a single brain region. Three regions (left lateral PFC and parietal cortex

Table 1. Regions in which gF predicted neural activity on lure trials.

Regions[a]	Coordinates			Size	Relation to behavior[b]				Mediator?[c]	Sustained activity[d]	
					gF	gF	gF	Accuracy		t_{47}	gF
	x	*y*	*z*		*r*	*pr*	r_{diff}	*r*	$\%R^2$	*t*	*r*
A priori											
Lateral PFC											
L 46	–32	42	18	59	0.55	0.52	0.49	(0.21)	(41)	(0.78)	(–0.13)
R 46	40	42	18	37	0.48	0.47	0.46	(0.12)	(14)	(–0.77)	(–0.13)
L 44 / 10	–44	42	0	10	0.50	0.46	0.44	(0.26)	(54)	(0.74)	(0.00)
L 46 / 45	–46	21	24	88	0.54	0.47	0.49	0.44	92	3.39	(–0.14)
R 9	46	18	33	32	0.45	0.34	0.45	0.40	(75)	2.93	(–0.05)
L 44 / 9	–40	9	27	83	0.51	0.43	0.46	0.38	(79)	7.91	(–0.06)
R 44 / 45	44	9	21	65	0.48	0.39	0.45	0.44	86	(0.90)	(–0.16)
Dorsal ACC											
L 24	–10	3	45	20	0.45	0.38	0.39	0.30	(56)	(–0.76)	(0.01)
Lateral Posterior Cerebellum											
R lobule VI	28	–54	–24	26	0.46	0.38	0.42	(0.18)	(32)	(–0.65)	(–0.07)
Whole-brain											
Frontal											
L 46 / 45	–46	18	24	21	0.51	0.42	0.46	0.43	88	4.69	(–0.14)
R 4	58	–12	45	8	0.49	0.42	0.40	0.34	(70)	–2.16	–0.31
Parietal											
L 40	–38	–39	42	21	0.51	0.37	0.40	0.38	(78)	4.43	(–0.11)
L 40	–56	–42	33	8	0.52	0.37	0.42	0.44	89	(–0.72)	(0.02)
R 40	46	–33	45	12	0.53	0.39	0.35	0.45	91	(1.25)	–0.31
R 31	20	–66	9	13	0.59	0.60	0.60	(0.24)	(55)	–2.82	(–0.15)
Temporal											
L 22 / 39	–56	–54	12	39	0.60	0.43	0.52	0.40	(91)	(–0.90)	(0.15)
R 22	50	–30	3	10	0.58	0.56	0.52	(0.26)	(60)	–2.70	(–0.28)

[a]PFC, prefrontal cortex; ACC, anterior cingulate cortex; L, left; R, right; approximate Brodmann area[42]. Talairach coordinates[42] are of the center of mass (*x*, left–right; *y*, posterior–anterior; *z*, inferior–superior). Size, number of $3 \times 3 \times 3$ mm voxels.
[b]Region-level relations between correct lure trial activity and behavioral measures, $n = 48$; *r*, zero-order correlation of gF with lure activity; *pr*, partial correlation of lure activity with gF after controlling for behavioral performance on lure trials (accuracy, mean RT) and for neural activity in the same region on other trials (correct non-lure, target); r_{diff}, zero-order correlation of gF with the lure minus non-lure difference in activity (see caveat, last paragraph of Methods); accuracy, zero-order correlation of lure-trial activity with the percentage of correct responses on lure trials.
[c]Percentage decrease in the variance (R^2) between gF and lure trial accuracy when lure trial activity within the brain region was partialled out (as a hypothesized mediator); statistical significance was calculated using the Sobel test[30].
[d]Region-level sustained activity. t_{47}, *t* value from a *t*-test against zero (0 = no sustained activity; positive *t* indicates greater activity during the task blocks than during fixation blocks); gF, zero-order correlation between gF and sustained activity.
Statistics in parentheses have associated $P > 0.05$, two-tailed.



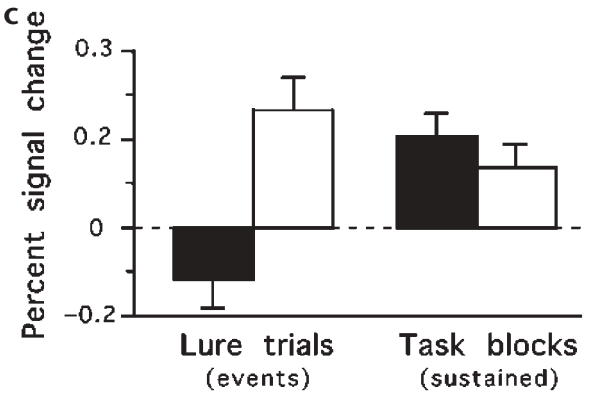


Fig. 4. Region-level relations between gF and brain activity in left lateral PFC (BA 46/45, 21 voxels from whole brain search, $n = 48$). Error bars indicate s.e.m. (**a**) gF versus the magnitude of correct lure-trial activity. (**b**) Time course of correct lure-trial activity by gF group (high versus low, based on a median split). (**c**) Neural activity by type (lure trial versus sustained) within high-gF (□) and low-gF (■) groups.

bilaterally, from the whole-brain search) simultaneously explained more than 99.9% of the gF–accuracy relationship (associated $P = 0.0089$, from the Sobel test[30]). To summarize, there were significant zero-order correlations between gF and neural activity in several regions. There was also a significant zero-order correlation between gF and accuracy ($R^2 = 0.09$), but there was virtually nothing about accuracy that gF could explain beyond that which neural activity in three brain regions explained. Conversely, neural activity predicted accuracy even when holding gF constant. This multivariate relationship is consistent with the hypothesis that the regions mediated[30] the relation between gF and lure-trial accuracy.

On non-lure and target trials, relations between gF and brain activity were far weaker. Across the whole brain, no region was reliably related to gF on either type of trial. In the *a priori* search space, gF correlated with activity in a single region on non-lure trials (nine contiguous voxels in the left lateral cerebellum, at –42 –49 –30 (*x y z*); region level, $r = 0.47$, $P < 0.001$) and a single region on target trials (eight contiguous voxels in the left lateral PFC, at –49 24 30; region level, $r = 0.46$, $P < 0.001$).

The observed correlations between event-related brain activity and gF were all positive in direction. Negative correlations held only in isolated voxels or in clusters outside the *a priori* search space.

A number of brain regions showed strong increases in sustained activity that were associated with three-back task performance (**Table 1**). The magnitude of the sustained activation, however, was only weakly if at all correlated with gF; no regions were identified using either the *a priori* or whole-brain search criteria. In an exploratory analysis (searching the whole brain at the *a priori* threshold), sustained activity was negatively correlated with gF in eight voxels in right medial dorsal thalamus (which is intriguing given its anatomical relationship to the prefrontal cortex). Some of the brain regions in **Table 1** (which were all identified using event-related activity) had sustained activity that was significantly different during the task as compound to fixation. In left lateral PFC, for example (**Fig. 4c**), sustained activity was substantial ($t_{47} = 4.69$, $P < 0.001$) but did not covary with gF ($r = –0.14$), whereas lure-trial activity did covary with gF ($r = 0.46$), with a significant interaction between activity type (sustained versus lure) and gF group (high versus low, based on a median split) ($F_{1,46} = 15.88$, $P < 0.001$).

Discussion

To our knowledge, this is the first large-sample imaging study to probe individual differences in general fluid intelligence, an important cognitive ability and major dimension of human individual differences. Our trial-type decomposition gave a high degree of experimental control over individual differences in motivation and other potential confounding factors. The data suggest that lateral PFC, a key brain region suspected to support reasoning and novel problem solving ability, does in fact show meaningful between-subject variability in neural activity. Critically, a formal statistical test suggested that neural activity in this region mediated the relation between ability (gF) and performance on a demanding working-memory task. Thus, the results reported here provide the first direct support for a major hypothesis about the neurobiological basis of gF.

Beyond confirming the involvement of lateral PFC, our results indicate that there is specificity in the type of cognitive situations in which neural differences are evident. gF-related differences in brain activity emerged almost exclusively on working memory trials with high interference, as predicted from behavioral evidence showing the importance of attentional control in protecting goals, or other information held actively in mind, from such interference[4,8,10]. Thus, our results also directly support a specific interpretation of the meaning of gF differences at a cognitive level.

Some neuroimaging studies have reported that higher gF is associated with less brain activity, possibly representing greater

neural efficiency[5]. This direction of effect is also found in studies of skill-learning and expertise in which activity in lateral PFC, ACC and cerebellum decreases with practice, regardless of task domain[17]. In the present study, however, higher gF was associated with greater activity, possibly as a result of our theoretically motivated focus on high-interference trials. Another possible explanation is that in previous studies, high-ability participants may have activated brain regions more strongly but for a shorter duration (related to faster performance), and hence came to show less total activation as integrated over time. Our event-related design and explicit control for behavioral performance avoided this possible confusion.

Apparently, our results both converge and conflict with a positron emission tomographic (PET) study[16] of 13 participants in which it was found that difficult, gF-sensitive tasks selectively recruit lateral PFC. Note that this study involved a comparison of group means in different task conditions and did not use individual variation to identify brain regions. Although we also implicate lateral PFC, we arrived at this result by a search for variability—a search that revealed several brain areas, some involved as strongly as the lateral PFC. It is possible (but not certain) that we had greater statistical power to detect effects and therefore found more regions. In the PET study[16], however, relaxing the statistical threshold did not reveal more regions, indicating that the selective activation of lateral PFC was not due to low power. Difficult tasks seem to require attentional control and recruit lateral PFC selectively, but individuals with greater fluid intelligence show greater activity across a wider network of brain regions while exerting attentional control to overcome cognitive interference. Thus, although the two studies converge, a complete picture of the relationship between neural activity and human traits and abilities must account for both central tendencies and individual variation.

To derive a mechanistic model of gF, a key step is to describe cognitive–anatomic covariation constrained by a specific theory[1]. We identified neural signals associated with gF in several brain regions during high-interference conditions selectively. The particular cognitive contribution of these signals probably varies by brain region; because the data are correlational, it is possible that some of the identified regions may not contribute causally to task performance. Of those that do contribute, there are many possible cognitive functions that a given region might be supporting: the inhibition of incorrect responses cued by familiarity[20,21], the detection, monitoring or reduction of conflict[22,31,32], increased mental checking under high-interference conditions, maintaining or updating task goals and subgoals[33], re-engaging task processes after a lure trial, other forms of switching between task components, and so on. Our present data do not distinguish between these possibilities. Such heterogeneity might partly explain the correlations observed in posterior areas. These areas are not thought to mediate attentional control, but parietal regions are likely to be recruited by control processes during working memory tasks. Moreover, individual differences in the effective connectivity between brain regions might contribute to differences in fluid intelligence and might further explain the posterior associations.

Large-sample neuroimaging studies are expensive and time-consuming, but they provide unique information. Whereas some questions about human mental function cannot be answered by studying individual differences, definitive answers to other questions require an individual-differences approach[1,34]. Correlational data are critical for understanding covariation at a fine-grained level, but cannot establish causation definitively. Nonetheless, the plausibility of causal models of brain–behavior relationships can be tested quantitatively in correlational data. Analyses of this type suggest that some regions that we identified are more likely than others to mediate gF, despite all having a significant correlation with gF. Also of note, the selective covariation of gF with lure-trial activity (controlling for non-lure) is a much more specific result than just a simple (zero-order) correlation. For example, from a simple correlation, it would be unclear to what extent individual differences in task strategy, motivation and so on, might contribute to the observed association between gF and lure-trial neural activity. However, other trials provide a control within the same scanning run. The selective covariation of gF with brain activity on high-interference (lure) trials but not other trials suggests that low-gF participants did not differ sufficiently from high-gF participants in their strategy and motivation to account for the key results.

Because gF is partly heritable[5], it is intriguing that gF was related to brain function in areas in which gray matter volume is under significant genetic control, notably lateral PFC[13]. The PFC in general has undergone considerable expansion throughout evolution, with human PFC being nearly twice the size of chimpanzee PFC as a percentage of the total cortical surface[15,35]. Given such convergence, future studies exploring the relationships among functional, structural, genetic and cognitive correlates of gF within the same sample would be valuable.

Finally, it is worth emphasizing that gF and related forms of intelligence are not completely determined by heredity. Behavioral interventions (such as schooling) and other factors can have markedly positive influences on intelligence[36–38]. Given such plasticity, a mechanistic understanding of gF could, in theory, lead to more specific and targeted approaches to enhancing gF.

Methods

Subjects. Participants ($n = 60$) were healthy, right-handed, native English speakers (aged 18–37 years, 29 male) from Washington University and the surrounding community. They were screened to ensure no history of neurological disorder, current psychoactive medication or factors contra-indicating fMRI. All participants gave written informed consent, and the experiment was approved by the Washington University Medical Center Human Subjects Committee. Two participants performed near chance on the three-back task ($d' < 1$) and so were excluded from all analyses. Ten participants had fMRI datasets that were compromised by excessive head movement, technical problems, or too few trials for estimating event-related responses.

Behavioral tasks. Raven's Advanced Progressive Matrices (APM)[39], a widely used measure of gF[5], was administered before the fMRI session. gF was taken to be the number of correct responses on APM set II made in 40 min (36 questions; observed range 11–34 correct, mean 25.5, s.d. 4.9).

The three-back task was administered using PsyScope[40] on a Macintosh G3 (Apple Computer, Cupertino, California). For a given scanning run, stimuli were either all words (concrete English nouns) or all faces (unfamiliar, male and female intermixed)[41]. Stimuli were shown one per trial for 2.0 s, with a fixation point (cross-hairs) shown between stimuli (**Fig. 1**).

Each scanning run had four unanalyzed trials, followed by four blocks of 21 task trials (16 task stimuli with 5 crosshair fixation trials randomly interspersed to introduce temporal jitter) and 23.6 s (10 trials) of resting fixation (a dash), for a total of 128 trials per scanning run (2.36 s per trial).

Data from two scanning runs per participant are reported here (one run with words, one run with faces, order counterbalanced), although additional runs were also obtained. Just before each scanning run, participants watched one of six 7-min videos, two of which were emotionally neutral and four of which were emotionally evocative (order counterbalanced). All data reported here are from the two neutral conditions. In analyses controlling for scan order and self-reported emotional state after the neutral video (before the scan), all partial

correlations between gF and activity remained significant and very similar to the corresponding zero-order correlations reported in **Table 1**. The only reduction in effect size was in right parietal cortex (BA 40; $pr = 0.51$, $P < 0.001$, versus $r = 0.53$).

fMRI data acquisition and analysis. Whole-brain images were acquired on a 1.5-tesla Vision System (Siemens, Erlangen, Germany). Structural images were acquired using an MP-RAGE T1-weighted sequence. Functional images were acquired using an asymmetric spin-echo echo-planar sequence (T.E. Conturo *et al.*, *Soc. Neurosci. Abstr.* **26**, 7, 1996) (TR = 2,360 ms, TE = 50 ms, flip = 90°), sensitive to blood-oxygen-level-dependent (BOLD) magnetic susceptibility. Each scanning run gave 128 sets of brain volumes (16 contiguous, 8 mm thick axial images, 3.75 × 3.75 mm in-plane resolution). After movement and artifact correction, functional images were normalized within each scanning run and temporally aligned within each brain volume. Functional images were re-sampled into 3 mm isotropic voxels, transformed into atlas space[42] and smoothed with a Gaussian filter (9 mm FWHM) before statistical analysis[43].

For each participant, we estimated the magnitude of both event-related and sustained neural activity at each voxel using a general linear model (GLM)[29]. A fixation trial–derived baseline was also estimated in the same GLM using the interspersed fixation trials. The GLM partitioned variance in the MR signal to estimate the magnitude of hemodynamic responses[44] on correct lure, non-lure and target trials, and activity sustained across the task blocks. These estimates are reported as the percentage of change from fixation. Statistically, these estimates were free from the influence of error trials, linear trend and other nuisance effects.

Across the group of participants, we then screened for voxels in which the magnitude of brain activity was correlated with gF. Each voxel had to meet multiple criteria, protecting against false-positive errors[41,45]. Criteria included having zero-order correlations between gF and neural activity in both the word condition and in the face condition, as tested by conjunction analysis[46]. Because gF is a domain-general ability, we required the word and face correlations to have the same sign, thereby eliminating two of four possible combinations. Based on simulations[45], the voxel-wise threshold for each correlation separately was set to $P < 0.05$ for regions of interest *a priori*, and to $P < 0.01$ for whole-brain analyses. When these criteria (word threshold, face threshold, same-sign restriction) are combined, the overall voxel-wise thresholds are equivalent to $P < 0.00125$ (= 0.05 * 0.05 * 0.5, *a priori*) and $P < 0.00005$ (= 0.01 * 0.01 * 0.5, whole brain). Contiguous clusters of eight or more such voxels were considered significant regions of interest.

Within each identified region, we used multiple regression to test whether the relation between gF and lure trial brain activity held on lure trials specifically. Although one might think to correlate gF with a lure – non-lure difference score (to assess a gF by trial type interaction), regression is preferred for this analysis[47]. The reason is that if there is a non-zero correlation between a control condition (non-lure) and a difference score (lure – non-lure), the nonzero correlation contaminates the interpretation of the correlation between another variable of interest (gF) and the difference score. In the extreme case, a difference-score approach could identify a spurious gF by trial type interaction that was due entirely to the non-lure trials, with no contribution of the lure trials. Regression protects against this possibility while retaining the interpretive advantages of assessing what is effectively a gF by trial-type interaction.

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Competing interests statement

The authors declare that they have no competing financial interests.

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