Research Focus

The intelligent brain in conflict

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Can individual differences in general reasoning ability be reduced to an elementary cognitive process or isolated to a neural circuit? A breakthrough neuroimaging study finds that fluid intelligence and attention control are behaviorally linked via the neural activity in brain areas involved in resolving cognitive conflict.

General fluid intelligence (gF) is a statistical construct, derived from factor analyses of reasoning and problem-solving tests [1,2]. Nonetheless, it reflects a real and robust empirical fact in need of explanation: Diverse tests of novel reasoning correlate positively with one another. This 'positive manifold' indicates that people who perform well (or poorly) on one reasoning test also tend to perform well (or poorly) on other reasoning tests, despite stark differences among the tasks in their surface and structural characteristics. Recent intelligence research from a cognitive perspective seeks to explain gF by reducing it to basic processes described by information-processing models [3–6]. In parallel, neuroscience work currently explores whether gF can be linked to neurological events, observed via such imaging techniques as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) [7,8]. A recent neuroimaging study by Gray, Chabris and Braver [9] has innovatively married the cognitive and neuroscience approaches. They provide compelling evidence that the linked constructs of working memory (WM), attention control, and goal maintenance, thought to rely especially on the brain's prefrontal cortex (PFC), hold promise as fundamental mechanisms of psychometric gF [10,11].

Previous theoretical efforts to link fluid intelligence to 'elementary' cognitive processes have been criticized as forms of illusory reductionism. That is, constructs such as WM and goal maintenance are measured with complex mental tasks that are similar to psychometric intelligence tests, and so they only re-name, rather than explain, gF [12]. And, although cognitive neuroscience can avoid the nagging question of whether it is reducing or simply re-describing intelligence by searching for its neural correlates, neuroimaging work to date has been limited to localizing brain activity that is elicited *within* a given fluid-ability test [13,14]. This research has therefore overlooked the critical question of whether such neural activity has anything to do with individual differences in performance or with the variance that is shared among gF tests. By analogy, most automobiles rely on a similar braking system, the critical components of which can be identified through observations of a stopping car. Yet, differences in braking distance among automobiles need not result only from variation in the performance of pads, drums and master cylinders. Differences might also (or instead) derive from variability in tire balance, the aerodynamics and weight of the chassis, or the ergonomic placement of the brake relative to the accelerator pedal, despite the fact that these are not basic mechanisms of braking. Because gF represents individual differences in performance that are shared among diverse tasks, then it must be studied as a multivariate construct and not in isolation.

Correlating variation across behavior and brain

Gray *et al.* recognized the centrality of individual differences to the gF construct, and thus their work goes well beyond previous research by merging behavioral and fMRI data to examine important individual differences in cognition [9]. More specifically, Gray and colleagues trace the WM–gF relationship to event-related activity in lateral PFC and parietal cortex, elicited in conditions of cognitive conflict. They tested 48 subjects in two cognitive tasks reflecting gF and WM, respectively, and this large (for imaging research) subject sample enabled the researchers to assess how well performance in the gF task predicted individual differences in WM performance and WM-related neural activity.

The Ravens Advanced Progressive Matrices (RAPM) test was used to assess gF, as it has in numerous studies of general cognitive ability [15–18]. The RAPM presents incomplete matrices consisting of novel figural stimuli, and subjects must induce the relations among the figures to select the correct completion (see Fig. 1). Subjects here completed the RAPM outside the fMRI scanner, before participation in the WM task. The WM task was an n-back task, in which subjects viewed a sequence of visual stimuli (words or faces) at a rate of one every 2.36 s, and indicated whether or not each stimulus matched the one seen 3 items ago in the sequence. The n-back task is considered a marker of WM processes because it requires subjects to continually maintain and update an evolving list of stimuli. Extensive neuroimaging research indicates that as the value of n increases between 1 and 3, so does activity in several brain areas, including lateral PFC [19,20].

As illustrated in Fig. 2, Gray and colleagues further measured the degree of attention control required by the n-back task by contrasting two different non-target trial types: 'lure' and 'non-lure' foils. Lure foils matched a stimulus 2, 4, or 5 items ago in the sequence, and thus presented substantial interference with the 3-back task demand. Non-lure foils were all other non-target trials (items never seen before, or matches seen 1-back or

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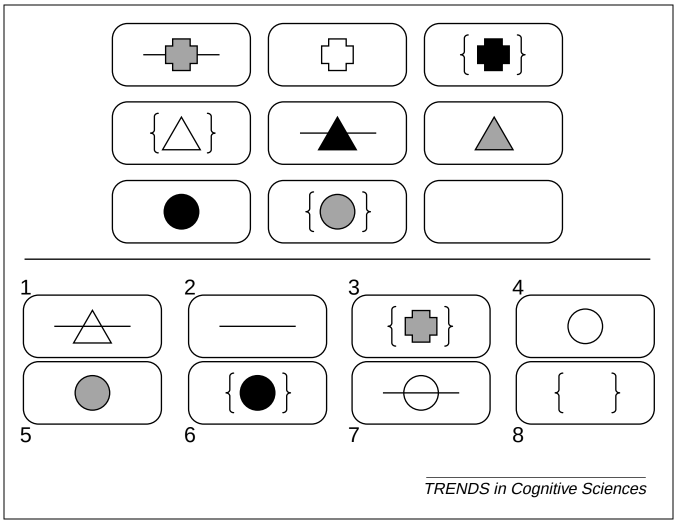

Fig. 1. A modified sample problem from the Ravens Advanced Progressive Matrices (RAPM) test. The subject must select the appropriate figure to complete the sequence from the set of figures labelled 1–8 below.

6-or-more-back, which therefore provoked less interference). If gF and lateral PFC functions are especially important when interference or conflict challenge attention control [21,22], then gF should most strongly predict accuracy and brain activity in *n*-back lure trials. In fact, lure foils were much less accurately rejected by subjects than were non-lure foils. For the crucial question, regarding individual differences in gF and its relationship to the attentional control of conflict, the key behavioral data were correlational: lure-foil accuracy correlated positively with gF, and remained significant after partialling out individual differences in non-lure foil accuracy or target accuracy. Thus, fluid intelligence clearly predicted attention-control effectiveness in the *n*-back task as indexed by interference resistance.

Neural mediation of the gF/control relationship

Gray *et al.* therefore examined the event-related brain activity during *n*-back performance that was specific to resolving lure-foil interference. They did so, first, in brain regions expected on *a priori* grounds to be involved in conflict detection and resolution: lateral PFC, dorsal anterior cingulate, and lateral posterior cerebellum. The authors additionally conducted an unconstrained search for event-related *n*-back activity in the entire brain. In the *a priori* search, lure-trial activity in several lateral PFC regions correlated significantly with both lure-trial accuracy and gF, as did activity in some inferior frontal areas and dorsal anterior cingulate (rs ≈ 0.40–0.50). High-gF subjects showed a markedly greater increase in fMRI signal in left lateral PFC on lure trials than did low-gF subjects (Fig. 3). Indeed, many low-gF subjects actually showed a decrease in signal on lure trials relative to their overall activity level in the *n*-back task. High gF individuals thus appeared to engage in more extensive ‘mental work’ in the presence of interference than did those of low gF.

The whole-brain analysis demonstrated similarly strong correlations between gF and lure-related activity in regions of frontal, parietal and temporal cortices. Moreover, the authors used path analysis to test formally whether brain activity in specific regions could mediate the expected (and observed) relationship between the two behavioral measures (gF and *n*-back performance). Several brain regions showed a simple correlation between lure-trial activity and gF, which is weakly consistent with a causal role of the brain region in mediating gF. In fact, some but not all of these regions also survived the path-analysis test for a mediator role. Strikingly, the lure-trial neural activity in lateral PFC and parietal cortex together accounted for 99.9% of the variance shared by gF and lure-trial accuracy. These results are consistent with the hypothesis that a mere three regions entirely mediated the relationship.

Gray *et al.* did not observe large gF x brain-activity correlations for other aspects of *n*-back performance, a fact that is particularly germane to theories linking WM and lateral PFC functions to gF via their involvement in the attentional control of interference [10,23]. Although gF predicted behavioral accuracy on non-lure and target trials, its correlation with brain activity during these trials was much weaker. Despite the fact that lateral PFC and parietal areas generally increased their activity in the *n*-back task compared to baseline, none of this sustained brain activity correlated significantly with gF, thus recalling the analogy of distinguishing basic braking mechanisms from sources of braking variation. In sum, only WM processes that were tied directly to interference control were supported by gF-related brain activity.

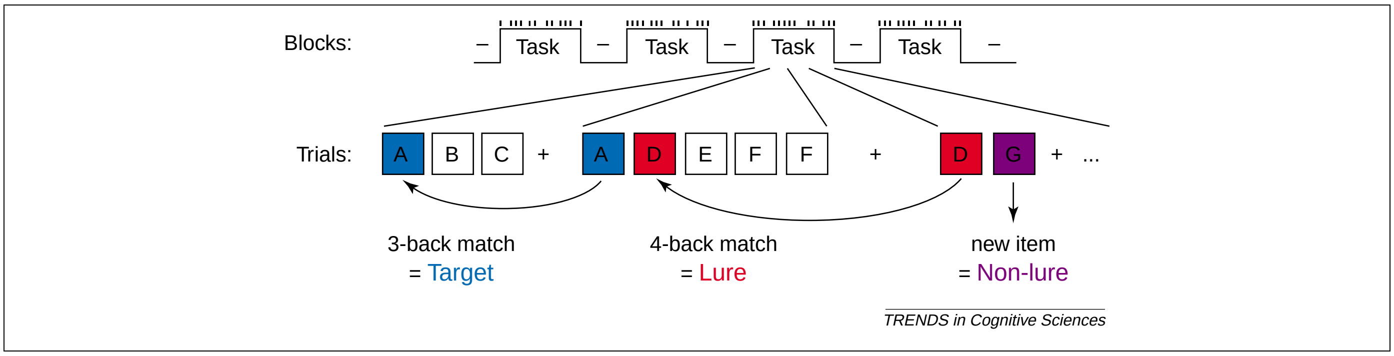

Fig. 2. The *n*-back task, used to assess working memory. The subject must indicate whether each stimulus in a sequence matches one seen 3 items ago (i.e. the target is a 3-back match). A ‘lure’ trial is one in which there is a 2-, 4- or 5-back match. Adapted with permission from [14].

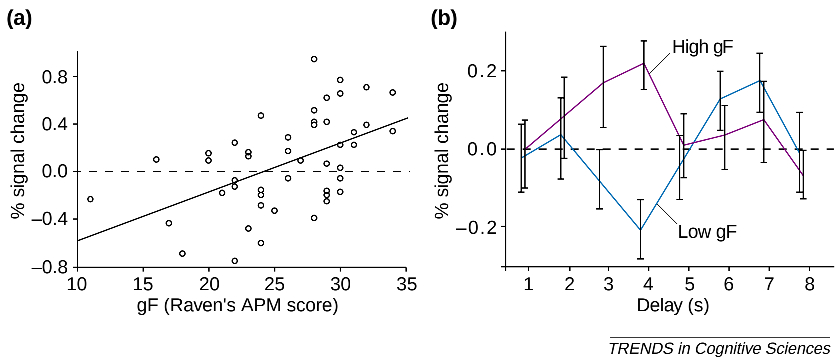

Fig. 3. **(a)** The relationship between gF, as measured by the RAPM test, and increase in fMRI signal in the left lateral prefrontal cortex. **(b)** Subjects with a high gF showed a markedly greater increase in activity than did low-gF subjects on lure trials (2-, 4- or 5-back match trials). Adapted with permission from [14].

Conclusions

Gray and colleagues' union of cognitive, neuroscience, and individual-differences methods has discovered that the correlation between gF and event-related neural activity in the *n*-back task is broadly obtained only under conditions of cognitive conflict that challenge attention control. Moreover, the correlation between gF and performance under conflict is mediated almost entirely by conflict-specific neural activity in lateral PFC and parietal cortex. The psychometric construct of gF might therefore be partially explainable as an ability to control attention that relies, at least in part, on activity within PFC and parietal circuitry.

Although the Gray *et al.* study represents a considerable methodological and conceptual advance in intelligence research, substantial challenges remain for future work. Pragmatically, the costs of running large-scale neuroimaging studies like this one are formidable and they are likely to increase as researchers move towards more sophisticated means of measurement, using multiple tests of each critical construct, testing very large subject samples, and subjecting the behavioral and imaging data to multivariate statistical techniques such as confirmatory factor analysis and structural equation modeling. A major conceptual difficulty also remains in the underspecification of the cognitive operations required to correctly reject a lure foil in the *n*-back task. The possibilities are numerous, as the authors indicate, including conflict monitoring and detection, assessment of familiarity versus recollection, response inhibition, and task-set switching between lure and target response demands. Coupled with the obvious complexity and multidimensionality of gF tasks, a truly reductionist explanation for general fluid intelligence awaits further groundbreaking research.

References

1 Carroll, J.B. (1993) *Human Cognitive Abilities: a Survey of Factor-Analytic Studies*, Cambridge University Press
2 Jensen, A.R. (1998) *The g Factor: the Science of Mental Ability*, Praeger
3 Deary, I.J. and Stough, C. (1996) Intelligence and inspection time: achievements, prospects and problems. *Am. Psychol.* 51, 599–608
4 Jensen, A.R. (1993) Why is reaction time correlated with psychometric *g*? *Curr. Dir. Psychol. Sci.* 2, 53–56
5 Kyllonen, P.C. and Christal, R.E. (1990) Reasoning ability is (little more than) working-memory capacity?! *Intelligence* 14, 389–433
6 Sternberg, R.J. (1977) *Intelligence, Information Processing, and Analogical Reasoning: the Componential Analysis of Human Abilities*, Erlbaum, Hillsdale, NJ
7 Haier, R.J. *et al.* (1992) Intelligence and changes in regional cerebral glucose metabolic rate following learning. *Intelligence* 16, 415–426
8 Vernon, P.A. (1990) The use of biological measures to estimate behavioral intelligence. *Educ. Psychol.* 25, 293–304
9 Gray, J.R. *et al.* (2003) Neural mechanisms of general fluid intelligence. *Nat. Neurosci.* 6, 316–322
10 Duncan, J. (1995) Attention, intelligence, and the frontal lobes. In *The Cognitive Neurosciences* (Gazzaniga, M., ed.), pp. 721–733, MIT Press
11 Kane, M.J. and Engle, R.W. (2002) The role of prefrontal cortex in working-memory capacity, executive attention, and general fluid intelligence: an individual-differences perspective. *Psychon. Bull. Rev.* 9, 637–671
12 Deary, I.J. (2000) *Looking down on human intelligence*, Oxford University Press
13 Duncan, J. *et al.* (2000) A neural basis for general intelligence. *Science* 289, 457–460
14 Prabhakaran, V. *et al.* (1997) Neural substrates of fluid reasoning: an fMRI study of neocortical activation during performance of the Raven's Progressive Matrices Test. *J. Cogn. Psychol.* 33, 43–63
15 Raven, J.C. *et al.* (1998) *Progressive Matrices*, Oxford Psychologists Press
16 Carpenter, P.A. *et al.* (1990) What one intelligence test measures: a theoretical account of the processing in the Raven Progressive Matrices test. *Psychol. Rev.* 97, 404–431
17 Engle, R.W. *et al.* (1999) Working memory, short-term memory and general fluid intelligence: a latent variable approach. *J. Exp. Psychol. Gen.* 128, 309–331
18 Marshalek, B. *et al.* (1983) The complexity continuum in the radix and hierarchical models of intelligence. *Intelligence* 7, 107–127
19 Braver, T.S. *et al.* (1997) A parametric study of prefrontal cortex involvement in human working memory. *Neuroimage* 5, 49–62
20 Jonides, J. *et al.* (1997) Verbal working memory load affects regional brain activation as measured by PET. *J. Cogn. Neurosci.* 9, 462–475
21 Engle, R.W. *et al.* (1999) Individual differences in working memory capacity and what they tell us about controlled attention, general fluid intelligence and functions of the prefrontal cortex. In *Models of Working Memory: Mechanisms of Active Maintenance and Executive Control* (Miyake, A. and Shah, P., eds), pp. 102–134, Cambridge University Press
22 Jonides, J. *et al.* (1998) Inhibition in verbal-working memory revealed by brain activation. *Proc. Natl. Acad. Sci. U. S. A.* 95, 8410–8413
23 O'Reilly, R.C. *et al.* (1999) A biologically-based computational model of working memory. In *Models of working memory: Mechanisms of active maintenance and executive control* (Miyake, A. and Shah, P., eds), pp. 375–411, Cambridge University Press

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