Intelligence tests predict brain response to demanding task events

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A functional imaging study relates general intelligence to brain systems involved in cognitive control. In prefrontal cortex and selected regions elsewhere that are known to be activated during cognitive conflict, intelligence test score predicts the response to a challenging task.

The importance of standard 'intelligence tests' is sometimes questioned because of the thought—undoubtedly correct—that no single measurement is likely to catch all that is important in human abilities[1]. Indeed, the earliest research on this problem[2] showed that many variations from one person to another contribute to performance in different tasks. As Spearman[2] clearly explained, whether these are regarded as different aspects of 'intelligence' is no more than a matter of convention. The fact remains that standard intelligence tests do measure something important.

Perhaps the most interesting are tests of 'general fluid intelligence' or gF. These tests of novel problem solving (**Fig. 1a**) correlate strongly with the more familiar 'IQ test,' in which average ability is measured across a variety of domains (verbal, spatial, numerical, etc.)[3]. Both measures are broadly correlated with success in a wide diversity of other tasks, including laboratory tests of perception, language, memory and so on and many activities of everyday life[3]. These facts suggest that standard intelligence scores, including the ability to solve problems like the one in **Fig. 1a**, measure some common processing ingredient in much, or perhaps most, cognitive activity[2]. One suggestion has been a link to the functions of prefrontal cortex[4,5]; certainly, prefrontal lesions can impair the structure of much goal-directed behavior[6]. In this issue, Gray *et al.*[7] use functional magnetic resonance imaging (fMRI) to show how gF predicts the brain's response to a momentary increase in cognitive demand.

The Gray *et al*. experiment[7] draws on previous neuroimaging[8] and theoretical[9] work addressing the detailed functions of different subregions of prefrontal cortex. A keystone of this work is the role of cognitive conflict, produced for example when a dominant response (such as the tendency to read a written word, or to make a saccade to a peripheral flash) must be withheld. Previous results[8] suggest that the dorsal anterior cingulate, on the medial surface of the frontal lobe, responds when conflict is encountered. Such activity has been ascribed to monitoring for conflict occurrence. Lateral prefrontal cortex, on the other hand, has been linked to conflict resolution through knowledge of task context. Gray *et al.* propose that cognitive control operations like these are basic to gF. They predicted that, when conflict is encountered, high-gF subjects would show stronger recruitment of anterior cingulate, lateral prefrontal cortex and associated structures than low-gF subjects.

The experiment used a test of working memory to assess the brain's response to unpredictable, high-conflict events. Subjects were asked to monitor a series of words or faces, presented sequentially every 2.3 seconds (**Fig. 1b**). For each stimulus, they were asked to indicate whether or not it matched the stimulus that appeared three items back in the series. This 'three-back' task requires constant updating and evaluation of the contents of working memory. Although this in itself is a challenging task, additional conflict was occasionally introduced by presenting a stimulus that matched, not the three-back item in the series, but another close by (two-, four- or five-back). As expected, accuracy declined and response time increased for these 'lure' stimuli. The key finding, however, concerns the relationship between brain activity engendered by lures and intelligence test score. In the same participants, gF was measured with a standard problem-solving test. An important feature, unusual in brain imaging studies, was the use of sufficient subjects (48) to give reliable correlation measures. Correlations around 0.50 showed that when lures occurred, the high-gF subjects showed stronger recruitment of several areas: the dorsal anterior cingulate, a large region of lateral prefrontal cortex in both hemispheres, and the inferior parietal lobule (often co-recruited with lateral prefrontal cortex[5]), along with regions of the lateral cerebellum and superior temporal gyrus. Furthermore, as shown by partial correlation analysis, this pattern could not be explained simply by the better performance of high-gF subjects. As predicted, high-gF subjects are characterized by a stronger brain response to cognitive conflict, conspicuously, though not exclusively, within prefrontal cortex.

Cognitive psychologists, in particular, often fear that neuroimaging is the modern phrenology, addressing static localization rather than function[1]. Appropriately used, however, neuroimaging is a method for physiological analysis of processing func-

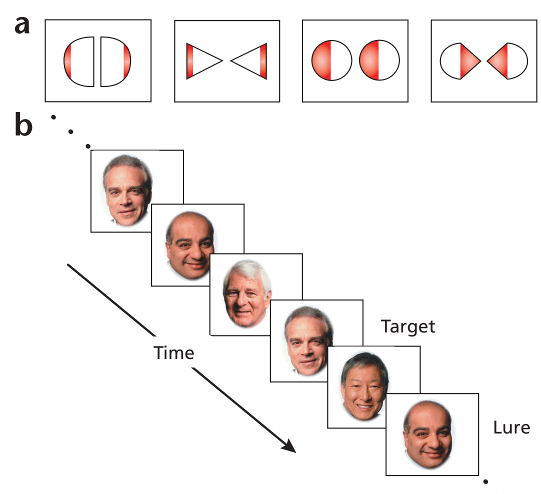

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Fig. 1. Tests for general intelligence. (**a**) Novel problem-solving is often used to measure fluid intelligence. Here the task is to decide which set of shapes does not belong with the others. (**b**) In the Gray *et al.* study, a series of stimuli (here faces) was presented one after the other. Targets matched the stimulus 3 back in the series; lures matched a different stimulus nearby (here 4 back).

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tions. The Gray *et al.* experiment[7] is of interest not only for relating gF and the functions of prefrontal cortex; it opens the door to detailed physiological analysis of what those functions are. The conflict monitoring/resolution model is certainly preliminary, and without doubt will be refined, revised or even replaced as our understanding develops. Relationships between prefrontal, parietal, superior temporal and cerebellar activations in the findings of Gray *et al.* need detailed investigation. Single-cell physiology, for example, shows that neural properties can be very similar in prefrontal and parietal cortex[10], raising the question of what differential contribution they make to cognitive control. It should also be remembered that, in the Gray *et al.* experiment, response to high-conflict trials will likely reflect a mixture of more general control functions and more specific processes (such as recency checking) required by this particular task. Investigating this will require generalization of the work to other types of task and cognitive conflict, which could also help to explain why high ability is sometimes associated with stronger neural activity (as it is here) and sometimes the reverse[11]. Already, however, this work begins a program for physiological study of the particular aspect of human intelligence measured by gF.

Gray *et al.*, like many others, suppose that prefrontal cortex has a central role in cognitive control, but how is such control achieved? Their task, like many used to study prefrontal function, requires 'working memory' in the simple sense of a short-term store of recent events. In symbolic artificial intelligence, however, 'working memory' in a much more powerful sense lies at the heart of planning and problem-solving programs like Newell's SOAR[12]. In such programs, cognition is controlled in domains from stimulus–response mapping and spatial navigation to language understanding and chess. In the program's working memory, perceptual input and long-term knowledge are used to build a temporary description or model of some aspect of the world and the actions planned upon it. Representing the relevant facts needed to understand how a part of the world is structured, this working memory controls cognition in the sense that it provides the current 'conditions' controlling action choice[12]. Inevitably, damage to this task model loosens the structure of the program's behavior[13].

Intriguingly, it may be animal studies that provide some of the strongest leads relating this aspect of intelligent cognition to prefrontal function. Single-cell recording studies in the monkey, largely focusing on the lateral frontal surface, indicate some remarkable facts[14,15]. No matter what arbitrary task the monkey is trained to carry out, large proportions of prefrontal cells respond to that task's features and events. These responses are of many kinds, coding the task's stimuli, responses or mapping rules, carrying information across task delays, reflecting reward availability and receipt, and so on. Despite some degree of regional variation, furthermore, cells of different types are closely intermingled within any one recording area. Such results suggest exactly the type of temporary task model used in problem-solving programs like SOAR[15]. Returning to the Gray *et al.* study[7], the proposal would be that, when lure trials are encountered, there is a sudden, increased demand on the task model detailing the exact behavior required in the current context. More generally, this modeling function would contribute to any form of effective, goal-directed behavior—in particular the kind of novel problem-solving conventionally used to measure 'fluid intelligence'.

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A new role for an old kinase: CK2 and the circadian clock

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A multifunctional kinase, casein kinase 2, regulates the *Drosophila* circadian clock and is exclusively expressed in the clock pacemaker neurons of the adult *Drosophila* brain.

Although we tend to rely on alarm clocks in the morning, most other organisms anticipate changes in the environment solely through endogenous circadian clocks. We also possess internal molecular clocks, which explains our initial difficulties when changing time zones. These molecular clocks are called circadian because they maintain rhythms of approximately 24 hours even in constant darkness.

Most of the molecules that form intracellular circadian clocks are conserved between humans and *Drosophila*, and it is studies of the *Drosophila* clock that have led the way in identifying clock genes[1]. Any new *Drosophila* clock gene becomes a potential mammalian clock gene, and this is one possibility raised by the identification of CK2 as a novel fly clock component in two papers—by Lin *et al.*[2] in *Nature* at the end of last year, and by Akten *et al.*[3] in this issue of *Nature Neuroscience*. *CK2*α and β are the ninth and tenth central clock genes identified in the fly, highlighting an important question: how many genes does it take to build a molecular clock?

Negative feedback is the principle that seems to underlie most biological oscillators, including circadian clocks. In the *Drosophila* clock, rhythmic transcription of the *period* (*per*) and *timeless* (*tim*) clock genes leads to the

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