several ganglion cells? Signals in adjacent photoreceptors tend to be correlated because of correlations in the natural scene. Calculations suggest that, when partially correlated signals sum in a ganglion cell, a dome-like weighting of the inputs leads to an optimal signal-to-noise ratio[15]. The same might be true for more central mechanisms that sum the partially correlated signals of ganglion cells. This hypothesis might be tested directly using the efficient experimental system that Chichilnisky and Baylor have provided.

The structure–function relationship shown here is unlikely to prove completely general. For example, ganglion cells are known to show nonlinear responses to certain stimuli, and it would be surprising if these were to be predicted simply from reading the anatomical circuit. Similarly, it is unlikely that the functions of cortical circuits will be obvious from their wiring, given that cortical synapses can undergo plastic changes in their physiological strength. Despite this, the present results encourage one to press on with the effort to correlate structure and function.

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The anterior cingulate cortex lends a hand in response selection

Edward Awh and William J. Gehring

The anterior cingulate cortex is involved in decisions between conflicting response tendencies. This exective function seems to involve separate pathways for manual and verbal responses.

The brain implements a variety of cognitive processes, which need to function together efficiently. Although routine cognitive activities are often relatively automatic, more demanding situations may require supervisory mechanisms to coordinate multiple sources of information or behavioral responses. In one laboratory task used to study this process (the Stroop task), people are asked to name the color of the ink in which a word is printed, while ignoring the word itself. People are slower to respond when the color of the ink and the word's meaning suggest different responses. For example, if the word "red" is printed in blue ink, then the proper response would be to say "blue." However, people are slow to say "blue" and often erroneously say "red" instead. In this situation, there is a conflict between the response suggested by one aspect of the stimulus and the response suggested by another aspect. Examples of this kind of conflict abound in everyday life. For instance, in driving from one place to another, one must ignore numerous signs directing traffic toward other destinations. A process termed 'executive control' is important for detecting and resolving this kind of conflict so that the correct response is ultimately produced[1,2].

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Several lines of research have suggested that the anterior cingulate cortex (ACC), a brain structure located on the medial surface of the frontal lobes, may be a critical neurobiological substrate of such executive control processes. This brain structure has rich interconnections with a number of cortical and subcortical brain areas, including association cortex (especially dorsolateral prefrontal, orbitofrontal and parietal), motor systems, limbic regions and the basal ganglia. The posterior ACC may be the subdivision that is crucial for cognitively demanding situations such as the Stroop task[3]. Functional neuroimaging and electrophysiological studies have provided support for ACC involvement in executive processes by demonstrating higher levels of activity in this area during Stroop tasks and situations that require divided attention, conflict resolution, response monitoring and error detection[1–6]. In addition, clinical studies have suggested that ACC dysfunctions are associated with psychiatric disorders, such as obsessive compulsive disorder and schizophrenia, that are associated with executive dysfunction[7–10].

In this issue of *Nature Neuroscience*, neuropsychological evidence from Turken and Swick[11] suggests an intriguing alternative view of the functional architecture of the ACC. They evaluated a patient (D.L.) who had a focal lesion in a circum-

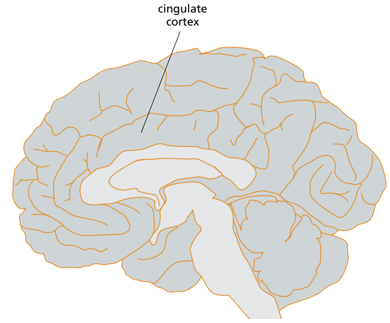

Fig. 1. Mid-sagittal view of the brain, showing the location of the anterior cingulate cortex.

scribed part of the right ACC caused by surgical resection of a glioma (**Fig. 1**). Such lesions do not generally cause major behavioral impairments or large movement deficits. The precise nature of the lesion allowed a direct assessment of the cognitive processes that depend on the integrity of the ACC. The authors explored an alternative to the executive control hypothesis of ACC function, in which the ACC controls motor responses that emerge as a result of earlier decision processes rather than coordinating the decision processes themselves[12,13]. Turken and Swick[11] tested D.L. in a variety of executive control tasks that activate the ACC in neuroimaging studies. In addition to manipulating the type of task performed by D.L., they varied the type of motor response required for each task (manual or vocal responses). They reasoned that if the ACC is responsible for general executive control, then D.L. should be impaired in all tasks with high executive demands; however, if the ACC is responsible for control of motor responses, the results should depend on the motor responses that were required. Their results supported the latter hypothesis. Compared to control subjects, D.L. was impaired specifically in tasks that required manual responses, but not in the same tasks when they required vocal responses.

One task required subjects to view successive displays of visual stimuli (see Fig. 3a of Turken and Swick) and detect changes in either a single dimension (that is, attention to color or to shape) or multiple dimensions (attention to color and shape). When D.L. indicated these changes with vocal responses, her performance was within the normal range. However, when manual responses were required, D.L. was significantly impaired on all versions of the task, even though the tasks required identical perceptual judgments. Another task (Fig. 3b of Turken and Swick) required subjects to give either vocal or manual responses to a composite display that consisted of a word ('left' or 'right') and an arrow pointing to the left or right. Subjects were required to ignore one stimulus and respond to the other. Neuroimaging studies have shown that such tasks activate the ACC, particularly in situations where conflict between the relevant and irrelevant stimuli is high[1]. Both D.L. and the control subjects were slower to respond when the two stimuli indicated different responses. However, the interference was significantly greater for D.L. than for controls—but only when she had to make manual responses to the words. When vocal responses were required, D.L. showed the same amount of interference as controls. In both tasks, D.L.'s impairment surfaced as a function of the output modality rather than as a function of the judgments that had to be made.

One crucial aspect of these data is that D.L.'s impairment was most evident when response selection requirements were most demanding: when fast and accurate responding required not only the initiation of the correct response, but also the suppression or abandonment of competing, erroneous responses. For example, whereas D.L. was impaired during all the manual response conditions of the divided attention task, she showed the greatest impairment during the manual response condition that required attention to multiple attributes. In this condition, the response suggested by one attended attribute may not have been the same as that suggested by the other, causing a greater demand for executive processes to select from multiple responses. Similarly, during the Stroop conflict task, D.L.'s abnormal interference levels were highest in the manual response condition that involved the highest level of conflict (an interpretation supported by the greater difficulty control subjects had in the same condition). Thus, although D.L.'s deficit was associated with manual responses, the degree of difficulty in selecting the manual responses was also critical.

The specific impairment of manual responses following a restricted lesion to the posterior part of the ACC in D.L. suggests that manual and vocal responses are mediated by independent parts of the ACC. This view is in line with previous neuroimaging evidence for somatotopic organization of the ACC (that is, different parts of the ACC activated during manual, vocal and oculomotor responses)[10,12]. This idea has important implications for theories of ACC function and executive control. Turken and Swick report that D.L. showed "intact executive function," along with impairment in the initiation and control of manual responses. They suggest that a command signal indicating the need for executive control originates in a lateral prefrontal system, rather than in the ACC. According to this view, the prefrontal command signal causes a modality-specific portion of the ACC to facilitate correct responses and to suppress errors[12]. Turken and Swick propose that in D.L. the command signal is intact, but the ACC is unable to facilitate or suppress responses appropriately.

Another possibility, however, is that the command signal originates within the ACC. That is, the executive system that detects conflicts and errors itself may be organized according to response modality. Thus, a manual response control system might detect conflict, facilitate correct responses and suppress errors in manual responses without having to interact with the system in the vocal subdivision of the ACC that performs these functions for vocal responses. One would expect that a patient with damage limited to the manual subdivision of this system would show maximal deficits in exactly the conditions where patient D.L. has the most difficulty: those where correct manual responses conflict with incorrect manual responses. According to this view, the executive processes that detect conflict or errors and the processes that control responses need not be separate from each other, but may instead be tightly interwoven within each modality[1,2,12,13]. The data of Turken and Swick[11] suggest that at least one part of the executive system is organized in a modality-specific fashion, such that the processes governing manual and vocal responses are implemented by different regions of the ACC[10]. The command signal may be intact, as Turken and Swick argue, or the command signal itself may arise in modality-specific ACC regions. In either case, their finding underscores an important characteristic of ACC organization that has not been fully appreciated in cognitive neuroscience.

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