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The cortical basis of motor planning: does it take two to tango?

René Marois

A new study using fMRI shows that the human frontal cortex—and not parietal cortex—is the primary locus of movement planning.

"I did everything Fred did, only backwards and in high heels," quipped Ginger Rogers about her dance partnership with Fred Astaire. Watching them in perfect unison, one could be hard pressed to know who was leading and who was following. In brain function, the frontal and parietal cortex are to the cortical control of action what Fred and Ginger are to dance: a dynamic and seemingly inseparable double act[1]. In fact, the recurrent co-activation of this frontoparietal network in functional imaging studies has made it difficult to tease apart their relative contributions to the control of action. Now, in this issue, Connolly and colleagues identify one stage of information processing that dissociates activity in the front and back of the brain: the bulk of movement planning is a property of the frontal, but not of the parietal, cortex[2].

The control of action has been extensively investigated in the frontal eye field (FEF) of the frontal lobe and the lateral intra-parietal (LIP) area of the parietal lobe, two key regions of the cortical network that controls where our eyes move and where our attention is directed[3]. Long studied in the monkey, putatively homologous brain regions have since been mapped in humans[4] (**Fig. 1**). When subjects rapidly shift their gaze from one object to another in a visual scene—an eye movement known as a saccade—or when they shift their attention to a different scene location from the one they are fixating, the FEF and LIP areas are invariably activated. Indeed, frontoparietal activation is ubiquitous in neuroimaging studies of attention and visual cognition[5]. Not surprisingly, the FEF and LIP are strongly interconnected and have similar physiological properties[6]. Should one thus conclude that the parietal and frontal cortex make equal contribution to the control of action? There is reason to believe that this may not be the case when we are preparing to act: although much evidence supports a role for the frontal cortex in the planning and preparation of movements[7,8], similar evidence for the parietal cortex is more equivocal[9–11]. However, strong support for this notion had been lacking, primarily because most evidence is derived from single-neuron studies in non-human primates that have examined only the frontal or parietal cortex, but not both. In addition, few imaging studies of visuomotor cognition have aimed at dissociating the planning of a movement from the target of that movement.

Connolly and colleagues[2] addressed this issue by measuring brain activity in both frontal and parietal cortex with event-related fMRI while human subjects performed an eye movement planning task. At the onset of each trial, subjects were instructed, via a central color cue, to execute an eye movement either toward (pro-saccade) or away from (anti-saccade) a peripheral target briefly presented either to the left or right visual field (**Fig. 2**). Crucially, a variable delay of 0, 2 or 4 seconds was introduced between the presentation of the cue and target. Subjects were faster at executing a saccade when there was a delay between the cue and target, demonstrating that some aspect of movement preparation beneficial to motor execution took place during the delay period. Connolly and colleagues found that for both pro- and anti-saccade trials, activation of the FEF ramped up during the cue and delay period, such that it was highest at the time of target presentation for the four-second delay and lowest at the zero-second delay. In other words, the delay between cue and target permitted a buildup of activity in the FEF before target presentation. In stark contrast, LIP showed no preparatory activity whatsoever during the delay period.

Any fMRI experiment that relies on a negative finding, such as the absence of parietal activation in this case, must safeguard against the trivial possibility

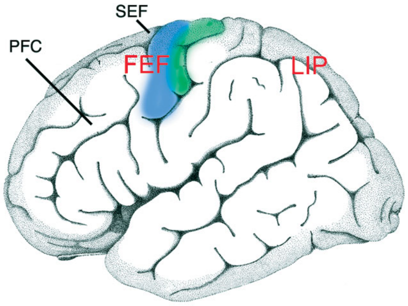
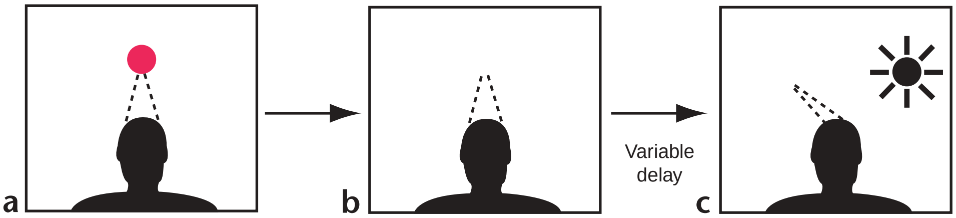


Fig. 1. Cortical centers of the oculomotor system. Connolly *et al.* measured brain activity in the FEF and presumptive LIP. Other cortical areas important in oculomotor control are the supplementary eye field (SEF) and the prefrontal cortex (PFC). The location of the primary motor cortex (green strip) and frontal premotor cortex (blue strip) is shown as a reference point.

The author is in the Department of Psychology, Vanderbilt University, 530 Wilson Hall, Nashville, Tennessee 37203, USA.
e-mail: rene.marois@vanderbilt.edu



Ivelisse Robles

Fig. 2. The trial design used by Connolly *et al.* Subjects fixated a central instructional cue. The cue changed either to green or red (**a**), instructing the subjects whether they would be required to perform a pro-saccade or an anti-saccade, respectively. The fixation cue was extinguished (**b**), and after a variable delay, a peripheral target was flashed briefly (**c**), indicating to the subject to initiate the eye movement (an anti-saccade in the example here).

of lack of sensitivity. Connolly *et al.* have done so in several ways. First, the same parietal region did activate during the pro-saccade or anti-saccade at the time of target presentation. Second, the authors used a localizer task to isolate the specific regions of frontal and parietal cortex associated with eye movements, thereby focusing on the cortical regions most sensitive to oculomotor function. Third, in a control experiment when subjects were instructed about the direction of the impending saccade by presentation of the target before the delay period, the parietal cortex activity increased during that delay, possibly to retain the location of the saccade endpoint. Thus, brief presentation of the target location, in the absence of eye movements, was enough to recruit the parietal cortex. Taken together, the findings of Connolly and colleagues[2] point to a genuine functional divide between the parietal and frontal cortex during movement preparation.

What exactly might be the operation performed by FEF but not by LIP? I can see two possibilities, which are not mutually exclusive: one is that FEF is involved in the translation of the colored cue (green/red) to the proper motor response (pro/anti-saccade)—stimulus–response mapping, in other words. Alternatively, it may be involved in the preparation of the proper motor commands to execute a saccade or anti-saccade[3]. Also, we should not assume that these operations are necessarily initiated in the FEF; it has been suggested that such signals may originate from higher level prefrontal and medial frontal centers of the oculomotor system[12].

Although these findings argue for the existence of motor planning–related activity in frontal cortex, they do not rule out a role for the parietal cortex in at least some stages of movement preparation[10]. For example, the parietal cortex may be involved in the representation of the location toward which the movement will be produced, as suggested by the control experiment of Connolly and colleagues. As an analogy, Ginger's frontal cortex would be summoned for the planning of her next leap, while her parietal cortex would be concerned with her landing softly in Fred's arms. However, there is an important caveat to this proposition: some single-neuron recording evidence indicates that the parietal cortex may also contribute to motor preparation independent of target location information[11,13], although this activity is not nearly as pronounced as the activity when the target location is specified. To be sure, fMRI is not as sensitive as single-neuron recording, but it does offer the possibility of much broader spatial coverage. Thus, whereas some preparatory parietal activity may have gone under fMRI's radar screen in the Connolly *et al.* experiment[2], it is the relative difference of activation between the frontal and parietal cortex that is truly remarkable. It therefore seems reasonable to conclude that the bulk of motor preparation is arising from the frontal, not the parietal cortex. Ultimately these imaging results will have to be reconciled with single-neuron non-human primate studies. What will be necessary is simultaneous single-neuron recording from both FEF and LIP[12] while monkeys perform a task similar to Connolly *et al.*'s, where activity during movement preparation can be compared in the absence and presence of target location information.

A pattern of primarily frontal cortex activation during planning of movement identity (pro- versus anti-saccade) and parietal cortex recruitment when the motor act acquires a postal address (target location) is reminiscent of the classic notion of the frontal cortex subserving predominantly planning or motor functions, and the parietal cortex subserving predominantly perceptual or representational aspects of action[14]. How is one to reconcile these ideas with the considerable amount of work indicating that the parietal cortex is essential for proper movement[10], just as the frontal cortex may be critical for perceptual decisions[1,8]? Most likely, action results from a coordinated activation of this (and other) neural networks, but with the gradient of activation shifting across the network depending on the perceptual or motor demands of the task. In support of this hypothesis, recent imaging data suggests that although frontal and parietal cortices are both activated by demanding perceptual and response-selection tasks, the perceptual task predominantly engages the parietal cortex[15], while the response-selection task preferentially affects the premotor frontal cortex (Marois *et al.*, *Soc. Neurosci. Abstr.* **32**, 180.19, 2002).

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