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Motor Planning: Insects Do It on the Hop

Planning a motor action in advance of its possible execution doesn't require cortical complexity: a recent paper demonstrates that even fruit flies prepare for movement some time before they decide whether or not to take action.

Tom Matheson

In a well-known comedy sketch called *The Ministry of Silly Walks*, English actor John Cleese, of Monty Python fame, demonstrated with remarkable long-legged flexibility and impeccable timing a myriad possible motor strategies for human forward locomotion. Indeed, almost any motor action can be achieved in an infinite number of ways because our bodies and nervous systems are much more flexible than strictly necessary to achieve any given task. In other words they possess high levels of redundancy. To control such redundant systems effectively, the central nervous system must be able to translate from relatively abstract behavioural requirements — 'move from point A to point B' — into a detailed pattern of muscle activation that takes into account the animal's current state and achieves the goal somehow 'optimally'. What sort of brain is required to carry out these seemingly intractable computations and thus plan a movement?

In this issue of *Current Biology*, Card and Dickinson [1] report observations on the fruit fly *Drosophila melanogaster* which demonstrate that key aspects of motor planning are carried out even in the tiny nervous system of this insect. Using high speed video capture they have demonstrated that flies reposition their legs during the approach of

a looming visual stimulus so that they are ready to escape from imminent collision in the best possible direction (Figure 1). According to the authors, this motor planning is one of the reasons why it is so hard to swat a fly!

Fruit flies, like many animals [2,3], respond with an escape manoeuvre to the sight of an object looming on a collision course. The jumping escape response of a fly is driven by extension of the middle legs to cause lift off within five milliseconds of the beginning of the response [4,5]. Activation of the main muscle involved in this leg movement is driven by activity in a pair of large-diameter interneurons known as the giant fibre system, which receive visual inputs in the brain. Until recently, it was thought that this giant

fibre system alone underpinned the sequence of actions involved in escape jumping. It is now known, however, that a different unidentified pathway from the brain to the thorax conveys an earlier signal that can drive wing elevation prior to take off [6,7].

The work of Card and Dickinson [1] reveals a new level of complexity in this escape behaviour: as well as raising their wings in preparation for a jump, flies reposition their legs relative to the body's centre of mass and sway so that subsequent middle leg extension leads to a directed jump away from the approaching visual stimulus. Importantly, the preparatory movements take into account the initial posture of the animal and are coordinated appropriately in the three pairs of legs. Take, for example, the case in which a stimulus approaches from in front of a standing fly. If the middle legs are initially positioned with the feet anterior to the centre of mass — a position that biomechanically favours a backwards jump as the legs extend — then the preparatory movements include only



Figure 1. *Drosophila* escape jumps.

Photomontages of three different *Drosophila* escape jumps show that regardless of starting orientation, flies jump away from a visual stimulus — which in all cases approached from the right-hand side of the image. The three video frames in each image show the fly's starting position 17–130 milliseconds before take-off (darkest), the moment of take-off when the tarsi first leave the ground (middle), and the fly in flight 2–5 milliseconds after take-off (lightest). Scale: *Drosophila* body length ~2.5 mm. (Illustration courtesy of G. Card.)

small repositioning steps of all six feet, and an overall backwards movement of the centre of mass prior to the jump. In contrast, if the middle legs are initially standing behind the centre of mass — which would favour an inappropriate forward jump towards the stimulus — the preparatory movements include large forwards movements of the middle legs and a large backwards motion of the centre of mass. Subsequent middle leg extension propels the animal correctly backwards and away from the threat. Such observations demonstrate that the fly has planned an escape trajectory prior to executing the main part of the jump.

Are there parallels to this motor planning in other insects? Locusts flex their large hind legs in preparation for a jump, and their take-off angle is governed by this flexed posture [8]. Simultaneous movements of the fore and middle legs govern the direction [9] — although somewhat less precisely than for the fruit fly. Although it is not known whether the locusts' movements take into account the initial posture of the animal, there is evidence to suggest that they could do so. During aimed scratching, for example, different limb trajectories are used to reach a common target site from different initial limb postures [10]. The start posture is signalled by internal sensory receptors that are known to influence ongoing movements.

Card and Dickinson's [1] work very neatly demonstrates that a fruit fly plans a successful escape that takes into account both the initial posture and the direction of approach of the stimulus. The preparatory movements made by a fly occur up to 100 milliseconds before the jump, and

indeed are not necessarily followed by a jump at all: some flies make the preparatory movements but don't leap into the air. Card and Dickinson [1] suggest that the whole escape behaviour is essentially modular, with earlier components such as leg re-positioning being activated at lower thresholds (earlier during an approaching stimulus) than are the later actions such as wing raising and leg extension.

So where in the central nervous system might these plans be computed? In primates like ourselves, motor planning involves activity spanning several regions of the brain, including the prefrontal cortex, premotor cortex and the cerebellum. The brains of insects contain many fewer neurons than those of vertebrates but are nevertheless highly complex, and are similarly organised into specialised regions. One of these in particular, the central complex, has been implicated in aspects of motor control including limb coordination. In *Drosophila*, mutations that disrupt central body function lead to locomotor deficits such as an inability to properly regulate step length or to orient towards attractive landmarks (reviewed in [11]). On the other hand, a large body of work tells us that many aspects of insect limb motor control are devolved to the chain of thoracic ganglia that form part of the ventral nerve cord. For example, just one of these ganglia is sufficient to generate aimed scratching movements in a locust [12], and a headless fruit fly can walk and groom [13]. A challenge for the future is to see if the genetically tractable *Drosophila* continues to give us new ways of identifying and dissecting apart the neuronal

structures responsible for motor planning.

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Golgi Inheritance: Rab Rides the Coat-Tails

A recent study describes a role for a Rab GTPase previously implicated in endoplasmic reticulum and mitochondrial inheritance and for a COPI coatomer subunit in the targeting of a type V myosin to the late Golgi in yeast.

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Organelle inheritance is the process whereby organelles are transferred

from mother to daughter cells during cell division. Much of what we know about this process has been determined in the budding

yeast, *Saccharomyces cerevisiae*, a cell type that undergoes polarized growth and asymmetric cell division. These studies have revealed mechanisms for organelle inheritance not just for mitochondria and endoplasmic reticulum (ER), which can be produced only from pre-existing organelles, but also for the Golgi apparatus, peroxisomes and vacuoles, which can be produced *de novo*.