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OUTSIDE JEB

The clutch and transmission of fly flight

Fly wings are technological marvels, flapping at frequencies over 100 Hz to produce enough lift to keep the tiny insects aloft. One of the innovations driving this extreme performance is the resonant oscillation of the thorax that allows the wings to reach frequencies beyond those attainable by direct nervous stimulation. Fly hindwings have also been modified over the course of evolution into halteres: gyroscopic sensors that oscillate in exact opposition to the wings, providing continuous fast feedback to the fly's flight apparatus. The tight association between forewing and haltere movement seems critical for fly flight. However, there are still peculiarities of fly flight that remain unexplained. For instance, how are the movements of the wings and halters so tightly coupled at frequencies much faster than those that can be achieved by neural systems?

Tanvi Deora and her colleagues at the Tata Institute of Fundamental Research in Bangalore, India, devised a beautiful series of experiments to test the roles of neural control, passive mechanical control and sensory feedback in wing–wing and wing–haltere coordination.

If the nervous system were to control wing–haltere coupling, flapping the wing of a dead fly would not elicit the synchronous motion of the wings and halteres typical during flight. And yet, upon actuating a single wing of a dead fly, the researchers observed that the opposite wing still moved in synch with the wing that they were moving, and the halteres moved perfectly in opposition to the wings. Given the synchronization of wings and halteres in the absence of a living nervous system, this suggested a passive mechanical means of precise coordination.

Figuring that a mechanical linkage must exist between wings and halteres, the researchers set about finding where that linkage might be. In live flies, the authors cut one of two sections of the fly thorax: either the large 'scutum' near the head or the smaller 'scutellum' toward the rear. Flies with a snipped scutum still flapped their wings synchronously, but flies with a cut scutellum could not. Thus, the scutellum was the site of wing–wing linkage.

However, even when the scutellum was cut, the wing and haltere on each side continued moving in perfect opposition – suggesting the presence of another mechanical linkage. Deora and her colleagues noticed a region of thickened cuticle on each side of the fly, the 'subepimeral ridge', linking the base of the wing with the base of the haltere, which seemed to be a good candidate for a second linkage. And when they cut the subepimeral ridge, the coordination between the haltere's movement with its wing was lost. Thus, the subepimeral ridge was another mechanical connection driving high-frequency coordination. Even after artificially increasing the frequency of the wingbeat, the wings and halteres stayed in synch. And the tight coupling between the wings and halteres must be important because when both subepimeral ridges were cut the insects could not fly at all.

However, despite both of these mechanical linkages working to keep the wings and sensors in synch, flies can still activate one wing independently of the other, suggesting that there must be a 'clutch'-like mechanism allowing the flies to disengage the wings from the thorax to decouple their motion. Taken as a whole, these elegant experiments show that thoracic anatomy acts as both transmission and clutch to overcome some of the seemingly unsurmountable physiological challenges of fly flight.

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Kara Feilich
Harvard University
kfeilich@fas.harvard.edu

Dragonfly hunting is based on predictive models

Goalkeepers doubtless need excellent responses to prevent the opposition from scoring that goal. However, exceptional responses are not enough. To reach and catch the ball at the right moment, the goalkeeper has to predict where the ball will end up and calculate where their movements will take them to capture the ball. This type of control has been found only in vertebrates so far. However, a recent study published in *Nature* by a team of researchers led by Anthony Leonardo from the Howard Hughes Medical Institute, USA, has demonstrated that dragonflies that are in pursuit rely on internal models that predict the effects of movements of their own body and their target, like the goalkeeper catching the ball.

Dragonflies are brilliant aeronauts that can hover, fly at high speed and perform agile manoeuvres to defend their territory, mate on the wing or chase prey. Their vision is also excellent: with their large eyes they can see in almost any direction. Usually they lurk on plants where they wait for prey insects to fly over. Once the prey is in focus, the dragonfly rapidly lifts off and

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manoeuvres to approach the prey at an angle from below, so that it can trap the victim with its capture legs.

To analyse this type of hunt in more detail, the team filmed dragonflies in slow motion during pursuits. It became obvious that the dragonflies did not rely exclusively on their reactions, because they did not always respond to unexpected changes in the prey motion. Rather, they tried to align their elongated body with the flight path of their prey to approach and strike from below, minimizing the chances of being discovered. To do so, the head of the dragonfly moves independently from the body, so that the eyes can continuously focus on the prey while the body is aligned with the prey's flight path.

The scientists then dissected the head movements in more detail. They set up a flight arena, which allowed them to record the paths of dragonflies and prey with high accuracy using high-speed cameras. They also placed micro-reflective markers on the head and body of the dragonflies to record the relative movements. Based on these data, they then calculated the angular position of the prey image on the dragonfly's eye.

What they found was quite surprising, as the head motions turned out to compensate precisely for drift of the prey image on the eye that resulted from the dragonfly's own body movements and the anticipated motion of the prey. The high synchrony and precision of the timing of these head movements suggest that dragonflies use internal calculations to generate models that predict how body and prey movements will influence the position of the image on the dragonfly's eye, and how the head must then be moved to cancel out these effects: classical sensory feedback. This predictive system largely compensates for the dragonfly's own body movements and thus relieves the visual system to detect sudden prey manoeuvres, to which the dragonfly can respond by reactive control.

Leonardo and his team have shown for the first time that invertebrates use internal models to predict the effects of their own body movements when targeting prey. The fact that all of the experiments were done under laboratory conditions where the prey's movements are more restricted may suggest that this predictive steering control could be dominated by reactive mechanisms in the wild, thus explaining why it had been overlooked for so long.

10.1242/jeb.112185

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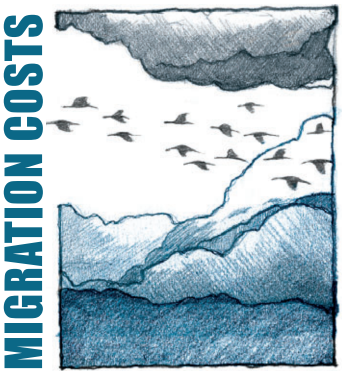
Hans Merzendorfer
University of Osnabrueck
merzendorfer@chemie-bio.uni-siegen.de

Taking the long way saves energy for high-flying birds



In these days of ever-present GPS and easy access to route-planning apps, taking the long way can feel like a waste of time. Efficiency, in terms of both time and energy expenditure, especially on long trips, is often a high priority. It is therefore somewhat surprising that when bar-headed geese (*Anser indicus*) make their remarkable twice-yearly migration across the Himalayan mountain range, they take the long route – ascending and descending along mountain valleys instead of flying in a straight path at high elevations. This somewhat counterintuitive route was reported back in 2013 by Lucy Hawkes and colleagues (Hawkes et al., 2013, *Proc. R. Soc. B* **280**, 20122114). At the time, the researchers hypothesized that the geese kept close to the ground because the costs of continuous flight at high elevations, where low oxygen levels increases the effort needed to maintain movement, were too high.

This hypothesis was recently put to the test by a large international team of scientists, led by Pat Butler of the University of Birmingham and Charles Bishop of Bangor University, UK. These researchers have been studying the energetics and biomechanics of bar-headed geese for a number of years in the hope of shedding light on how the birds accomplish their remarkable migration. In the past, the team has used laboratory-based experiments on the bar-headed geese and other birds to be able to obtain reliable estimates for metabolic rate (an approximation of energy expenditure calculated using heart rate) and metabolic power (how much work is needed to perform a task estimated using wingbeat frequency). Thus, the team had access to most of the information needed to estimate the costs of the migration; all that was needed were direct measurements of these values from the geese during migration.

Using sophisticated data loggers – that provided not only location and elevation but also core body temperature, heart rate, pressure, acceleration and wingbeat frequency – the team successfully obtained data from seven birds over 391 h of flight during migration. Similar to the previous study, the tagged birds took the long route, up and down along mountain valleys, and generally remained close (within ~60 m) to the ground throughout the migration. This path added nearly 112 km to the total distance travelled, when compared with a straight line flight at high elevation, but was by far the less costly of the two routes. From their previous work, the team knew that the lower density air at high elevations causes an increase in metabolic power, similar to what humans experience when exercising at high altitude. They had also determined that for continuous flight at a single elevation there is a high correlation between metabolic power and metabolic rate. Therefore, remaining at high elevation throughout migration would have cost the birds more than ascending the odd mountain peak. Thus, the birds' 'roller coaster' path up and down the peaks and valleys of the Himalayas was actually the path of least resistance. Perhaps even more surprising was that, overall, the heart rate of the birds remained at relatively low levels, showing just how well adapted these birds are to flight under what for most species would be challenging conditions.

10.1242/jeb.112193

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Danielle L. Levesque
University of Malaysia at Sarawak
lldanielle@ibec.unimas.my

The rat makes the decisions around here

Decision making can be infuriating, debilitating and often disappointing in retrospect. And yet, animals of all stripes are constantly faced with critical decisions that determine whether they survive or perish. Many of these decisions are reflexive or instinctive: for example, the decision to jump into a river to escape an approaching train, or to duck to avoid a blow to the head. However, other decisions require more deliberation. In these cases, an animal might take time to accumulate information, which it can use to evaluate prospective options and select the one that seems most likely to produce a favorable outcome. For example, when making an important decision like selecting a mate, it is important to consider all of the available evidence.

A recent study from Carlos Brody's lab, at Princeton University, USA, has combined electrophysiological and behavioral experiments to investigate how the brain integrates evidence to make informed decisions. The decision maker they studied was a humble, thirsty rat. In order to quench his thirst, the rat was asked to play a simple game. The team positioned speakers to the left and right of the rat that randomly emitted gentle clicking sounds. The rat's task was to count the number of clicks from the left and right speakers and then, after a brief pause, poke the button that corresponded to whichever side emitted more clicks. If he answered correctly, a drop of water was released. The goal of the parched rat was simply to maximize the amount of water that he received.

While the rat performed this decision-making game, Hanks and colleagues recorded from neurons in two brain areas: the posterior parietal cortex and the prefrontal cortex. Previous work in monkeys had shown that these brain areas are active during perceptual decision making. Similar to findings in the monkey, the neurons in the parietal and prefrontal cortex increased their firing as the rat gathered sensory evidence during the click task.

The team then used a clever analysis technique to determine the relationship of each neuron's firing rate to the gradual accumulation of evidence. They observed that, at any point during the decision-making process, the activity of neurons in the parietal cortex faithfully encoded the current level of accumulated evidence. However, neurons in the prefrontal cortex had a more binary response, which reflected the actual decision outcome. Thus, although neurons in both areas fired during evidence accumulation, activity in the prefrontal cortex was more predictive of the animal's behavior.

To further investigate the functional role of the prefrontal cortex, the authors used optogenetics to silence prefrontal neurons during different epochs of the click task. They discovered that decisions were affected only if the prefrontal cortex was silenced toward the end of the evidence-accumulation period. This result is consistent with the view that the frontal cortex is not directly involved in evidence accumulation, but instead contributes to decision execution. However, it remains unclear whether the parietal cortex plays a causal role in perceptual decision making. To test this hypothesis, it will be necessary to silence the parietal cortex during evidence accumulation.

For several decades, neuroscientists have recorded from brain areas that might be involved in decision making and used these data to build models of how the brain executes informed judgments. However, because most of these experiments have been performed in monkeys, it has been difficult to casually test these models through targeted manipulation of the underlying circuits. By transiently silencing specific cortical regions during an elegant decision-making task, all the evidence suggests that Hanks and colleagues have made an important step in the right direction toward understanding how the brain controls decision making.

10.1242/jeb.112177

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John Tuthill
Harvard Medical School
john_tuthill@hms.harvard.edu