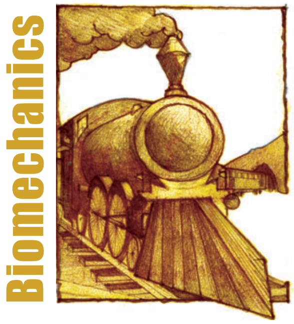
The kangaroo's fifth leg



When you hear the word 'kangaroo', you might picture that charismatic Australian marsupial hopping bipedally across the grassy plains. It may be surprising to hear that most of the time kangaroos spend moving is not time spent hopping. Instead, they move slowly while grazing and lazing about. This slow motion is not a hop, but instead, a gait called pentapedal locomotion. Unlike jumping, where the tail is held straight behind the body as a counterbalance, during pentapedal locomotion the tail is placed on the ground in sequence with the kangaroo's arms and hind legs. While researchers have known about pentapedal locomotion with the tail for decades, they did not know what the tail was doing – if it was functioning merely to support body weight, or as a propulsor like a leg.

Shawn O'Connor of Simon Fraser University in Canada and a team of international colleagues wanted to test the tail-as-leg hypothesis, to determine the extent to which the tail contributes to kangaroo pentapedal locomotion. They recorded the ground reaction forces of red kangaroo forelimbs, hindlimbs and the tail during this unique gait, and estimated the power generated and work done by each individual limb and the tail.

Surprisingly, the group found that the tail was functioning not just like a regular leg, but actually as a quite powerful one. While the forelimbs and the hindlimbs of the kangaroo generated some forward thrust, the tail generated more thrust than both pairs of limbs combined. However, the forelimbs and the hindlimbs played a much greater role than the tail in supporting body weight. In terms of mechanical power, the kangaroo's hindlimbs produced almost three-quarters of the total positive mechanical work. But even here the tail made a substantial contribution, accounting for most of the remaining work output. To put this pentapedal propulsion into perspective, the authors compared the kangaroo's tail with a human leg. The kangaroo tail performs as much mass-specific work as one human leg does while walking at the same speed.

Together, the force and power measurements lead to one conclusion – the kangaroo tail functions precisely as a biomechanical leg, to both support body weight and provide forward propulsion. But why walk pentapedally at all? The authors hypothesize that pentapedal locomotion may be partly the result of a body shape that improves bipedal hopping. While the huge hindlimbs and small forelimbs of the kangaroo are an asset for bipedal hopping, they give the kangaroo a very uneven distribution of weight. If not for the propulsive tail, this weight distribution might make the kangaroo fall backwards during slow 'quadrupedal' locomotion. So, the kangaroo tail turns out to be quite the multipurpose structure. Its utility as a balance while hopping and a propulsor while grazing has given kangaroos a literal leg-up over the quadrupedal competition.

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Electric fish confront the paradox of selfhood

Among your brain's many responsibilities, one of the most important is distinguishing between external and self-generated signals. The sound of one's own laughter might closely resemble the shrieking of an irascible badger, but the two auditory stimuli require wildly different responses. One way that the brain might differentiate between these two scenarios is by actively monitoring the motor command signals that generate self-movement. By transforming and subtracting this so-called 'corollary discharge' from incoming sensory signals, the brain could predict and eliminate the sensory confounds of self-generated behavior.

The best evidence for this important theory comes from a bizarre and handsome animal: the weakly electric fish. In order to navigate through muddy streams, Mormyrid fish use a specialized organ to produce a weak electrical pulse and monitor deformations of the resulting current flow with passive electroreceptors in the skin, thus forming an electrical 'image' of their environment. Previous studies have found that a corollary discharge signal from the electric organ is subtracted from sensory inputs within a specific circuit of the fish brain called the electrosensory lobe. However, in addition to predicting the stereotyped discharge of the electric organ, the brain must also take into account the seemingly infinite number of different movements produced by a frisky fish. Is there a different pattern of corollary discharge signals for each of these possible movements? If so, how are these myriad combinations integrated with electrosensory information in the brain?

A recent paper by Tim Requarth and Nate Sawtell at Columbia University, USA, addressed these questions by measuring the responses of neurons in the electrosensory lobe to movements of the tail. The authors evoked rhythmic swimming movements within paralyzed fish by electrically stimulating locomotor circuits in the brain. They then recorded extracellularly from mossy fibers, neurons that convey motor signals from the spinal cord to the electrosensory lobe. They discovered that some mossy fibers encode unique movement parameters, such as the frequency, amplitude or direction of tail wagging. Thus, different mossy fibers carry corollary discharge signals related to specific aspects of the fish's self-movement.

Requarth and Sawtell next investigated the convergence of motor and electrosensory signals within the principal neurons of the fish's electrosensory lobe. Mossy fibers connect to tiny neurons called granule cells, which subsequently route self-movement signals to principal neurons. When granule cell signals are repeatedly paired with electrosensory input, the strength of the synapse between the granule cell and the principal neuron decreases. This allows the principal neuron to subtract predictable components of the sensory response that are due to the fish's own behavior. The authors observed that repeated pairing of a tail movement with coincident electric organ discharge led to a highly specific depression of granule cell inputs. Furthermore, they found that each principal neuron was capable of subtracting multiple unique motor signals from a given sensory event.

These findings provide a tantalizing hint of how the brain might cope with the extreme dimensionality of possible motor behaviors. Because a single principal neuron in the electrosensory lobe receives synaptic input from many granule cells (~20,000), each principal neuron could potentially subtract gazillions of different movement combinations from a given sensory signal. The basic circuit structure of the Mormyrid electrosensory lobe is much like that of the cerebellum, a cauliflower-like structure at the rear of the mammalian brain, which is thought to play a similar role in predicting the sensory consequences of motor commands. Therefore, insights from the electric fish might help us understand brain circuits in furrier animals, such as humans or badgers.

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Anthropogenic pollutants disturb moth navigation

Nocturnal pollinators such as moths have developed a highly sophisticated olfactory system that allows them to locate nectar-providing flowers. They are able to navigate correctly in complete darkness, even in the presence of background scents produced by non-target flowers. The mechanism by which moths find the correct flowers against a background of other odors was recently examined in an exciting study published in *Science* by Jeffrey Riffell and colleagues from the Universities of Washington and Arizona, USA. They found that scent tracking was dependent on odor frequency and background odors. However, they also made the disturbing observation that anthropogenic pollutants can perturb the moth's odor-navigation system.

To find food sources or mates, moths and other insects need to discriminate and locate different scents within a complex mixture of odours. For instance, Carolina sphinx moths (*Manduca sexta*) roam up to 80 miles a night to find the nectar of angel's trumpets (*Datura wrightii*) flowers. However, finding these flowers is challenging, as they are often isolated within dense populations of the creosote bush (*Larrea tridentate*), which disperses a very strong scent. Odors are not evenly emitted from flowers, the plumes are broken into filaments by air turbulence. To measure the patchy odor traces produced by *Datura* in the field, the scientists used a proton-transfer reaction mass spectrometer that allowed monitoring of volatile organic compounds such as oxygenated aromatics and monoterpenes in ambient air. They found that the rate at which specific *Datura* monoterpene odor filaments are encountered in the air (odor frequency) increases with the distance from the flower. Also, the ratio of monoterpenes to oxygenated aromatics changed in the presence of background volatiles, such as those emitted by the creosote bush.

Next, the team tested the moth's ability to locate the flower in the laboratory using a wind tunnel where they could control odour plumes. The team examined how freely flying *Manduca* moths responded to *Datura* secnt embedded in different background mixtures, including odors from the creosote bush. They found that the volatile background significantly influenced the moth's ability to discriminate and track the odor, particularly when oxygenated aromatics that occur in both *Datura* and *Larrea* scents were present. To dissect the neuronal pathways activated in the moths by antennal odor perception, the scientists went on to collect electrical recordings from the antennal lobe, the area in the insect brain that receives the input from the olfactory sensory neurons on the antennae. They also developed computational models that allowed them to compare the neural activity patterns collected in response to flower scents in isolation and flower scents embedded in various backgrounds. Combining the results of their experiments and simulations, the team found that the model agreed well with their experimental observations. They also found that odor frequencies above 1–2 Hz and certain backgrounds modified the neuronal representation of the *Datura* mixture in the brain and thus altered perception of the flower. Unexpectedly, traffic pollutants containing volatiles such as toluene or xylene, which are only weakly similar to odors that attract moths, elicited responses from the same olfactory neurons as oxygenated aromatics that are found in *Datura* and *Larrea* scents, fooling the insect's olfactory system.

Riffell and colleagues have demonstrated that the olfactory system is less sensitive to flower-specific volatiles than previously thought. They have also shown that, surprisingly, moths respond to volatiles present in the exhaust gases of cars and trucks. They speculate that this may affect the moth's navigation system and possibly account for the widespread disruption to other pollinators such as bees, which are economically essential.

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Energy availability drives timing of moult in a songbird

Feathers are essential for flight and thermoregulation as well as for communication. However, producing and maintaining feathers is costly. As with any outer covering, wear and tear necessitates their replacement on a regular basis. The shedding of worn feathers and their subsequent replacement happens through a process called moult. Moulting, especially when it occurs over the entire body at once, incurs a high energetic cost. Not only is it costly to produce the feathers themselves, but birds also sustain additional costs: their thermoregulatory costs rise because of skin exposure and their ability to fly can also be impaired. Thus, especially in temperate climates where the availability of energy is seasonally limited, moult rarely coincides with other energetically costly life stages such as migration and breeding. In most species moulting is deferred until after the breeding season, often late in the summer, to repair damage sustained during reproduction as well as to ensure adequate plumage coverage before the winter. However, species that produce showy breeding plumage also need to moult before reproduction (pre-alternate moult), so that they are equipped to display their readiness to breed.

The factors that trigger initiation of the pre-alternate moult have received little attention to date. Changes in season, primarily indicated by changing photoperiod, are likely to be the main drivers of moult timing but other possible factors include breeding and energy availability. It was the latter hypothesis that led a team of American researchers, headed by Raymond Danner of Virginia Tech University and the Smithsonian Migratory Bird Center to initiate a study into the patterns and timing of moulting in free-living swamp sparrows (*Melospiza georgiana*) in coastal North Carolina. Specifically, they sought to test whether the pre-alternate moult was limited and/or initiated by energy availability.

The team established four research plots, separated by several kilometres and provided a rich supply of food – in the form of millet and mealworms – on two of the plots to determine the effects of energy availability on moult timing. Then they monitored when the birds dropped their feathers prior to developing their breeding plumage. Food-supplemented birds were able to initiate the pre-alternate moult earlier than birds from the more impoverished plots, potentially allowing earlier migration to breeding grounds and an early start to the breeding season. The researchers also discovered that there was a distinct pattern to the moulting sequence in all individuals, regardless of treatment. The birds first lost feathers from their bodies, before losing them from the head and then the face, ensuring that the energetic costs are spread out over a long period of time and that high-priority areas (such as the body) moult first and that regions of the body that are important for sexual signalling (such as the head and face) moult closest to breeding.

These findings confirm that energy availability is indeed a trigger for moulting. The study also has implications for lab-based studies, where the animals are often fed freely, as well as for songbird populations that experience fluctuations in the availability of food as a result of well-stocked backyard feeders, invasive species and climate change. It remains to be seen how the availability of food triggers the initiation of moult and whether this is characteristic of all species that exchange their plumage prior to breeding.

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