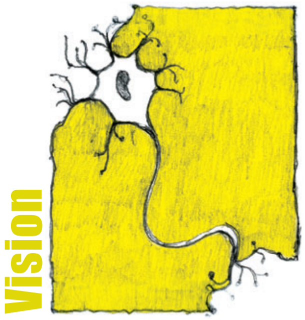
A unique way to see colors



Color vision is a vital capability for animals, as it significantly increases the information received from the environment. To discriminate between different colors, the eyes of most animals rely on two to four photoreceptors with different spectral sensitivities, whose electrical responses are compared in a neural process yielding an astonishingly fine color resolution, particularly in vertebrate eyes. In a remarkable study published recently in *Science*, a team of scientists led by Hanne Thoen from the University of Brisbane, Australia, provide evidence for a completely different mechanism of how animals can see colors. Instead of having only a few visual receptors with different spectral sensitivities, mantis shrimp use 12 different photoreceptors, which enables them to recognize light of different wavelengths without time-consuming neural processing.

Mantis shrimp belong to an ancient group of crustaceans; they look like lobsters that were beautifully painted with vivid colors. They are predominantly found in tropical coral reefs, where they hunt with the help of forceful raptor claws that can explosively unfold to maim and even kill comparably large prey animals. Colors play important roles for these shrimp, because they help the animals to recognize different types of corals, prey species, predators and competitors. To orientate in this colorful environment, the shrimp have stalked ‘compound eyes’ that are capable of moving independently of each other. The eyes resemble those of other arthropods, as they are made of numerous visual units called ommatidia, which produce individual pictures that are finally combined in the brain. The shrimp eyes, however, are special in that they possess a ‘midband’ of six ommatidial rows, two rows of which analyze polarized light and four rows account for color vision.

To examine the mode of color-coding in these shrimp, Thoen’s team measured spectral sensitivities using intracellular electrophysiological recordings in the photoreceptor cells. They demonstrated that the 12 different types of photoreceptor cells are contained in the color-detecting ommatidial rows of the midband, and each photoreceptor cell is narrowly tuned to a different wavelength between 300 and 700 nm. As the vertical visual field captured with these ommatidia is very narrow, the scientists concluded that the shrimp need to scan an object of interest with slow eye movements. Indeed, such scanning movements of the shrimp’s eye have been noticed in previous studies. This mechanism may generate a temporal signal for each spectral sensitivity, enabling the shrimp to recognize particular colors very rapidly.

Next, the scientists wanted to know how the eyes perform in color discrimination. They trained the shrimp to recognize a certain color by rewarding them with food. Then they used various test colors to determine at which wavelength difference the animals fail to discriminate between the test color and the color they were taught to associate with food. Counter-intuitively, the team found that the shrimp’s ability to discriminate between different colors is very poor, despite the fact that they possess these 12 different color receptors.

Thoen’s team demonstrated that mantis shrimp see their environment with an array of peripheral color detectors that scan an area of interest. They also discovered that the animal’s colour discrimination is not very sensitive, but its temporally efficiency is high because further neural processing steps are not required. Obviously, it is less important for the mantis shrimp to discriminate colors with high accuracy, but advantageous in their environment to instantly recognize the movement of colored patterns that are characteristic of either prey animals or potentially life-threatening predators and competitors.

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Low energy use fuels a slow existence

Much of an organism’s life is given to the acquisition, assimilation and transformation of energy. Energy is collected, via foraging and feeding, and is in turn allocated to reproduction, somatic growth and the collection of yet more energy. A long-standing hypothesis in the field of physiological ecology has been that the rate at which organisms use energy (their metabolism) dictates the speed at which they live. Thus, those with high metabolic rates relative to their body size would have quick, high rates of energy turnover, usually falling onto the ‘live fast, die young’ side of the slow–fast life history continuum. Conversely, those with low rates of energy usage would have slow life histories: growing slowly, maturing at a later age and producing fewer young.

Consequently, in mammals it would be expected that those with low metabolic

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rates relative to their body masses would have slow life histories and vice versa. However, attempts to validate this relationship using basal metabolic rate (BMR – measured in animals at rest in favourable thermal conditions, which is the energetic equivalent to the idling speed of a car) have proven to be inconclusive. Take for example the primates; as an Order they have significantly slower rates of living than other mammals of similar body sizes, maturing late, producing only a few young and living for relatively long periods of time. However, after controlling for the effects of phylogenetic relatedness and body mass, primate BMR is no different from that of other mammals. But what if BMR was not the best indication of energy usage? Is there a better way to test whether metabolism is indeed linked to the speed of life?

These were the questions put forward in a study by Herman Pontzer from Hunter College in New York and a large number of colleagues from across the USA, recently published in *PNAS*. Pulling together countless hours of gruelling fieldwork, the study presented measures for total energy expenditure (measured on a daily basis) from 18 different species of primates spanning a range of body sizes. The results confirmed earlier studies and failed to find a relationship between BMR and a number of life history traits (such as growth rate, litter mass and maximum lifespan). What they did find, however, was a significant relationship between those traits and total energy expenditure. Despite a wide range of activity patterns and lifestyles, and after controlling for body mass and phylogenetic relatedness, the primate total energy expenditure was on average almost 50% lower than that of other mammals. Interestingly, the results did not differ between captive and wild populations of a small subset of these species, indicating that a low rate of energy use is characteristic of these primates regardless of habitat or ready access to food.

The authors suggest that this capacity for surprising energetic frugality contributes to the slow pace of life in primates. The broader implication of this study is not only that energy use might indeed be linked to the pace of life but also that the BMR that we find in the laboratory is not always a true reflection of total energy expenditure that occurs in the wild, leaving open the possibility for more to be learned about the interactions between metabolic rate and life histories as we continue to take the lab to the field.

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Sneaky fish use suction for stealthy hunting

Imagine you are a small crustacean. You might be minding your own business, until suddenly you feel it: a wave of water signaling the approach of a predatory fish. Luckily, your escape response is incredibly fast. All you need is that brief warning wave to scoot away in the nick of time. Furthermore, your fishy pursuer probably uses a suction-based strike, and suction feeding requires a fish to be very close to its prey for success. Given the rapid approach of the fish, and the comparatively huge wave it must send toward the copepod, it seems remarkable that fish can catch anything at all. Yet many fish survive by suction feeding, and they are remarkably successful predators. This raises an interesting question: how can fish ever get close enough to prey for suction feeding while avoiding detection?

The wave produced by the front of a swimming fish is called a bow wave, and it should provide ample stimulation to frighten away prey. And somehow, the prey doesn't escape. They hardly seem to notice the bow wave at all. Fish must have some way of sneaking up on small prey that does not elicit an escape response.

Brad Gemmel and his colleagues at the University of Texas suspected that fish might be able to actively avoid detection by manipulating their own bow wave. The group of researchers filmed predatory interactions between zebrafish and copepods using tomographic particle image velocimetry, a technique to visualize fluid movement in a 3-D volume. By measuring the bow wave and fluid strain between the fish and the prey, they hoped to find some clue as to the fish's apparent stealth.

Surprisingly, the researchers noticed that during predatory strikes, the fluid forces from the bow wave on the prey were much smaller than expected. However, a normally swimming fish that was not approaching prey had a much stronger bow wave. In fact, somehow, the feeding fishes were targeting the change in their bow wave. The fluid strain was weakest in the plane of the prey. But how were the fish doing it? Gemmel and colleagues decided to look for some change in behavior just before the suction strike that did not appear during normal swimming and found there was one chief difference in the fish between predatory and non-predatory swimming. When a fish approached a copepod, it opened its mouth just slightly before the actual feeding strike. During routine swimming, the fish's mouth did not open.

By opening its mouth ever so slightly, the zebrafish created suction: sucking its own bow wave in to hide it from the copepod. This hydrodynamic stealth has never been observed before. It's a clever co-option of a mechanism that was already being used for feeding – and given the prevalence of suction feeding among fishes, hydrodynamic stealth may be more common than anyone expected.

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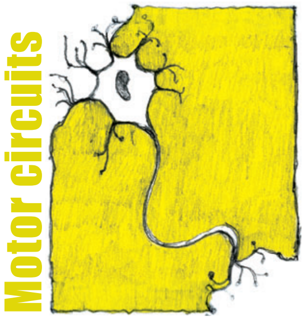
Fishing for complements in the spinal cord



In comparison to the clownish stumbling of most of us landlubbers, fish are elegant beasts. They appear to cruise through the water by simply wiggling their bodies back-and-forth in a single (axial) plane. Walking on solid ground looks and feels far more complicated, requiring independent control of multiple limbs along several axes.

Given the evident ease of the fish's locomotor lifestyle, it has been assumed that the spinal networks that control their movements are relatively simple. In particular, it was thought that fish could independently control muscles on the left and right sides of their bodies, but dorsal and ventral muscles within a body quadrant always contracted together. However, a recent study of zebrafish motor circuits has gutted this assumption by showing that fish spinal networks are fully equipped to control movements along more than just the axial plane.

Martha Bagnall, a post-doc in David McLean's lab at Northwestern University, USA, used whole-cell patch-clamp electrophysiology to record from primary motoneurons in the larval zebrafish spinal cord. By measuring the synchrony of input currents to pairs of motoneurons, she discovered that motoneurons that innervate dorsal and ventral muscles are driven by different premotor inputs. This surprising result means that motor circuits are organized in parallel, allowing independent control of muscles along both the anterior–posterior and dorsal–ventral axes.

The discovery of these parallel circuits in the fish spinal cord raised the possibility that movements could be initiated by differential activation of dorsal and ventral muscles within a single body quadrant. To test this hypothesis, Bagnall and McLean used calcium imaging to measure motoneuron activity when a fish rolled over, from a side-lounging position to a ready-to-swim stance. They observed that dorsal and ventral motoneurons were asymmetrically activated when the fish flipped. Further experiments showed that the descending input to motoneurons during flipping behavior depended on the vestibular system, which allows the fish to monitor self-motion and body orientation. However, the segregated organization of dorsal and ventral motoneurons remained whether or not the vestibular system was intact.

Together, these impressive electrophysiology and behavior experiments reveal a previously unappreciated level of intricacy in fish motor circuits. The authors suggest that fish spinal networks may have provided a template for the evolution of limb control circuits in tetrapods. It might be possible to shore up this idea by comparing the genes that specify development of fish dorsal and ventral motoneurons versus tetrapod flexor and extensor motoneurons. However, this theory is likely to remain on the bone-heap of speculation, as fish motoneurons are not well preserved in the fossil record.

Another important question raised by this study is the role that dorsal and ventral motoneurons play in fish rolling behavior. The authors show that dorsal and ventral motoneurons exhibit unequal activity when the fish rolls, but it is not clear whether this pattern of activity is really sufficient to cause the fish to flip over. Indeed, it is difficult to understand how simply flexing muscles on half the body would cause the animal to roll. It seems more likely that fish shift their weight or use their fins to generate torque, and, in the process, may asymmetrically activate dorsal and ventral motoneurons. Further work is needed to understand the biomechanics and neural control of this self-righting behavior. Fortunately, the ability to record from spinal circuits in behaving zebrafish provides a unique opportunity to investigate the interaction of multiple elements within an active motor circuit.

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