Neurobiology: Jumping Spiders
Getting On Board

A new technique has overcome decades of failure to allow, for the first time, electrophysiological access to the brains of jumping spiders, a group of animals renowned for generating highly complex, seemingly vertebrate-like behavior from their tiny arthropod brains.

Stanley Heinze

Jumping spiders are amazing. These animals have a pair of huge, forward facing eyes that make them appear adorable even to arachnophobics. Although this might be a selective advantage when facing ready-to-scream-and-swat humans, the remarkable visual abilities that result from these eyes have evolved to enable highly precise hunting behaviors and bizarrely complicated mating rituals. How those behaviors are controlled by a brain less than a millimeter in diameter is completely unknown, but a fascinating new study reported in this issue of Current Biology by Menda et al. [1] finally paves the way towards illuminating the neural basis of a behavioral repertoire unmatched amongst invertebrate land animals.

The jumping spider’s visual capabilities are indeed astounding. They possess excellent color vision [2], precise depth perception [3], and with a spatial resolution of down to 0.04 degrees they have the sharpest vision of any arthropod, even surpassing many vertebrates, including numerous mammals [4]. Additionally, their large, forward facing pair of eyes (the anterior medial eyes) is complemented by two to three lateral eye pairs, which are specialized for motion vision and provide the animal with a near full panoramic field of view [5] (Figure 1). Similar to our saccades, jumping spiders have eye movements that allow them to scan interesting parts of the environment. As the lenses of the eyes are fixed to the head, they use tiny muscles to move their retinae, which sit at the end of telescope-like eye tubes [6]. Coordinated by their minute brains, they use this highly acute, telescopic sight to sit in ambush and watch out for prey, potential mates, or rivals. Once they have detected prey, these animals have an amazingly variable range of hunting strategies [7].

Most species of jumping spiders sneak up on their prey in a cat-like manner and pounce at it once they have reached a certain close distance. Unlike many other invertebrates with their stereotypical routines, however, jumping spiders adjust their attack strategy to the type of prey; for example, some attack larger prey only from behind, while they jump at smaller prey from any direction; or chase fast moving prey, whereas they slowly stalk stationary prey. Probably the most fascinating strategy has been observed in an Australian rain-forest species, which hunts by walking along trees until it detects its prey, a certain species of web-building spider with capable defense mechanisms. Then, instead of walking straight towards its victim and invading its web, the jumping spider stops, leaves its position near the prey, visually inspects the environment above the web, and, once it has spotted an appropriate structure above the center of the prey’s web, climbs up another tree towards that point. From its new position it drops from its silk-line until it is alongside the web and attacks its prey from midair [7].

This behavior is remarkable in several ways. First, the attacker moves away from its prey in order to move towards an appropriate abseiling position, a detour during which it can completely lose sight of the prey. Second, without moving, the spider visually inspects its surroundings and anticipates the best dropping point, as well as a suitable path through dense vegetation to get there. At last, as no two prey webs are located in an identical position in the forest, the spider has to find a novel detour during each hunt. All these behavioral decisions rely on detection and categorization of objects and require sophisticated interactions between these recognition processes (mediated by the large frontal eyes) and motion vision (mediated by the secondary eyes). The anticipatory nature of detouring demands a highly capable working memory, potentially involving an internal representation of the chosen path long before any movement along that path is initiated. Interestingly, only in very few other groups of animals has this last aspect been unambiguously revealed, most prominently amongst higher primates and corvid birds [8]. Given these intriguing similarities between jumping spider behavior and essentially our own behavior, it is highly desirable to illuminate the neural basis of the complex strategic decisions made by those animals. This is particularly fascinating when we consider the small size of jumping spider brains, which function with only a tiny fraction of the number of neurons of mammalian brains.

Unfortunately, the high hydrostatic pressure of the spider’s body fluid, which enables it to jump without the need for large muscles, has prevented any electrophysiologist from recording from its brain. This is because catastrophic fluid loss almost immediately kills the animal after opening the spider’s head to gain

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access to the nervous system. Despite these challenges, Menda et al. [1] have started to unravel the neural basis of the jumping spider’s enigmatic behaviors. They developed a novel method to finally enable electrophysiological access to the spider’s brain. With an astonishingly simple strategy, they were able to overcome decades of failure: to avoid fluid loss, they simply made the opening in the head very, very small — going to an extremely tiny size of around 100 μm. Then they were able to successfully carry out the delicate procedure of inserting a tungsten wire through that hole and target defined areas of the spider’s brain, resulting in many hours of in vivo extracellular recordings of neural activity. But where would one aim the electrode at?

Although no functional studies exist on brains of jumping spiders, spider brain anatomy is at least partly described. One structure in the middle of the brain, the arcuate body, receives prominent input from early visual brain centers and has been discussed to be the spider counterpart of the central complex of insects [9]. Intriguingly, the insect central complex is involved in coordination of motor actions as well as higher order visual processing [10]. With the study of neural correlates of complex behaviors in mind, Menda et al. [1] consequently chose the arcuate body as their recording site. During those recordings, they essentially sat the spider down in front of a large television screen and displayed a variety of images, which the spider could scan with its elaborate combination of eyes. They presented either classic visual stimuli used to characterize visual systems across the animal kingdom (such as gratings, oriented bars, and so on) or they presented naturalistic, behaviorally relevant stimuli of potential prey, mates, or rivals. They indeed found neural activity that correlated with the presence of prey images, whereas the same cells showed no response to a scrambled image with identical low-level image characteristics such as overall contrast and brightness distribution.

Additionally, using white-noise stimuli, Menda et al. [1] measured receptive fields of some of the neurons while they either covered up one eye-pair (frontal or lateral eyes) or left all eyes open. Surprisingly, the receptive fields of both individual eye-pairs combined would not add up to the receptive fields measured when all eyes were open (within the same neuron). These non-linear interactions of outputs from the object-scanning frontal eyes and the motion-detecting lateral eyes are intriguing, as they provide a first hint towards how information about different aspects of prey are integrated to generate a coherent behavioral response. The mental binding of distinct features of the environment into one coherent representation of objects is carried out by our own brains as well, yet it is far from understood [11]. The fact that in jumping spiders those input pathways can be easily separated by covering up one pair of eyes opens fascinating avenues of research towards unravelling fundamental features of parallel processing and integration of different visual input streams.

Overall, the combination of a small, accessible brain, highly complex behavior, and a unique division of labor between different sets of powerful eyes makes the jumping spider a model organism highly relevant for neuroscience far beyond spider research. Menda et al. [1] now cleared the path for applying the powerful tools of electrophysiology to these animals. So far, we have merely scratched the surface of the neural principles that enable these amazing little creatures to achieve their cunning hunting efficiency and flexibility. But finally the door has been opened and jumping spiders are on board!

Figure 1. Jumping spider (*Phidippus audax*). The large anterior medial eyes (center) have the highest resolution of all arthropod eyes and surpass that of many vertebrates, while the anterior lateral eyes are specialized for motion vision. (Photograph by Thomas Shahan, published under the Creative Commons license (http://creativecommons.org/licenses/by-sa/3.0) on http://en.wikipedia.org/wiki/Phidippus_audax#mediaviewer/File:Phidippus_audax_male.jpg.)

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Neuronal Plasticity: How Do Neurons Know What To Do?

A recent study confirms activity-dependent co-regulation of membrane conductances as a mechanism underlying homeostatic regulation of neuronal properties. How multiple cellular and synaptic homeostatic mechanisms interact in a neuronal circuit is best studied with a combination of experimentation and modeling.

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Nervous systems face two challenges: to be plastic and able to change, adapt, and learn, while at the same time functioning reliably to ensure an animal’s survival in an ever-changing environment. A growing body of experimental and computational work indicates that to do so brains rely on multiple plasticity and homeostasis mechanisms that act on both synaptic and cell-intrinsic parameters. While the triggers and molecular mechanisms of some prominent forms of synaptic plasticity are increasingly well understood [1], what factors govern — and what mechanisms underlie — the plasticity and stability of neuronal properties is less clear. Recent work reported in Current Biology by Schulz and colleagues [2] shows that electrical activity plays a role in regulating correlated expression levels of ionic membrane channels that had previously been found to also depend on the presence of neuromodulators [3,4]. This warrants a brief review of various triggers and regulators of neuronal plasticity and stability.

An important finding in the area of neuronal plasticity and homeostasis is that electrophysiologically relevant parameters of neurons — for example, the magnitudes of different ionic conductances in a neuron’s membrane — can vary widely between different neurons of the same type [5]. Such variability of parameters that support similar and physiological network output has also been confirmed in computational models [6]. This introduces the notion of a ‘solution space’, i.e. the idea that instead of being limited to a particular and narrowly defined combination of cellular and synaptic parameters, networks can achieve functional output in an often extensive subset of their high-dimensional space of cell and synapse parameters [7]. Despite this variability in individual parameters, the electrical activity produced by neurons of the same type can be highly stereotyped.

One mechanism through which neurons appear to achieve reliable and functional activity is the imposition of constraints on how cellular and synaptic parameters can vary. Such constraints often take the form of linear relationships between pairs or higher numbers of parameters [3,8], thus reducing the dimensionality of the solution space occupied by the biological system. Such linear correlations between cellular and synaptic parameters have been independently demonstrated at the level of electrophysiological properties such as ionic membrane conductances [3,9] and synapse strengths [10], and at the level of mRNA copy numbers for ion channels, like in the recent paper by Schulz and Colleagues [2].

Why might correlations between neuronal parameters be important for the ability of neurons and networks to generate and maintain proper biological output? Computational models of neurons and networks show that imposing pairwise correlations on neuronal or synaptic parameters can increase the likelihood that a given neuron or network generates functional activity despite variability in individual parameters [11]. In some cases, sets of cellular parameters that are found to be correlated in biological neurons appear to be functionally tied into ‘modules’ [12]. For example, in bursting neurons, the conductances of the slow inward current $I_s$ and the potassium current $I_K$ constitute a burst generation module, while conductances for the transient calcium current $I_{CaT}$ and the delayed rectifier current $I_{Kr}$, if co-regulated, determine the peak and duration of the slow voltage oscillations underlying bursts [12]. Imposing correlations between the conductances within a given module will therefore help ensure proper neuronal behavior.

Intriguingly, the recent Schulz et al. paper [2] and previous reports by this and other groups [3,4] show that correlations between cellular parameters that appear to support functional network output in an intact and unperturbed circuit are sometimes abandoned when the circuit is exposed to — and has to overcome — massive perturbation or injury. For example, in the stomatogastric nervous system of crabs, rhythmically active central pattern-generating neurons exhibit several pairwise linear correlations between mRNAs coding for various ion channels when the circuit is intact, under the influence of neuromodulators, and generating appropriate motor patterns [3,8].

In contrast, most of these pairwise correlations disappear when the circuit is challenged to produce its motor pattern in the absence of neuromodulation and after a period of quiescence [3,4]. It is as if the circuit ‘knows’ that it needs to abandon its previously implemented correlation rules in order to explore a larger swath of its parameter space and find a new solution to generating functional activity under perturbed conditions. What tells a neuron whether — and how — to adjust its properties in order to maintain proper function? Figure 1