

Weakly Electric Fishes and Auditory Processing

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Electrosensory systems share numerous similarities with auditory systems, including a shared evolutionary history reflected in hair cell sensory receptors and similar brain pathways; key roles for spectral and temporal stimulus features in information processing; and similar neural computations for determining the spatial location and identity of stimuli. Moreover, many people are familiar with strongly electric fishes such as the electric eel and torpedo ray that use electricity as a weapon. Indeed, the writings of ancient Greeks and Romans make it clear they were aware of the special powers of strongly electric fishes, although not yet of the nature of electricity (Finger and Piccolino, 2011). Even earlier evidence of this knowledge in the form of artwork dates back more than 5,000 years to ancient Egypt (see bit.ly/3StnlKf).

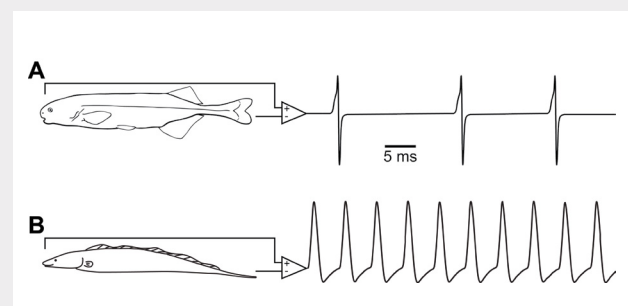
Less commonly known than the strongly electric fishes are the weakly electric fishes, so named because they generate electric fields with much less voltage than strongly electric fishes. The electric fields in these species are so weak that they usually cannot be felt by humans even when these fish are handled. In fact, detecting their electric fields requires electrodes and special equipment.

Some weakly electric fishes can be found in the aquarium trade. It is not uncommon to spot a black ghost knifefish (*Apteronotus albifrons*; see bit.ly/3kjBcGC) or elephant-nose fish (*Gnathonemus petersii*; see bit.ly/3IubLde) in your local pet store. Their behavior is fascinating to watch, but few observers realize that these fish are constantly generating an electric field in the water surrounding them (see bit.ly/3EV3YV9). In addition to electric organs that actively generate an electric organ discharge (EOD), these fish also have electroreceptors that detect EODs (see bit.ly/3ZfFcGR). These EODs are too weak to serve as any kind of a weapon. Instead, weakly electric fishes use EODs to communicate, much like we use sound to communicate. These fishes are also

able to navigate and detect objects in their environment by detecting distortions of their EOD in a process called active electrolocation, which shares some similarities with echolocation.

Weakly electric fishes come in two basic types. Pulse-type fishes generate brief EODs separated by longer gaps of silence (**Figure 1A**). In wave-type fishes, the interval between each EOD matches the duration of a single EOD, resulting in a continuously oscillating, almost sinusoidal, EOD (**Figure 1B**). Electric organs have evolved at least six times independently among fishes (Gallant, 2019). Research on two lineages in particular, the African mormyrids and neotropical gymnotiforms, has led to numerous foundational insights into neural mechanisms for sensory processing and the control of behavior (Bullock et al., 2005; Carlson et al., 2019). Many of these insights have, in turn, fostered subsequent discoveries in auditory processing and have helped place our understanding of auditory processing into a broader evolutionary context.

Figure 1. Electric organ discharge (EOD) recorded from two weakly electric fish species. Placing a pair of wires in the water near a fish and connecting them to an amplifier allows visualization of the EOD on an oscilloscope or computer. **A:** pulse-type EOD recorded from the mormyrid *Paramormyrops kingsleyae*. **B:** wave-type EOD recorded from *Gymnarchus niloticus*, the closest living relative to mormyrids.



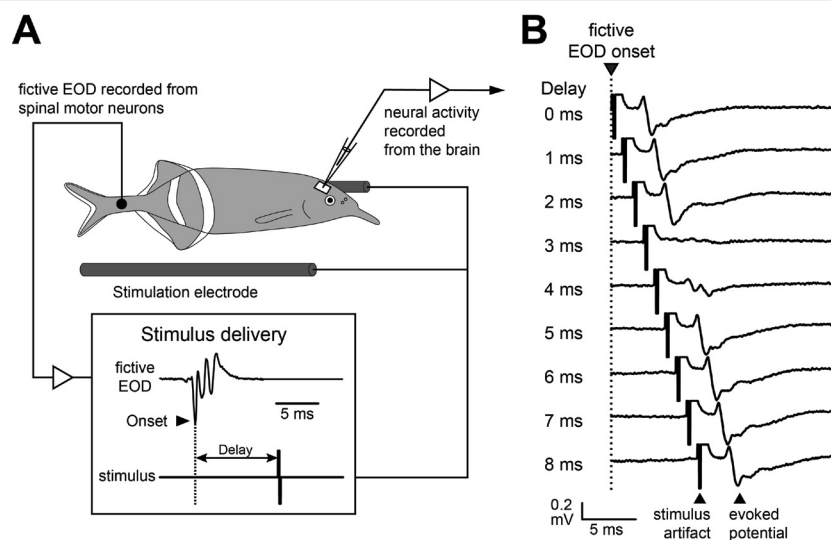


Figure 2. Studying the effects of corollary discharge on sensory processing in mormyrid fishes. **A:** fish is paralyzed and its EOD is silenced. However, the activity of spinal motor neurons that normally result in an EOD can be recorded using an electrode placed next to the tail. Electrosensory stimuli can be delivered at fixed delays relative to this fictive EOD while recording the responses of sensory neurons in the brain to these stimuli. **B:** recording of electrosensory responses from neurons in the exterolateral nucleus in the brain. Stimuli are delivered at various delays following the fictive EOD. An electrical stimulus artifact is visible at the timing of stimulus delivery, and this is followed shortly by an evoked potential that represents the summed activity of numerous neurons near the recording electrode. This evoked potential is blocked at delays of 3-4 ms due to corollary discharge inhibition. Modified from Fukutomi and Carlson (2020).

How to Distinguish Self from Others

When humans move their eyes, there is a dramatic shift in the visual stimulus hitting the retinas, but we perceive a stable, unmoving world. When external objects move, however, we perceive that as visual motion. Although humans and other animals distinguish between these different sources of visual stimulation effortlessly, this ability relies on sophisticated neural processing. Whenever an animal performs a behavior, a signal is sent from motor regions of the brain that control that behavior to sensory regions of the brain. Referred to as a “corollary discharge” (Sperry, 1950), this signal informs sensory regions about the timing of behavioral output, causing sensory neurons to respond differently to self-generated stimuli versus stimuli coming from the outside world.

Corollary discharges are critical for sensory processing and the control of behavior (Crapse and Sommer, 2008). There is even evidence suggesting that corollary discharge dysfunction may play a role in schizophrenia by impairing an individual’s ability to distinguish self from other (Ford et al., 2001). However, corollary discharges can be challenging to study because this requires the

monitoring of sensory and motor systems in animals that are actively behaving. Electric fishes, however, are unique in that they produce a behavior, the EOD, that does not involve any muscle contractions and is much simpler than most behaviors. Because of this, decades of research in African mormyrids has led to numerous insights into corollary discharge functions and mechanisms (Fukutomi and Carlson, 2020).

Mormyrids produce pulse-type EODs (Figure 1A). When performing a neurophysiological experiment, the fish is immobilized with a drug that blocks the neuromuscular junction and prevents movement. This drug also silences the electric organ, so the fish no longer produces an EOD. However, neurons in the spinal cord that normally excite the electric organ continue to fire, and their activity can be recorded noninvasively by placing a small wire next to the tail, much like an electroencephalogram (EEG) is used to record human brain activity. Electrical activity in these spinal motor neurons is referred to as a “fictive EOD” because it reflects when an EOD would normally occur in a fish that hadn’t been silenced and thus can be used to monitor the timing of behavioral output. At the same

electrolocation pathway. Because this excitation is only active when the fish generates its own EOD, it selectively boosts sensory responses to the fish's own EOD (Fukutomi and Carlson, 2020). Similarly, in the auditory system of bats, corollary discharge appears to suppress responses during calls (Suga and Schlegel, 1972) but enhance responses during echoes (Schuller, 1979).

Generating Expectations

A short window of inhibition is sufficient to block responses to brief, fixed stimuli like an EOD. However, sensory inputs resulting from an animal's own actions are often more complex, varying over space and time. For example, when an animal moves its eyes, the entirety of the images hitting the retinas shift, and the nature of that shift depends on whether the animal moved its eyes directly using ocular muscles or indirectly using neck muscles to move the head. The nature of that shift also depends on how fast and in which direction the eyes moved. In many cases, a corollary discharge activates a so-called "efference copy," which is a "negative image" of the sensory response predicted to result from a behavior (von Holst and Mittelstaedt, 1950). It is more complex than a brief window of inhibition that simply blocks sensory responses and is instead a precise template that can cancel out responses to self-generated stimuli that vary in space and time. As a result, responses to self-generated stimuli are subtracted out, whereas responses to external stimuli get through.

Research in mormyrid fishes yielded the first experimental demonstration of how brains can implement an efference copy (Fukutomi and Carlson, 2020). In addition to the electroreceptors that mediate communication and active electrolocation, mormyrids have a third electroreceptor type that mediates passive electrolocation. Passive electrolocation is to active electrolocation what hearing is to echolocation: the identification and localization of objects in the environment using external cues rather than feedback from self-generated stimuli. Passive electrolocation is far more widespread than active electrolocation, being an ancestral vertebrate sense found in living lampreys; cartilaginous fishes such as sharks and rays; certain bony fishes such as sturgeons and paddlefish; aquatic salamanders; and mammals such as the platypus (Bullock et al., 1983). Much like neurons that maintain an electrical potential across their membrane due to an uneven distribution of ions inside and outside the cell, living organisms in an aquatic or marine environment maintain an electrical

potential across their skin surface because the concentrations of ions in their bodies are different from those in the surrounding water. These small potentials can be used to precisely locate living organisms. Passive electrolocation is typically used to detect prey at short range but can also be used to detect predators and potential mates.

These passive electroreceptors are far more sensitive than the electroreceptors mediating active electrolocation and communication because they must pick up faint signals naturally emanating from living organisms rather than from comparatively "loud" EODs being actively generated by electric organs. As a result, these receptors respond strongly to the fish's own EOD. However, unlike the electroreceptors that mediate communication, which have very brief responses to EODs, the responses of the passive electroreceptors are complex and can last as long as 100 ms. Simply blocking responses throughout this window of time would render the fish unable to detect external stimuli for an extended period of time.

Instead, an equally complex and long-lasting efference copy is used to cancel responses to self-generated EODs while maintaining sensitivity to external stimuli (Fukutomi and Carlson, 2020). What's more, as environmental conditions change, the responses to self-generated EODs can also change. Thus, this efference copy is not hard-wired but is continuously updated in real time. Recently, a similar process was found to occur within the mouse auditory system, in which an efference copy was generated and continuously updated in response to sounds that were associated with licking behavior (Singla et al., 2017).

Temporal Hyperacuity

Timing plays a critical role in both auditory and electrosensory processing. The most extreme example of temporal sensitivity in the auditory system is the detection of interaural time differences (ITDs) that many land vertebrates use to determine where a sound originates from (see bit.ly/3EugfQ8). Sounds originating directly in front of the listener arrive at both ears simultaneously. Sounds that come from one side, however, hit the near ear before the far ear, resulting in an ITD. Humans can detect ITDs as small as about 10 μ s (Klumpp and Eady, 1956).

Much like humans detect differences in the timing of auditory inputs to the two ears to determine where a sound is

coming from, weakly electric fishes also use differences in the timing of the responses of electroreceptors on different parts of the body surface to get information about the outside world. In mormyrids, such timing differences are used to determine the EOD waveform of neighboring fish, which varies with species, sex, age, reproductive status, and relative dominance (Hopkins, 1986a).

In contrast to the pulse-type EODs of mormyrids, their closest relative, *Gymnarchus niloticus*, generates a wave-type EOD (Figure 1B). Wave-type EODs are also found in numerous gymnotiform species from Latin America. During active electrolocation, wave-type fish use small timing differences in the feedback from their self-generated EODs to detect electrical capacitance, which allows them to distinguish living from inanimate objects (von der Emde, 1998). Timing differences are also important during social interactions. When two fish are in proximity to one another, their EODs interfere to create modulations in signal amplitude and phase (Heiligenberg, 1991). The rate of modulation is equal to the magnitude of the frequency difference between the EODs and is identical for frequency differences of equal magnitude but opposite sign. Distinguishing positive from negative frequency differences requires a fish to analyze the relationship between amplitude and phase modulation and thus depends on the ability to detect small-phase modulations (Heiligenberg, 1991). Because EOD frequency varies in wave-type fish with species, sex, and relative dominance, this ability is crucial in identifying neighboring fish. It also underlies performance of the jamming avoidance response, in which fish with similar EOD frequencies shift their frequencies away from each other to avoid jamming their active electrolocation abilities (see bit.ly/3Eu35Cw).

Weakly electric fish outperform humans in their temporal sensitivity. They can detect differences in the timing of electrosensory stimuli as small as tens to hundreds of nanoseconds (Kawasaki, 1997). This remarkable sensitivity may have evolved because, unlike acoustic signals, electric signals do not propagate as waves but exist as localized, nonpropagating electrostatic fields (Hopkins, 1986b). Whereas acoustic communication signals are degraded due to absorption, reflection, refraction and reverberation, the fine temporal structure of electric signals is preserved, allowing information to be accurately transmitted at much shorter timescales (Hopkins, 1986b).

Detecting Submillisecond Timing Differences

Neurons transmit information using electrical spikes that are called action potentials. Typically, action potentials are generated close to the cell body, or soma, of a neuron and then propagate at a finite speed down a long biological wire called an axon. The end of that axon comes into close contact with a target neuron, forming a synapse for communication from the presynaptic neuron to the postsynaptic neuron. Sometimes these synapses are located on the soma of the postsynaptic neuron, but often they are located on dendrites, which are small, branching fibers that emanate from the soma.

A typical action potential in a neuron lasts about 1 ms. Even the fastest synapses operate in the range of milliseconds to tens of milliseconds. Thus, the degree of temporal acuity found in the auditory system of humans and the electrosensory systems of weakly electric fishes is remarkable. How can nervous systems detect differences in the arrival times of stimuli at different sensory receptors that are several orders of magnitude shorter than the signals the nervous system itself uses to process information?

Following the discovery of ITD sensitivity in humans, Jeffress (1948) devised a model for how a neural circuit could detect a range of ITDs. According to this model, auditory inputs from the two ears enter a neural circuit on opposite sides (Figure 4A). An action potential traveling along an axon coming from the left ear will reach neurons on the left end of the circuit first and neurons on the right end of the circuit last. However, an action potential coming from the right ear goes in the opposite direction. These axons traversing the length of the circuit are referred to as “delay lines,” because the inputs they provide to their postsynaptic targets arrive at increasing delays as an action potential travels down the axon. Postsynaptic neurons within the circuit respond maximally when they receive simultaneous inputs from both ears, which is referred to as “coincidence detection.” Thus the Jeffress model (1948) is a model based on “delay-line coincidence detection.”

A sound coming from in front of the listener will reach both ears at the same time. The resulting action potential from the left ear will enter the left end of the circuit at the same time as the action potential from the right ear enters the right end of the circuit. These action potentials

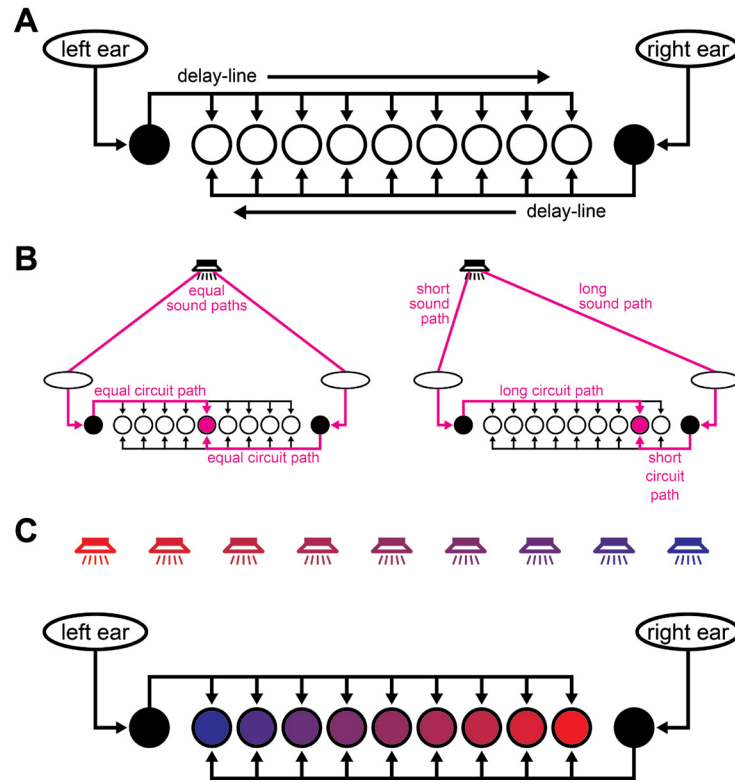


Figure 4. The Jeffress model relies on delay-line coincidence detection to convert interaural time differences (ITDs) into a map of sound source location. **A:** axons relaying auditory input from the left and right ears enter the circuit at opposite ends and traverse the length of the circuit, synapsing on postsynaptic neurons throughout. This establishes delay lines running in opposite directions for the two ears. **B:** postsynaptic neurons are coincidence detectors that respond maximally when they receive simultaneous excitatory input from the left and right ears. **Magenta lines**, paths that a sound takes to first reach the two ears and then the paths of action potentials traveling through the circuit to coincide at the neuron in the circuit (**magenta circles**). For a sound coming from straight ahead, the sound path to the two ears is equal in length and arrives at the two ears simultaneously. The inputs arising from the two ears will therefore be coincident in the middle of the circuit where the two circuit paths are also equal in length. If a sound comes from the left, however, then there is a shorter path to the left ear. Therefore, the inputs arising from the two ears will be coincident at a location in the circuit where there is a shorter circuit path from the right ear compared with that from the left ear, at which differences in circuit path length compensate for differences in sound path length. **C:** this combination of delay lines and coincidence detection leads to a spatial representation of sound source locations. **Top row:** sounds coming from different positions in space as a spectrum of colors from the left side of the head (**red**) to the right side of the head (**blue**). **Bottom row:** colored circles indicate which postsynaptic neuron responds maximally to sound coming from each of these different locations. From Carlson (2019).

will arrive simultaneously at postsynaptic neurons in the middle of the circuit, which will respond more strongly to sounds coming from this particular location compared with neurons on either side of the circuit (**Figure 4B**). If a sound comes from one side, however, the closer ear will get a head start over the farther ear. For a sound coming from the listener's left, the action potential arriving from the left ear will enter the left side of the circuit before the action potential arriving from the right ear enters the

right side of the circuit. As a result, these action potentials will arrive simultaneously at postsynaptic neurons toward the right side of the circuit, and these neurons will respond more strongly compared with other neurons in the circuit (**Figure 4B**). Sound sources that are even further to the listener's left will maximally excite neurons that are even closer to the right edge of the circuit, and sounds that are to the listener's right will maximally excite neurons that are toward the left side of the circuit.

Thus, the Jeffress model (1948) provided a hypothetical mechanism by which a neural circuit could convert small differences in the arrival times of sounds at the two ears into a map of sound source location (**Figure 4C**).

Forty years after Jeffress published his model, Carr and Konishi (1990) discovered that the auditory system of barn owls processes ITDs using this mechanism. Additional comparative studies in alligators, chickens, and emus revealed that they use the same mechanism, suggesting that all reptiles and birds detect ITDs this way (Carr et al., 2009). However, later work in mammals revealed that they detect ITDs using different mechanisms. The exact mechanisms by which mammalian auditory systems detect ITDs remain unclear because there is evidence supporting a variety of different mechanisms (Carlson, 2019). However, it is clear that mammals solve this problem in a fundamentally different way from birds and reptiles.

The neural circuits responsible for processing submillisecond timing differences in weakly electric fishes have been studied in pulse-type mormyrids, wave-type gymnotiforms, and the wave-type *Gymnarchus*. These different fishes solve this problem in fundamentally different ways that also differ from the ITD processing circuits of reptiles/birds and mammals (Carlson, 2019). Like reptiles and birds, mormyrids rely on axonal delay lines to shift the timing of excitatory input to their postsynaptic neurons (Friedman and Hopkins, 1998). However, mormyrids also rely on precisely timed inhibition to postsynaptic neurons. Thus, the mormyrid circuit for processing submillisecond timing differences implements “delay-line *anti*-coincidence detection” (Lyons-Warren et al., 2013). In other words, the neurons in this circuit respond best when delayed excitation and inhibition is *not* coincident. Another key difference is that the axonal delay lines in mormyrids follow a convoluted and tortuous path and do not establish a spatial map of timing differences, unlike the spatial map of ITDs found in the brains of reptiles and birds.

Wave-type electric fish solve the problem of detecting submillisecond timing differences in yet another way. Both gymnotiforms and *Gymnarchus* use delay-line coincidence detection, similar to reptiles and birds (Carr, 2004). However, they use dendritic delays rather than axonal delays. A synaptic input to the dendrite of

a neuron will require the resulting electrical activity to travel down the dendrite before reaching the soma, thus causing a delay compared with a synaptic input directly onto the soma. If the stimulus driving a dendritic input occurs before the stimulus driving a somatic input, then that dendritic delay will compensate for this difference in stimulus timing, and the two inputs will reach the soma at the same time, maximally exciting the neuron. Despite this similar mechanism in the two groups of fishes, there are key differences in the circuitry for implementing this delay-line coincidence detection. Most notably, the relevant circuit is found in completely different parts of the brain in *Gymnarchus* and gymnotiforms.

The Evolution of Temporal Processing

Mammals and birds/reptiles evolved tympanic ears along with the neural circuitry for processing ITDs independently (Christensen-Dalsgaard and Carr, 2008). Similarly, gymnotiforms evolved their electrosensory systems independently from mormyrids and *Gymnarchus* (Lavoué et al., 2012). Thus, it is remarkable that all five of these circuits share numerous similarities at the cellular level, including large somas, large-diameter axons with thick insulation (called myelination), minimally branching dendrites (or no dendrites at all), large synapses, and fast-acting synapses (Carr et al., 2001). These features increase the speed and reliability of action potential propagation and synaptic transmission and thus reduce timing errors. These similarities thus reflect the power of natural selection to predictably shape the evolution of neural circuits.

Nevertheless, these similar building blocks are used to construct different circuits. Why do five different circuits that all serve a similar function do so using different mechanisms? Chance may have dictated which one evolved in a given lineage. However, these differences may also reflect adaptation and evolutionary history (Carlson, 2019). The earliest reptiles appear to have had larger heads and sensitivity to lower frequency sounds compared with the earliest mammals, and ITDs work best for sound localization with low-frequency sounds and large distances between the ears. Thus, the earliest reptiles may have already been using ITDs for sound localization, whereas mammals that evolved enlarged heads and low-frequency hearing may have had to repurpose existing circuitry to process ITDs (Grothe and Pecka, 2014). Moreover, although mammals and birds/reptiles need to make a single timing comparison

between the two ears, weakly electric fishes have dozens of electroreceptors, requiring far more timing comparisons. Furthermore, although pulse-type mormyrids need to detect a range of timing differences to identify a variety of EOD waveforms, wave-type electric fishes simply need to detect stimulus advances or delays to identify capacitive objects or determine the frequency difference between their EOD and that of a neighboring fish. These functional differences may have necessitated different computational strategies for efficiently processing this information (Carlson, 2019).

Regardless of the ultimate reasons these circuits evolved to solve this problem in different ways, it is clear that findings in one species cannot simply be extrapolated to other species. Comparative studies across the electro-sensory and auditory systems of multiple species have revealed numerous similarities and differences. In the study of any behavior and its neural basis, comparative studies are necessary to identify which features are shared across species, which features differ between species, and why these differences exist.

Conclusion

Research on electric fishes has led to fundamental insights into how nervous systems distinguish self from other, generate expectations about sensory input, and detect submillisecond timing differences, as well as other important discoveries not described here, such as how nervous systems process stimulus envelopes, integrate amplitude and timing information, and modify behavioral output. Indeed, the jamming avoidance response remains, to date, the only vertebrate behavior for which we have a complete understanding of its neural basis, from sensory input to sensory processing to motor control to behavior (Heiligenberg, 1991). Electric fish research has proven synergistic with research into auditory and other sensory systems. In some cases, the findings in electric fishes have stimulated research on other sensory systems. In other cases, these findings have helped contextualize our understanding of other sensory systems, improving our knowledge of how and why brains have evolved. Electric fishes are a testament to the neuroethological approach to behavior: choosing a study organism not because it is convenient to house in a laboratory or because of genetic tools but because unique aspects of its behavior make it amenable to addressing specific questions of broad relevance to understanding all nervous systems.

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