Chapter 8
Using Control Theory to Characterize Active Sensing in Weakly Electric Fishes

Sarah A. Stamper, Manu S. Madhav, Noah J. Cowan, and Eric S. Fortune

Abstract Animals routinely use their own motor outputs to modulate the sensory information they perceive, a process termed "active sensing." This chapter highlights the use of control theoretic approaches to reveal the functional relationships between active sensing, task-related behaviors, sensing, and motor control. Specifically, recently developed experimental systems use artificially controlled feedback loops to perturb natural reafferent feedback in freely behaving animals. Such perturbations allow quantitative and systematic descriptions of control strategies for active sensing.

Keywords Closed loop · *Eigenmannia* · Electroreception · Feedback control · Gymnotiformes · Image stabilization · Jamming avoidance response · Open loop · Ribbon fin · Station keeping

8.1   Introduction to Active Sensing

Animals use behavior to control the acquisition of sensory information through a variety of processes collectively referred to as "active sensing." The simplest definition of active sensing is the use of motor outputs for the purpose of acquiring or

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modulating sensory information. Active sensing is found across animal taxa and sensory modalities. A handful of species are active sensing specialists; these species have adaptations for the generation of sensing signals. The best known of these species have evolved specialized organ systems for electroreception, echolocation, whisking, and hydrodynamic imaging (Nelson and MacIver 2006). Each of these species has complementary motor and sensory adaptations that work together to gather information from their environment. For example, weakly electric fishes have specialized neuromotor systems known as electric organs that generate an electric field (Heiligenberg 1991a) that can extend to over a meter around the fish (Tan et al. 2005; see also Gallant, Chap. 4). The corresponding sensory adaptations in these fishes are modified electroreceptive cells that detect the electric fields produced by these organs (Meyer and Zakon 1982). Together, the electric organ and specialized electroreceptors can detect nearby objects and conspecifics and are used in behaviors that range from prey capture to social communication (Heiligenberg and Bastian 1984; Caputi 2017).

The most common form of active sensing, however, does not involve specialized organ systems but is mediated through movement. An animal's movements often dramatically alter and/or regulate the information that its sensory receptors receive from the environment (Hofmann et al. 2014). For example, many animals move their pinnae in relation to attention; such movements have been described in a variety of species including echolocating bats (Ghose and Moss 2006) but also in animals such as foxes (Koop and Velimirov 1982) and cats (Populin and Yin 1998). Indeed, movement often determines what information is available to a sensorium.

Active sensing can also be profoundly affected by social context. When animals are near each other, they can perceive, and sometimes even exploit, the sensing signals used by nearby animals. This occurs, for example, when animals move in a herd or fish swim in a school. The competing signals from conspecifics often interact with the animal's own sensing signals (Griffin et al. 1963; Heiligenberg 1991a). Active-sensing signals are also public and therefore subject to "eavesdropping" where other animals can intercept, and potentially exploit, information carried in these signals. Examples of eavesdropping are found in both invertebrate (Stowe et al. 1995; Lichtenberg et al. 2011) and vertebrate (Fenton and Ratcliffe 2004; Götz et al. 2006) animals.

Social context can introduce a new category of sensorimotor challenges for animals vis-à-vis their use of active sensing (Partan and Marler, 1999). Specifically, there is a categorical difference in the sensory environment of animals when they are alone compared with when they are in groups (Tan et al. 2005; Stamper et al. 2010). Adding to the complexity is the fact that animals frequently use signals that serve dual purposes: sensing and social signaling (Metzner 1999; Dawson 1991). Animals routinely use their own movement to modulate both the effects of nearby interference produced by conspecifics and the social signals between individuals.

Weakly electric fishes rely on each of these forms of active sensing. These animals generate a weak electric field produced and detected by specialized organs that is used in the control of many locomotor and social behaviors (Heiligenberg 1991a). The fish also use movement for active sensing, both in the context of locomotor control and in social behaviors. Both the electric field and movement are also used in social behaviors in these fishes.

One of the advantages of weakly electric fish is that the spatial distribution of the active sensing signal, the electric field, is directly related the position of the fish (Madhav et al. 2018). As a result, the sensory consequences of movement can be computed by monitoring the position of fish relative to objects and conspecifics over time (Nelson and MacIver 1999).

8.2 Properties of Active Sensing

8.2.1 *Active Sensing via Movement*

The most common form of active sensing is movement, which is often tuned to the sensory demands of the task. For example, if a task is to determine the texture of an object, people tend to move their hand back and forth in a lateral rubbing movement (Lederman and Klatzky 1987; Hollins and Risner 2000). This movement activates mechanoreceptors in the hand (e.g., Merkel disks) that respond to indentation of the skin and have restricted receptive fields that allow for the very fine spatial resolution required for tactile discrimination. However, if instead the task is to determine the weight of an object, people tend to make "hefting" movements where they move the hand holding the object up and down (Gibson 1962). This type of movement primarily activates muscle stretch receptors that can detect the load on a given limb but do little in terms of discriminating textures.

Indeed, there are many ways in which animals move specifically for the purpose of gathering sensory information (Fig. 8.1). Animals can move to
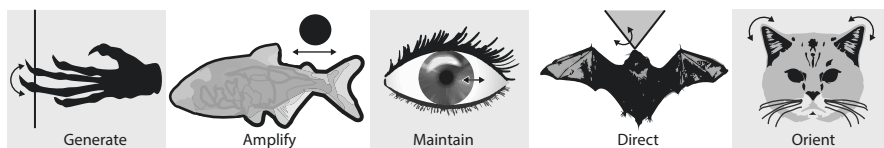

Generate   Amplify   Maintain   Direct   Orient

Fig. 8.1 Examples of categories of active-sensing movements. *Left to right:* aye-ayes generate both tactile and auditory feedback by tapping their fingers; blind cave fish use hydrodynamic imaging to amplify feedback; involuntary fixational eye movements reduce perceptual fading and possibly statistically whiten afferent signals (Mostofi et al. 2016); bats move their heads to direct echolocation calls to prey items and other targets while flying; and cats orient their pinnae in relation to sound sources to improve auditory perception

(1) Generate a sensory signal. Consider the "aye-aye" lemur *Daubentonia mada-gasceriensis*, which is nocturnal and forages for insects that live in the subsurface of tree cavities. To detect an insect, the aye-aye makes a rapid tapping motion (termed "percussive foraging" or "tap scanning") on the surface of the wood and listens for the returning echoes (Erickson 1994; Erickson et al. 1998). This behavior is not specific to aye-ayes; it has also been observed in woodpeckers and some monkeys (Phillips et al. 2004).

(2) Amplify a sensory signal. The blind cave fish *Astyanax jordani* uses its mechanosensory lateral line for hydrodynamic imaging (Windsor et al. 2010). To investigate novel objects, these fish rapidly accelerate and glide past the object (Von Campenhausen et al. 1981; Hassan 1989). It appears that this rapid acceleration produces a flow field around the fish's body that is modified by the presence of stationary objects (Hassan 1985; Windsor et al. 2008). The fish controls its swimming speed and pattern (acceleration glide) in order to optimize the activation of their mechanoreceptors (neuromasts; Teyke 1988).

(3) Maintain a sensory percept. Sensory receptors commonly have high-pass filtering properties and therefore reject stationary or very low frequency signals. This filtering is often known as "adaptation," which can have profound effects on sensing. If an image is stabilized perfectly on the retina, then there is no relative movement and the photoreceptors would adapt over a period of a few seconds. The perceptual consequence is that the visual pattern would disappear, which is known as "perceptual fading" (Ditchburn and Ginsborg 1952). One-way animals overcome adaptation, which leads to perceptual fading, is by maintaining high-frequency movements, such as in the form of temporally punctate saccades (Ahissar and Arieli 2012) or continuous, broadband motions (Stamper et al. 2012).

(4) Direct a sensory signal. In echolocating bats, the sonar beam is highly directional and narrow (a 60–90° cone from the midline; Surlykke et al. 2009a), which is beneficial for detecting targets within the range directly in front of the bat but less so for detecting objects located off-axis. To solve this problem, bats use movement to direct the beam across a wider swath of the environment. Specifically, they move their head back and forth in a scanning motion to increase the sensory volume for the detection of prey and other objects in their environment (Ghose and Moss 2006; Surlykke et al. 2009b). The sonar beams of dolphins are also highly directional and narrow (Au and Moore 1986).

(5) Orient their receivers or receptor arrays. Bats (Pye and Roberts 1970; Ghose and Moss 2006), foxes (Koop and Velimirov 1982), and cats (Populin and Yin 1998) each use ear movements to help localize the direction of a sound source. For example, surgically immobilizing the bat's ears before an obstacle-avoidance task leads to decreased performance, especially for targets that require elevation processing (Mogdans et al. 1988). In short, movement is used to modulate the spatial relationships between the signal source and the sensorium to improve sensory perception.

8.2.2   Relationships Between Task-Directed and Sensing Movements

A common feature of active sensing via movement is that the movements for sensing are distinct from the movements the animal uses to complete a behavioral task. In some behaviors, the movements for sensory acquisition and task completion are performed during separate temporal epochs. For example, if the task is to report features of a stationary image (e.g., time of day, number people in the image), the eye movements for active sensing are nonoverlapping with the motor task of verbally reporting the answer (Fig. 8.2; Yarbus 1967).

Such behaviors are amenable to information-theoretic approaches based on information maximization (Yang et al. 2016). However, when the active sensing and task-dependent movements occur contemporaneously, such theoretical approaches are more challenging to apply. Consider, for example, the change in a person's reaching pattern as they flip a light switch. In the light, the person would first use eye movements to find the light switch and then plan arm movements to execute the task of flipping the switch (Yang et al. 2016). However, in the dark, the person would scan a hand along the wall while trying to move toward the switch and flip it. In the latter case, sensing movements are not temporally independent from task-directed movements.

Another feature of active sensing is that such movements depend on the availability of information across modalities. In the above example, individuals compensate for the loss of *visual* information by using manual scanning to generate
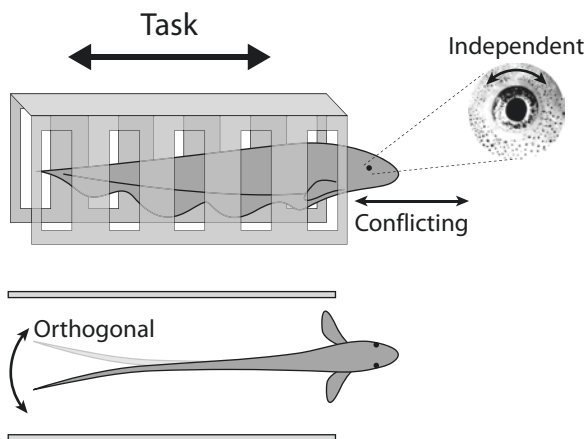

Fig. 8.2 In refuge tracking in weakly electric fish, fish swim forward and backward to remain within the refuge: the Task. Active movements for sensing can be independent of such task-related swimming movements, such as moving the eyes. Active-sensing movements can also be orthogonal to the task-related movements, such as swaying the tail back and forth within the refuge, or be conflicting, in the same dimensions as the task-related movements, as is the case for va-et-vient active-sensing movements

somatosensory feedback. In both the light and dark, the task goal, flipping the switch, is identical. But in the dark, the person adds active-sensing movements that are not mechanically related to performing the task goal but are nevertheless necessary to obtain sufficient sensory information to achieve the task.

Animals simultaneously engage in both categories of movements: those related to the task mechanics and those related to active sensing. These two categories of movement may be related in the following ways:

(1) *Independent.* The sensory apparatus is on a different part of the body from that performing the mechanical task, such as ocular movements in support of manual tasks.

(2) *Orthogonal.* The sensory apparatus is mechanically coupled to the task effector, but the movements are largely orthogonal, such as tapping perpendicular to a wall while reaching along the wall to flip a light switch or tail bending of electric fish during refuge-tracking behavior (Stamper et al. 2012).

(3) *Overlapping/Conflicting.* The sensory apparatus is mechanically coupled to the task effector, and the movements for active sensing overlap with the physical degrees of freedom required to achieve the task. In this way, an active-sensing movement may be in the opposite direction as that required to achieve the task goal and therefore in direct conflict. The back-and-forth active-sensing movements that electric fish use during refuge-tracking behavior is an example of this sort of conflict (Stamper et al. 2012).

During the execution of any mechanical task, animals can exhibit different active-sensing behaviors contemporaneously, each having a potentially different relationship (independent, orthogonal, overlapping) with the task goal. For example, tail-bending and fore-aft movements are simultaneously used in electric fish during refuge tracking (Stamper et al. 2012). Just as movements for active sensing depend on task-oriented movements, progress toward achieving task goals can modulate active-sensing movements.

Given the dynamic relations between active-sensing and task-oriented movements that evolve during behavior, how can a biologist identify the neural mechanisms for the control of these two categories of movement? This is particularly challenging because both categories routinely stimulate the same receptor systems.

8.2.3   Correlations in Sensing and Motor Systems

Movement, irrespective of whether it is generated with respect to achieving a task or for active sensing, results in strong correlations in activity between the motor and sensory systems in the brain. Indeed, it is increasingly appreciated that animals rely on the correlations between an animal's behavior and sensing to enhance task-dependent sensory perception. The relationship between motor activity and sensory

information arises through "reafferent" feedback (sensing produces movement, and movement, in turn, creates sensory signals; Pearson 2008; Hofmann et al. 2014). Reafferent information is often used in the control of movement (Gritsenko et al. 2009; Knill et al. 2011). Sensory–motor correlations also can arise internally, through descending and other pathways within the brain, for example, sensory predictions and corollary discharge (Alviña and Sawtell 2014; see Perks and Sawtell, Chap. 11).

These sensory–motor correlations, however, present a challenge for scientists because they can obscure the role of brain activity in sensory perception versus motor control. In other words, because strong temporal correlations between motor output and sensory inputs occur at all levels of biological organization, from the mechanics of the behavior to the activity of neurons in the brain, these sorts of correlations cannot be naively used to disentangle the respective roles of sensory and motor control systems. For example, neurons in a song control nucleus in the brains of songbirds respond to playback of the bird's own song, an exclusively sensory signal, with a pattern of activity that is almost identical to the activity seen when the bird is singing (Dave and Margoliash 2000). This result might be surprising: the auditory activity during playback is mediated by spiking activity that originates from the cochlea and reaches these neurons via ascending auditory pathways, whereas motor activity affects downstream targets to control the contractions of muscles in the syrinx to produce sound. It seems surprising that neurophysiological codes used to represent ascending sensory information would be identical to the descending motor output used to control the production of forces in the syrinx given the distinct physics between sound production and sound transduction. However, the fact that output from the syrinx always stimulates the cochlea suggests that there will be strong correlations in sensory (auditory) and motor (singing) activity in the brains of these birds.

The relationships between the motor and sensory systems are dynamic because they serve multiple behaviors with differing task-dependent goals. Because the spatiotemporal structure of behaviors differs, so must the spatiotemporal structure of correlations between the motor and sensory systems. In other words, the computational structure of neural substrates for control are dynamically tuned in relation to the behavioral tasks (Chacron et al. 2003). These dynamic changes in correlations pose an additional challenge for neuroscientists because neurons within brain circuits retune in relation to behavioral context.

The tight coupling between the sensory and motor systems pushes neuroscientists toward conducting experiments in awake, behaving animals rather than in anesthetized animals. One consequence of using anesthesia for experiments is the immobilization of the animal, which opens feedback loops. This experimental opening of feedback loops eliminates correlations between sensory and motor activity in the brain, which can both alter patterns of neural activity and lead to fundamental misinterpretations of the roles of sensory responses in the control of behavior (Szwed et al. 2003; Mosconi et al. 2010).

8.3 Using Control Theory to Study Closed-Loop Sensorimotor Systems

The challenge of understanding active-sensing mechanisms is that the sensory and motor circuits operate together to produce behavior. Motor circuits generate movement (i.e., the behavioral output) that results in sensory feedback that is processed by the nervous system to modulate ongoing motor output. These "closed-loop systems" offer dramatic improvements in the regulation of behavior, including increasing the speed of responses and stabilizing motor performance (Cowan et al. 2014).

8.3.1 Control-Theoretic Approaches

Understanding the dynamics of these types of systems are the focus of control systems theory. The application of control-theoretic approaches allows scientists to quantitatively and independently probe control subsystems to understand their roles in the performance of the intact closed-loop system (Roth et al. 2014). Control-theoretic approaches to the study of closed-loop dynamical systems take advantage of the linkages between the inputs and outputs of a system (Cowan et al. 2014). These analyses often involve the application of small perturbations in feedback information. This approach has proven to be extremely successful in predicting the performance of designed systems, where the feedback topology and the system dynamics are specified by humans.

This approach differs from those commonly used in behavioral neuroscience. Although neuroscientists are keenly aware of feedback loops at multiple levels of organization, from within neurons to the brain circuits to the entire organism and beyond, many experiments focus on a unidirectional flow of information from sensory systems through to motor systems. Experiments that do explicitly engage the roles of feedback most commonly use techniques that completely eliminate the flow of information through feedback pathways. Examples include the use of lesions or injections of anesthetics into brain areas or the application of masking signals such as noise. Of course, many of the approaches and strategies that are used by neuroscientists to analyze how animals control behavior are limited by technical and practical issues.

Although the application of control-theoretic approaches to the analysis of feedback control in animals may be useful in decoding neural mechanisms, these approaches involve additional challenges. First, unlike in artificial systems, the feedback topology and system dynamics of animal behavioral systems are rarely known. Biological feedback loops that can impact the control of behavior occur at levels of organization from molecules to ecosystems; it is fair to say that the full topology for feedback control has not been revealed for any organism. Second, experimental perturbations of feedback may be difficult or impossible to achieve during behavior or within neural circuits due to lack of experimental access to feedback pathways. Third, perturbations of feedback can lead to categorical shifts

in behavior. Experimental perturbations can drive the animal to switch tasks or adopt different strategies for achieving the task goal. This is particularly challenging in relation to the study of active sensing when the animal is typically behaving with two simultaneous goals (achieving a task goal and controlling active sensing). Perturbations are likely to interact with both goals in ways that drive nonlinear changes in behavior.

8.3.2 Closing the Loop on Active-Sensing Systems

Systems that rely on closed-loop modulation of reafferent feedback are being developed to help understand control strategies across a wide range of behaviors in animals from flies (Roth et al. 2012; Reiser and Dickinson 2008) to fish (Ahrens et al. 2012; Madhav et al. 2013) to rodents (Chen et al. 2013; Ravassard et al. 2013; Aronov and Tank 2014; Sofroniew et al. 2014; Aghajan et al. 2015). The benefit of these systems is the tight control over the sensory experience of the animal, often during neural recordings (Maimon et al. 2010; Ahrens et al. 2012; Sofroniew et al. 2014).

These newly developed closed-loop systems typically constrain the animal (e.g., glued to a stick, mounted in agar, or head fixed to a microscope) to reduce the routes for sensory feedback and behavioral state of the animal. Once within the system, the motor output of the animal is monitored in real time. Information from the behavior of the animal is translated into sensory signals delivered to the animal as a form of feedback (Kim et al. 2018). The behaving animal then responds to this modified feedback that it perceives as being generated through natural sources of reafference.

Creative modulation of these feedback systems can give the experimenter almost complete control over an animal's behavior. Perhaps the most compelling application of this approach is the ability to induce the animal to repeatedly produce nearly identical behaviors (Madhav et al. 2013). This is important for the analysis of brain mechanisms because neurophysiological activity is inherently noisy. Neuroscientists rely on repeated measures and averaging to identify and characterize neural encoding strategies, which can be difficult to achieve in awake freely behaving animals. Using real-time manipulation of the animal's feedback, it is possible to either elicit *repeated motor signals* for analysis of activity in areas of the brain that contribute to motor control and/or deliver *repeated sensory stimuli* to awake, behaving animals to analyze activity in areas of the brain used in sensory perception.

8.3.3 Reconciling Terminology of Control Theory and Biology

The mathematical analysis of transformations between input and output fall naturally within the purview of control theory. Control theory was originally developed to control a known machine (the "plant," as in a manufacturing plant), and it allows
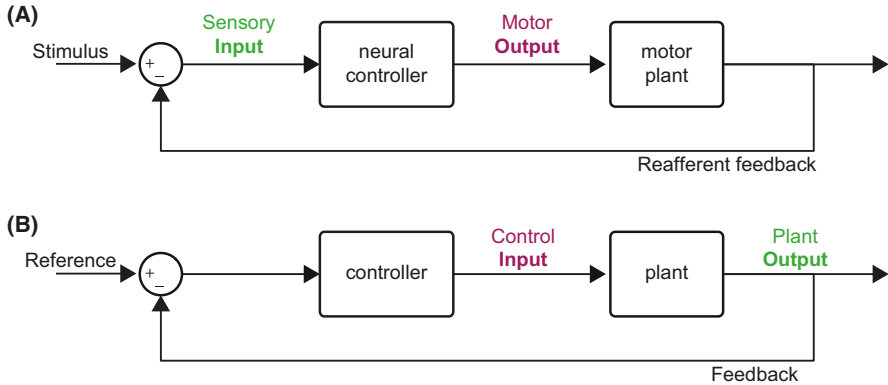
(A)

(B)

Fig. 8.3 Simplified block diagram representations of a biological system (**A**) and an engineering feedback control system (**B**) with the same topology. Biology and engineering differ in their nomenclature of inputs and outputs. In biology, input typically refers to the sensory signals and output refers to the motor commands from the neural controller. In engineering, input refers to the signal generated by the controller that drives the plant and output refers to the signals generated by plant dynamics

the user to design a "controller" that drives states (relevant parameters) of the plant to desired values. The same techniques of design can be inverted to analyze neural control. In this case, the plant is the animal, more precisely, its motor system and its physical interaction with environment.

Importantly, neuroscientists and engineers use semantically opposite terminology to refer to the same network (Fig. 8.3). In engineering, *inputs* refer to the signals sent by the control system to the plant, whereas *outputs* refer to signals measured by sensors. In neuroscience, *inputs* refer to signals measured by the nervous system, whereas *outputs* refer to motor activity.

8.4 Electric Fishes as a Model System for the Study of Feedback Control

The challenges of studying the closed-loop dynamics that dominate active sensing can be, in part, mitigated through the choice of animal model systems and behavioral tasks. Specifically, behavioral systems that facilitate the manipulation of feedback signals are particularly useful for the application of control-theoretic approaches.

Weakly electric fishes are unusually well-suited animals for these sorts of approaches due to at least three features. The first and most important is the self-generated electric field that facilitates the manipulation of sensory feedback. Second is a ribbon fin for locomotion that permits these fish to swim omnidirectionally (Blake 1983; Snyder et al. 2007). This high degree of maneuverability affords nearly

symmetrical forward and backward swimming performance that allows (Lannoo and Lannoo 1993; MacIver et al. 2001) the animal to accurately track a longitudinally moving refuge. Finally, these fish use a combination of movement and sensory feedback mediated by the electric field in multiple behaviors. Such behaviors include refuge tracking, social interactions, and prey capture, each of which features categorically different task parameters and goals.

8.4.1 Electric Field

The primary feature that makes weakly electric fish well suited for the exploration of the relationships between the motor and sensory systems via manipulation of feedback signals is the electric field. The electric field is generated by an electric organ in the tail and along the sides of the animal. The electroreceptors that detect the electric field are embedded in the skin across the body. Electrosensory systems share properties with both the visual and auditory systems. Like the visual system, the signal propagates at the speed of light and there a topographic representation of the external spatial world across the receptor array. Objects that are closer to the receptor array cast sharper gradients along their edges than objects that are further away (Babineau et al. 2006).

Like auditory systems, electrosensory information is encoded in relation to the frequency and amplitude of signals. Indeed, for social signals in which the electric fields of two or more individuals interact, the interaction can be described with regard to the frequency of modulations of both amplitude and phase and/or timing (see Metzen and Chacron, Chap. 9). Similarly, reafferent feedback caused by changes in the animal's electric organ discharge (EOD) and/or by the movement of the animal also affect the amplitude and phase perceived by the fish.

These spatiotemporal properties of electrosensory signals are often linked to task-dependent categories of electrosensory feedback. For example, the interaction between a swimming weakly electric fish and small prey items leads to relatively slow (approx. <10 Hz), localized activation of electroreceptors (Nelson and MacIver 1999), whereas social signals can lead to faster (approx. >10 Hz), global (entire receptor sheet) activation of the electroreceptors (Chacron et al. 2003; Cowan and Fortune 2007). The spatiotemporal properties of feedback from different tasks can overlap, leading to degradation of performance.

Electrosensory feedback is pervasive across tasks in weakly electric fishes. Because the spatiotemporal parameters of the electric field are closely tied to the movement of the fish, almost all behaviors performed by these fish result in modulations of electrosensory feedback. This includes social communication in which the relative motion of two fish can be perceived by both individuals.

Critically, electrosensory feedback from both movement and social communication, are amenable to the types of perturbations used in control-theoretic approaches to the study of the motor and sensory systems. This is due, in part, to analog and digital technologies for the generation and control of electrical signals. Specifically,

electrosensory feedback can be detected and characterized through direct measurement of the electric field and via video monitoring of the position of the fish. This feedback can, in turn, be modulated in real time via artificial electric signals generated in the tank or via manipulations of the movements of nearby objects.

8.4.2   Ribbon Fin

Weakly electric gymnotiform fishes and one group of mormyroid fishes (*Gymnarchus*) use longitudinal undulating fins to generate primary locomotor forces. These fins use traveling deformations along the length of the fin to produce force in either a rostral or caudal direction (Blake 1983). In many species of gymnotiform fishes, fish produce counterpropagating waves that can increase manueverability in the fore-aft direction (Sefati et al. 2013). Indeed, some species, such as *Eigenmannia*, are like aquatic hummingbirds, using the counterpropagating waves to hover in position and make small, precise fore-aft movements.

   Ribbon fin locomotion offers a distinct advantage in the study of sensory feedback because locomotion can occur without bending or movement of the body axis. In this way, propulsive movements, which can be restricted to the ribbon fin, are decoupled from task-oriented and active sensing-oriented movements. In *Eigenmannia*, this specialization enables the fish to use tail-bending movements for active sensing (Stamper et al. 2012) because they do not need to rely on them for locomotion as in so many other species (Colgate and Lynch 2004). In weakly electric fishes that use ribbon fin locomotion, measurements of body position and pose are strongly correlated to task-oriented and active sensing-oriented goals rather than to locomotor mechanism. Indeed, ribbon-finned propulsion may have evolved, in part, as a mechanism to stabilize electrosensory information by decoupling locomotor-based contamination.

8.5   Experimental Control of Feedback in Weakly Electric Fishes

As described in Sect. 8.3.2, the manipulation of feedback signals is an important component of control-theoretic approaches to the study of animal systems. Unlike stimulus/response paradigms where a predetermined stimulus is played to the animal and the response is measured, control-theoretic approaches use stimuli that are generated (at least in part) by measuring behavior in real time and manipulating feedback to the animal. The result is that the stimulus reflects the consequences of the ongoing behavior of the animal (Kim et al. 2018), as is the case in naturally occurring behaviors. There is a rich history of such manipulation in electric fish, particularly with the study of the jamming avoidance response, and more recently, this approach has been used in the analysis of refuge tracking.

8.5.1   *Closing the Loop on Social Behavior*

When two or more weakly electric fish are in close proximity, within about 1 meter of each other, the electric fields sum, often producing emergent modulations of the amplitudes and phases/timing of electrosensory signals (Tan et al. 2005). For wave-type fish, the amplitude and phase modulations occur at the difference frequency between a fish's EOD and that of a conspecific (Heiligenberg 1991a). These modulations can be detected by electroreceptors in the skin of these fishes and such modulations used in social communication (see Metzen and Chacron, Chap. 9). Unlike the amplitude and phase modulations that are produced by small prey items, social signals are broad and diffuse, often affecting the entire electrosensory array of the animal (Chacron et al. 2003).

The diffuse, spatially distributed electrosensory interference caused by conspecific signals is a key feature that facilitates the study of the neural mechanisms of social signaling. Because social signals are spatially diffuse, artificial social signals can be delivered using simple pairs of electrodes around the fish, with little sensitivity to the specific geometry. Indeed, many studies rely on stimulus geometries that are experimentally convenient but not biologically plausible (e.g., across the body of the fish).

The social behavior that has been studied most intensively is the jamming avoidance response (JAR) in *Eigenmannia*. The JAR remains one of the best understood behaviors, from the level of the entire organism to the contributions of single neurons within computational networks in the central nervous system. The analysis of the JAR was facilitated not only by the geometry of social signals but also critically by the ability to manipulate feedback signals. This was possible, in part, due to two "quirks" of the organization of the control system for the JAR. First, *Eigenmannia* do not have internal feedback signals (efference copy or corollary discharge) within the brain of the fish (see Perks and Sawtell, Chap. 11). As a result, the sensory feedback used in the control of the JAR is mediated solely through external sensory cues that are experimentally accessible. Second, the JAR behavior does not require movement of the animal; it can be elicited reliably in immobilized fish.

But perhaps the most important tool used in the decoding of the JAR is the modulation and even replacement of the natural electrosensory (reafferent) feedback loop. This can be achieved using a combination of pharmacological blockade of the electric organ and replacement of the autogenous electric field with an artificial mimic (fictive EOD). In this way, the natural electrosensory feedback loop is eliminated (see Fig. 8.4). This manipulation enables the replacement of natural feedback with experimentally defined signals. Critically, although the production of the electric field is blocked, the neural signal that controls the electric organ remains intact and can be monitored using electrodes placed adjacent to the animal. As a result, the responses of the fish to manipulations and modulations of electrosensory feedback can be directly measured and used in real time for the generation and modulation of the experimentally defined signals presented to the animal.

The classic experiments of Heiligenberg (1991a,b) relied on manipulation of feedback loops for the control of the JAR. Electrosocial signals were presented in two different external feedback topologies. In a closed-loop topology, artificial signals were tied to the output of the neural control system of the animal by triggering the production of the simulation of the fish's own electric signal based on the timing of spinal activity for the control of the electric organ. In an alternate, open-loop topology, the signals were generated independent of the activity of the neural control system (see Fig. 8.4).
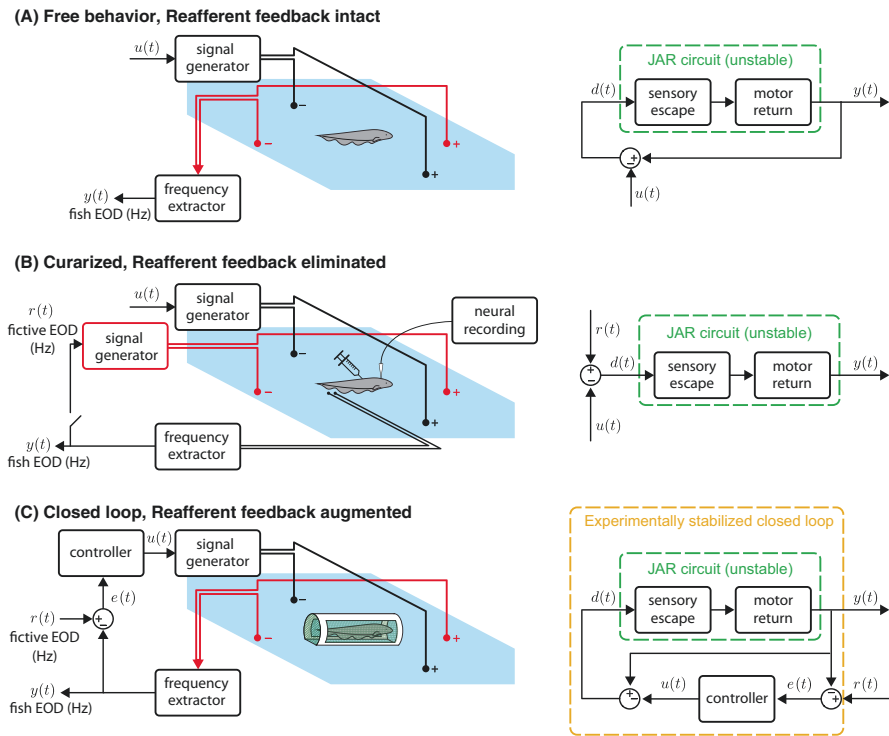

Fig. 8.4 Three different experimental topologies for investigating the jamming avoidance response (JAR) circuit. *Left:* experimental setup; *right:* control topology. **A:** an intact animal responds to the interaction between its own signal [$y(t)$] and artificially generated conspecific electrosocial signals [$u(t)$] that sum to produce $d(t)$. EOD, electric organ discharge. B: pharmacological blockade (syringe) of the electric organ eliminates natural feedback from the fish's own signal [$y(t)$]. Electrodes placed very close to the electric organ can detect the residual EOD $y(t)$ to control the generation of an artificial mimic [$r(t)$] of the fish's own EOD (fictive EOD). Alternatively, $r(t)$ can be independent of the fish's EOD, thereby creating an open-loop experimental condition. **C:** addition of an augmented feedback control system that controls the artificial signal [$r(t)$] in relation to the fish's intact EOD [$y(t)$] allows moment-to-moment manipulation of reafferent electrosensory feedback [$e(t)$]

Precise manipulations of feedback were the key to unlocking the computational organization of the JAR. For example, the spatial organization of feedback was modified to show how the relative phase of the autogenous and heterogeneous signals are computed from the spatial distribution of phase differences across the electroreceptor array (Heiligenberg 1991b). Similarly, the sensitivity to beat rate (at the difference frequency) and not the individual frequencies of the autogenous and heterogeneous electric fields was demonstrated by generating the same temporal pattern of beats using equally spaced pairs of frequencies in open-loop experiments.

There are very few vertebrate behaviors (the JAR among them) for which the complete computation and neural control system has been elucidated from sensory afferents, through central nervous system circuits, and to motor outputs. The classical description of the JAR was made without a formal quantitative model of the behavior. In contrast, the physiological description of the vestibulo-ocular reflex (VOR) relied on detailed engineering control systems modeling (Robinson 1976). Such modeling has been vital in the analysis of a wide range of other sensorimotor systems (Cowan et al. 2014; Roth et al. 2014) and served an essential role in interpreting neurophysiological activity underlying the VOR (Robinson 1977). Analogous modeling of the dynamics of the JAR (e.g., in the form of differential equations and feedback control theory) was not completed until recently (Madhav et al. 2013), decades after the pioneering work describing the underlying circuitry.

Unlike the VOR, which is a *stable* sensorimotor control system, the JAR is an "escape behavior" and is *unstable* in the sense that trajectories are dynamically driven away from the equilibrium condition that would occur if the heterogeneous signal were precisely matched in frequency to the fish's own EOD (i.e., identical frequencies, 0-Hz beat frequency; Madhav et al. 2013). Standard stimulus–response techniques rely on small perturbations from an equilibrium; these perturbations would inevitably drive an unstable system away from this unstable equilibrium. Thus, modeling the dynamics of the unstable JAR is challenging.

To overcome this, a novel experimental topology was developed that utilized a new layer of feedback (Madhav et al. 2013). The concept involves stabilizing the naturally unstable biological system by applying artificial, low-latency closed-loop feedback signals during an experiment. This allows the application of system identification techniques to the artificially stabilized system. The model thus computed is of the combined system, the animal along with the artificial feedback. However, because the feedback is a deterministic quantity that is computed via an algebraic relationship to the biological variables, the model for the underlying, unstable biological system can be "reverse engineered" post hoc.

In this particular work, the JAR was stabilized around the unstable equilibrium of being "exactly jammed" by using a closed-loop artificial feedback system (Fig. 8.4). Specifically, the system measures the frequency of the EOD of the fish and generates an artificial sine wave at that frequency, which is presented to the fish. To stabilize the EOD frequency of the fish, when its frequency drifts lower, for example, the frequency of the artificial signal can be moved slightly lower yet, eliciting a JAR that drives the fish's frequency back to the original frequency. Through this constant

measurement of the frequency of the EOD while eliciting the JAR behavior to drive the fish's EOD frequency up and down, the EOD frequency can be artificially stabilized. Once stabilized, the JAR dynamics can be elucidated using standard engineering system identification analysis (Cowan et al. 2014), resulting in a new, parsimonious representation of this classical system.

This parsimonious representation affords two advantages. First, the response of the system to any input stimulus can be simulated. Second, the structure of the model constrains the possible neural mechanisms. For example, the model for the JAR is composed of two abstract mathematical components. The "escape," which causes the fish's frequency to diverge from that of the interfering conspecific, and the "return," which is a spring-like component that causes the fish's frequency to converge back to a preferred frequency in absence of interference, a return that can be altered with long-duration jamming signals (Oestreich and Zakon 2005).

It was discovered that the escape function is different for each individual and is also asymmetrical in the direction of frequency shifts. The return, on the other hand, is symmetrical and highly stereotyped across individuals. This high-level model thus indicates developmental or social factors that might shape the plastic neural mechanics of an individual's escape function while keeping the circuitry responsible for the return essentially unchanged.

8.5.2   Closing the Loop on Refuge Tracking

Another example in which natural feedback loops can be experimentally modulated is in refuge-tracking behavior (Rose and Canfield 1993; Cowan and Fortune 2007). In this behavior, which occurs in several species of weakly electric fishes, individuals swim forward and backward to maintain their position within a refuge (Roth et al. 2011; Stamper et al. 2012). The neural goal of the refuge-tracking task is similar to the VOR: to stabilize a sensory image on receptor arrays. When either the refuge or fish moves, the sensory image of the refuge is translated proportionally along the receptor surface. The fish detects this "sensory slip" and swims to stabilize the position of the image on receptor arrays (Cowan and Fortune, 2007; Roth et al. 2011).

Contemporaneously, fish commonly produce transient "va-et-vient" back-and-forth movements (Toerring and Møller 1984) that are used for active sensing. These movements are often in direct conflict with the task-oriented goal of following the position of the refuge (Fig. 8.2). Indeed, these back-and-forth movements significantly increase the swimming effort used in tracking the movement of the refuge (Stamper et al. 2012).

These back-and-forth movements were shown to be a form of active sensing because they are modulated by the sensory information available to the fish (Stamper et al. 2012). The fish produce larger back-and-forth movements in the dark than in the light. Similarly, the magnitudes of these active-sensing movements increase as the conductivity of the water is increased (Stamper et al. 2012). Increasing conductivity decreases electrosensory salience by decreasing sensory volume (Snyder et al. 2007),

thereby affecting the contrast of nearby electrosensory images such as the refuge wall (Babineau et al. 2007). These results are interpreted to indicate that the active-swimming movements are specifically produced to alter the spatiotemporal patterns of feedback through the electrosensory system (Stamper et al. 2012).

Both the task-directed movement, swimming to maintain position with the refuge, and the movements for active sensing determine the relative velocity of the object and the fish and therefore determine the temporal patterns of spiking in electroreceptors. Because the reafferent stimulation for both task-oriented and active-sensing movements is mediated by the same sensorimotor systems in the same linear dimension (rostrocaudal axis of the fish), it is difficult to determine whether any specific movement is related to the task goal or active sensing.

To carefully examine the roles of reafferent feedback in refuge tracking, the feedback needs to be controlled deterministically and repeatably. This was done (Biswas et al. 2018) by detecting the position of the fish and altering the trajectory of the refuge in real time to produce an experimentally controlled error signal. The feedback was thus altered to produce an "augmented reafferent feedback" system (Fig. 8.5). Normally, if a fish were to swim 1 cm forward within a normal refuge, the fish would experience a 1-cm head-to-tail relative slip of the sensory image from the refuge. Using this closed-loop experimental setup, as the fish moves, the sensory slip can be reduced (by moving the refuge in the same direction) or amplified (by moving the refuge in the opposite direction).

Experimental changes in reafferent gain likely have different impacts on task-dependent swimming and active sensing. On the one hand, because the goal of refuge tracking is to maintain position within the refuge, changes in reafferent gain are expected to result in commensurate changes in swimming: the fish may cancel the experimental gain through increases or decreases in its own swimming. On the other hand, the impacts of experimental changes in reafferent gain on the production of back-and-forth active-swimming movements depends not on the tracking task but on the sensory goal. How might sensory feedback be used to manage these two simultaneous behavioral goals, tracking and active sensing?

To answer this sort of question, it is useful to "separate" the roles of movement toward achieving the task and in active sensing as much as is possible. For example, in an effort to examine the control of active sensing in refuge tracking, one can reduce the task-level behavior (remaining in the refuge) by not moving the refuge. That is, the fish could achieve the task by simply remaining in place. Any movements of the fish were therefore a result of either active sensing, tracking error, or other unrelated movements.

Fish produced active-sensing movements under these conditions that were, as expected, modulated by lighting conditions. When the fish were in the light and could use visual cues, their active movements were small. In the dark, however, fish rely more almost exclusively on electrosensory cues and produced large active movements. By changing the reafferent feedback gains while measuring active movements, it was shown that fish maintain the sensory slip between the fish and the refuge. Fish use a strategy that minimizes energy expenditure: the fish performed longer drifts with fewer reversals of direction (Biswas et al. 2018).
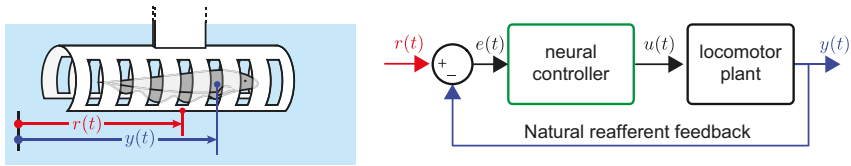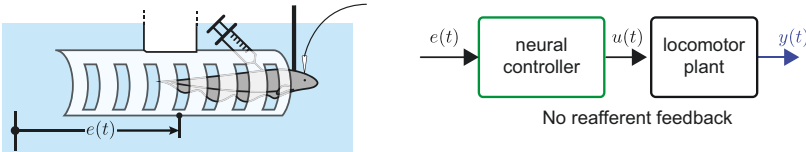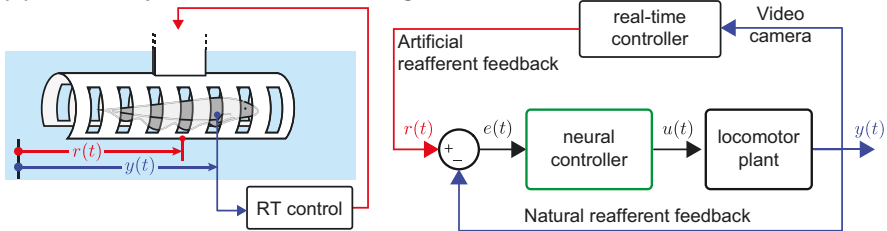
(A) Free behavior, Reafferent feedback intact

(B) Curarized, Reafferent feedback eliminated

(C) Closed loop, Reafferent feedback augmented

Fig. 8.5 Three different experimental topologies for investigating the refuge-tracking behavior. *Left:* experimental setup; *right:* control topology. A: an intact animal moves freely [$y(t)$] back and forth in a refuge [$r(t)$] at position $y(t)$. The fish receives natural reafferent feedback in the form of sensory slip: $e(t) = r(t) - y(t)$. **B:** reafferent feedback can be eliminated by immobilizing fish via pharmacological blockade of neuromuscular junctions. Neural recordings can be made while moving the refuge with previously recorded $e(t)$ or other trajectories. **C:** addition of a real-time controller for the refuge position [$r(t)$] based on feedback of the animal's position [$y(t)$] allows moment-to-moment manipulation of the $e(t)$ signal in the intact, freely swimming fish

These sorts of augmented reality systems can also be used as a form of behavioral clamp. For example, reafferent feedback arising from the fish's own swimming can be eliminated by moving the refuge to precisely match the fish's own movements. Under this "reafferent clamp" condition, the refuge can be used to impose any arbitrary stimulus by superimposing desired signals on top of the behavioral clamp. In this way, for example, previously recorded reafferent signals can be replayed to the freely swimming fish.

The ability to play back an arbitrary reafferent signal to a freely moving animal is generally applicable and could be a powerful tool in neurophysiological studies. Neuronal spiking activity is inherently noisy, and therefore, any signal stimulus–response pair will not fully represent the underlying relationships between them. To address this issue, neuroscientists typically present multiple repeats of a stimulus

while recording the activity of neurons, permitting the characterization of the firing statistics, including the structure of the noise and the response.

This approach has proven challenging in awake, behaving animals: the timing and production of behavior is both subject to its own variation and under the control of the animal. This has been addressed by observing long bouts of free behavior and "binning" the resulting behaviors into similar epochs, effectively relying on behavioral serendipity to probe the stimulus space.

A potential advantage of behavioral clamps in virtual or augmented reality systems, in contrast, is that they allow the presentation of test signals designed to address specific questions about neural coding in freely behaving animals. It is sensible (and standard) to replay exafferent signals that mimic the sensory experience of a stationary animal to an immobilized animal. In contrast, feedback from active-sensing movements only makes sense in the context of freely moving animals, and augmented reality systems provide a novel means by which to replay stimuli in a behavioral relevant context.

8.6 Summary

Sensing is not a static process but rather is dynamically tuned by the animal depending on the task it is performing and its social and sensory context. Active sensing can be used in at least five ways, including to generate, amplify, maintain, or direct sensory signals or orient receptor arrays. Animals can use a variety of strategies for active sensing that often include the generation of reafferent feedback via movement. These movements for active sensing are produced contemporaneously with movements for achieving behavioral tasks and can be independent of, orthogonal to, or in conflict with the goals of the task. The interplay between task-oriented and active-sensing behavior requires specialized strategies to disentangle the relationships between sensory and motor signals. Control theory, the study of the behavior of dynamical systems and feedback regulation, provides the tools and approaches for decoding the structure of these systems. Specifically, control theory highlights the critical role of reafferent feedback in behavioral control and enables the application of experimental modulation of feedback topology as an approach to understanding the organization of biological control systems.

Compliance with Ethics Requirements Sarah A. Stamper declares that she has no conflict of interest.

Manu S. Madhav declares that he has no conflict of interest.

Noah J. Cowan declares that he has no conflict of interest.

Eric S. Fortune declares that he has no conflict of interest.

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