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Active Sensing: Constancy Requires Change

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We constantly generate movements in order to enhance our ability to perceive the external environment. New research on electric fish has used augmented reality to demonstrate that animals dynamically regulate their movements to maintain variability in their sensory input.

During day-to-day life, our senses continually inform us about the external environment — a process that is very much influenced by our own movements. In some cases, movements act in a compensatory manner to stabilize the sensory input: for example, when fixating a given target by making compensatory eye movements while moving our head. In other cases, movements act to enhance sensory information: this is known as active sensing (Figure 1A): for example, when looking for keys and coins in our pocket, we make complex exploratory hand and finger movements to gather information about the characteristics of these objects, such as their shape, texture, weight and so on. Active sensing is found ubiquitously across sensory modalities and contexts [1,2]. Nevertheless, how such movements are controlled and adapted depending on context — for example when manipulating a dull *versus* a sharp object — is not known. A new study by Biswas *et al.* [3], reported in this issue of *Current Biology*, brings important insights into the control of active sensing movements. By studying weakly electric fish in an augmented reality setup, these authors were able to show how active sensing movements are dynamically regulated in relation to the sensory feedback that they generate.

Gymnotiform weakly electric fish such as *Eigenmannia virescens* (Figure 1B) rely on their active electric sense to explore their environment — they generate a three-dimensional electric field around their body
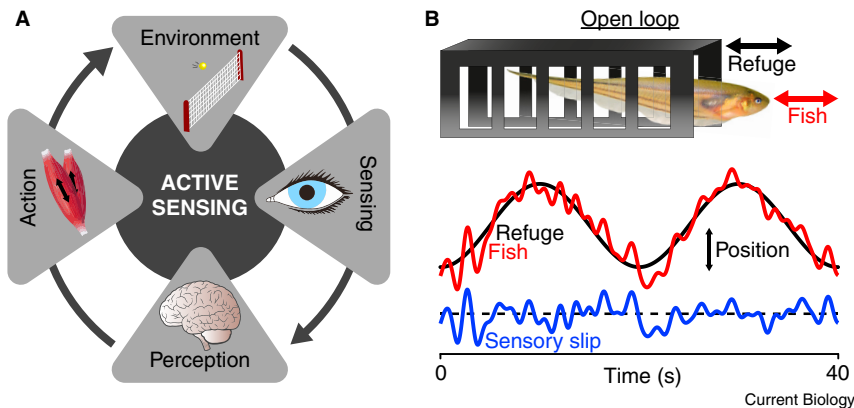
Figure 1. Active sensing movements in weakly electric fish.
(A) The action-perception cycle of active sensing: movement ('action') causes an interaction with the physical world ('environment'), which generates sensory feedback ('sensing') used to integrate ('perception') into the next purposeful movement step. For example, during smooth pursuit of a target such as a tennis ball, the visual system generates microsaccades on top of the smooth motion that prevent visual adaptation. (B) During refuge tracking, *Eigenmannia virescens* (top) track the position of the refuge (bottom, black) but generate high frequency movements on top of the smooth motion (bottom, red). The movements are hypothesized to be active sensing movements and create a difference in position between the fish and the refuge termed 'sensory slip' (bottom, blue).

and detect perturbations of this field through an array of peripheral electroreceptors on their skin. During the day, these fish typically hide in refuges such as plant thickets to avoid predators. Motion of these thickets, for example due to water currents, are tracked to maintain a constant relative position [4]. The research group led by Eric Fortune and Noah Cowan has studied how these fish track moving refuges in the laboratory [5] (Figure 1B).

They found, surprisingly, that fish perform pronounced longitudinal 'va-et-vient' movements on top of those used to track refuge movement (Figure 1B, lower panel) [6]. Why would the animal make such energetically costly movements that also destabilize sensory input (Figure 1B)? Previous studies by this research group [6] have shown that these longitudinal movements, which result in changes in the relative movement between the fish and refuge known as sensory slip, are tightly regulated. Indeed, movement amplitude decreases when visual information is available and increases with decreasing water conductivity (which effectively decreases the saliency of electrosensory stimulation). These results and others strongly suggest that these movements are used for active sensing.

The challenge of studying the role and regulation of active sensing is that the animal's own behavior is the source of sensory stimulation, thereby requiring experimental approaches that both allow the animal to behave freely while also facilitating the experimental manipulation of sensory feedback. In their current study, Biswas *et al.* [3] built an augmented reality system to directly manipulate the sensory feedback received by the animal due to its own movements [3]. Specifically, they coupled the movement of the refuge to the animal's own motion and then systematically varied the gain of this coupling (Figure 2A). For example, when the gain was negative, the refuge moved in the opposite direction to the fish (Figure 2A, top left) whereas, when the gain was positive, the refuge moved in the same direction as the fish (Figure 2A, top right).

The surprising result is that, as the gain of the augmented reality system is varied, the animal dramatically changes the amplitude of its own movements in order to maintain a similar variance in its sensory slip (Figure 2B). These results provide further support for the hypothesis that the sensory slip is not simply error in tracking, but results from voluntary movements used for active sensing. More importantly, however, they also raise the interesting possibility that the animal is able to extract information contained in the input resulting from the actively generated sensory slip in order to achieve tracking.

How do active movements affect electrosensory input to the animal? One possibility is that such movements are used to increase the sensing volume — the area of space around the animal's body within which stimuli can be detected. For a person, the visual sensing volume is typically much greater than our body: this is because, on a clear day, we can see up to a kilometer away. In contrast, for an electric fish, the sensing volume only extends several centimeters beyond the animal's body [7]. In feeding behaviors, active movements can increase this 'short-range' sensory volume, thereby allowing the animal to better detect prey [7]. In contrast, in refuge tracking, active movements have no net effect on sensory volume because the fish are swimming back and forth over roughly the same location.

Another possibility is that such movements serve to counteract the 'high-pass' adaptation properties of peripheral electrosensory neurons [8]. Such peripheral filtering enhances responses to fast time-varying signals, but attenuates, if not eliminates, responses to slowly varying signals [9] such as those due to refuge movement. Active movements shift the frequency of feedback from low-frequency signals to higher frequency signals that are not subject to peripheral filtering. Alternatively, and more interestingly, it is also possible that 'va-et-vient' movements create information about the sensory environment that would not be present otherwise, and that this information is decoded by the electrosensory system as shown in another context [10]. Indeed, the results of Biswas *et al.* [3] shows that fish maintain a constant variance of the sensory slip (Figure 2B), which may represent an independent stream of information that has not been previously considered.

To shed light on how active sensing movements enhance sensory input, future research will need to focus on recording neural activity in freely swimming fish during refuge tracking. While these experiments seemed impossible just ten years ago, advances in technology have made such recordings more and more feasible in aquatic animals [11]. As sensory input is generally a compound of external (ex-afferent) and self-generated (re-afferent) signals, one key question is how the nervous system distinguishes between these during processing. In the case of refuge tracking,

A

B
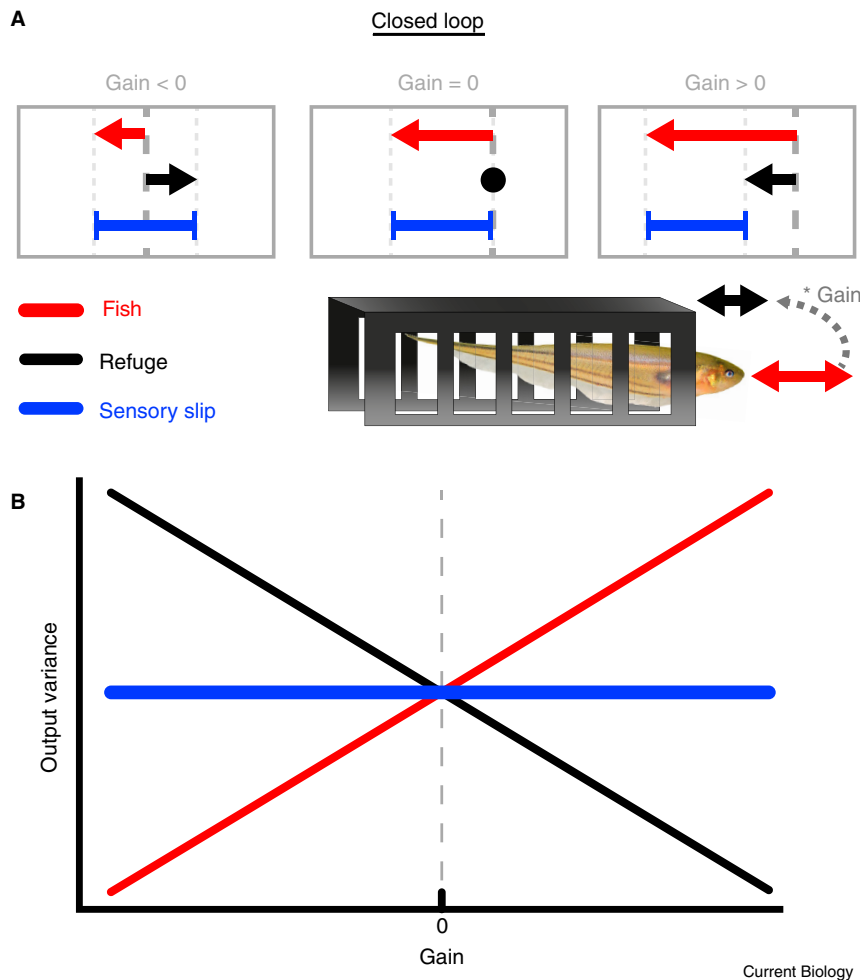
Figure 2. Control of sensory feedback through regulation of active sensing movements.
(A) In their experiments Biswas *et al.* [3] coupled the movement of the refuge to the movement of the fish to create a closed loop augmented reality setup. By varying the gain of the coupling, the authors could artificially increase (left, gain < 0) or decrease (right, gain > 0) the usual level of sensory feedback. (B) When varying the gain of the shuttle coupling (black) the authors found that fish adjusted by changing the amplitude of their movements (red): if the sensory feedback was increased (left part of graph) fish decreased the amplitude of motions and vice versa (right part of graph). As a result, the sensory slip (blue), which is the variance of the sensory input, was maintained at a constant level in all conditions.

these play a critical role in extracting salient information for behavioural control from the re-afferent sensory input created by the animal's own movements. Weakly electric fish, which share functional similarities to mammalian systems [14] and benefit from well-characterized anatomy, physiology and behavior, are thus likely to become a key model system for discovering how active sensing movements are used and generated by the nervous system to enhance sensory information and perception.

the sensory input caused by the external movement of the refuge would be ex-afferent while that caused by the 'va-et-vient' movements on top of the smooth pursuit would be re-afferent.

The separation of re-afference and ex-afference is a general problem studied across systems and species [12]. In electric fish, responses of electrosensory neurons to ex-afferent sensory input have been well-characterized in immobilized weakly electric fish [13,14]. How electrosensory neurons respond to stimulation during movement is, however, unknown. One possibility is that re-afferent input is 'cancelled out', thereby allowing central electrosensory neurons

to respond selectively to ex-afferent input, as observed in other systems [15]. Previous studies have shown that descending pathways — input from more central brain areas to more peripheral brain areas — can mediate such a subtraction of re-afference from the afferent input stream [16,17].

Interestingly, recent studies [18–20] have uncovered novel roles for descending inputs such as generating and optimizing neural responses to sensory input that is typically experienced during movement. Such descending inputs likely play a much bigger role than simply subtracting out re-afferent sensory input. A compelling hypothesis is that

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Ecology: Termite Patterning at Multiple Scales

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A vast and ancient array of regularly spaced dirt mounds — the result of termite activities— has been discovered in Brazil. Might this inform our understanding of general mechanisms of spatial patterning at different scales?

A major area of interest in biology is that of self-organization: local interactions between individuals — molecules, cells, organisms — leading to emergent patterns and properties at much larger scales. One instantiation of this phenomenon are regular spatial patterns — periodic distributions of features that share a characteristic cluster size. Regular patterns are common in natural systems, at levels of organization ranging from cells and organisms [1–3] to entire landscapes [4,5] and seascapes [6] (Figure 1). Often the same patterns — spots, labyrinths, stripes — can be found across these diverse organizational scales, leading to the notion that a single, universal mechanism might cause all these patterns. This notion has become more tempered, however, with the discovery of diverse self-organizing mechanisms that can produce superficially identical patterns at each of these scales [7–10]. In a recent study in *Current Biology*, Stephen Martin and colleagues [11] reveal a regular spatial pattern of astonishing proportions and suggest an unexpected underlying mechanism: in northeastern Brazil, spread across an

area equivalent to that of Great Britain, tens to hundreds of millions of meters-high and millennia-old dirt mounds,

apparently the result of termite foraging, are organized into an overdispersed, hexagonal pattern, such that every dirt
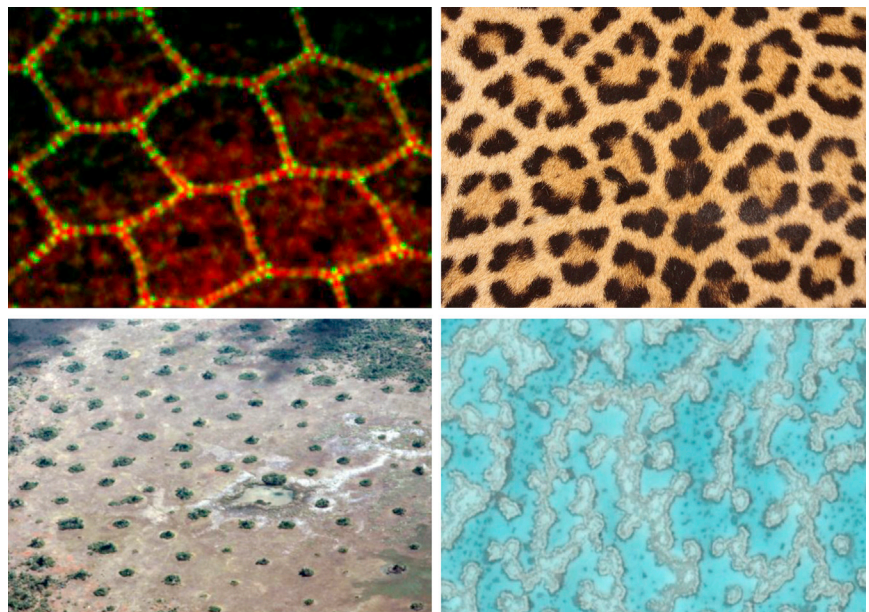
Figure 1. Regular pattern formation across scales.
Cell organization in an epithelial tissue (top left; reproduced from [3]), animal coats (top right), termite mounds appearing as islands of vegetation in Gorongosa National Park, Mozambique (bottom left; photo: Rob Pringle), coral reefs (bottom right; copyright 2015 Digital Globe image (latitude = −23.47; longitude = 151.89).