

RESEARCH ARTICLE

Active sensing *via* movement shapes spatiotemporal patterns of sensory feedback

Sarah A. Stamper^{1,*}, Eatai Roth², Noah J. Cowan² and Eric S. Fortune¹

¹Department of Psychological and Brain Sciences and ²Department of Mechanical Engineering, Johns Hopkins University, Baltimore, MD 21218, USA

*Author for correspondence (sstamper@jhu.edu)

SUMMARY

Previous work has shown that animals alter their locomotor behavior to increase sensing volumes. However, an animal's own movement also determines the spatial and temporal dynamics of sensory feedback. Because each sensory modality has unique spatiotemporal properties, movement has differential and potentially independent effects on each sensory system. Here we show that weakly electric fish dramatically adjust their locomotor behavior in relation to changes of modality-specific information in a task in which increasing sensory volume is irrelevant. We varied sensory information during a refuge-tracking task by changing illumination (vision) and conductivity (electroreception). The gain between refuge movement stimuli and fish tracking responses was functionally identical across all sensory conditions. However, there was a significant increase in the tracking error in the dark (no visual cues). This was a result of spontaneous whole-body oscillations (0.1 to 1 Hz) produced by the fish. These movements were costly: in the dark, fish swam over three times further when tracking and produced more net positive mechanical work. The magnitudes of these oscillations increased as electrosensory salience was degraded *via* increases in conductivity. In addition, tail bending (1.5 to 2.35 Hz), which has been reported to enhance electrosensory perception, occurred only during trials in the dark. These data show that both categories of movements – whole-body oscillations and tail bends – actively shape the spatiotemporal dynamics of electrosensory feedback.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/215/9/1567/DC1>

Key words: active sensing, electroreception, sensory volume, shaping.

INTRODUCTION

Active sensing is broadly defined as the expenditure of energy into the environment for the purpose of sensing (Nelson and MacIver, 2006). Active sensing can include the generation of signals, such as echolocation chirps in bats (Moss and Surlykke, 2001; Ulanovsky and Moss, 2008), and the generation of movements, such as whisking in rodents (Grant et al., 2009). Active sensing in weakly electric fish includes the generation of a sensory signal (their electric field), as well as movement through the environment for the purpose of sensing (Heligenberg, 1975; Assad et al., 1999; Babineau et al., 2007).

Recent studies have identified the important role of movement-based active sensing (Peters et al., 1999; Madsen et al., 2004; Ghose and Moss, 2006; Wachowiak, 2010) for increasing sensory volumes (MacIver et al., 2010; Yovel et al., 2011). Animals can also move their sensory organs, e.g. eyes, pinnae, antennae or whiskers, through independent actuation for purposes other than increasing the sensory volume. For example, eye microsaccades prevent perceptual fading (Ditchburn and Ginsborg, 1952) and larger eye movements place salient features on the fovea (foveation) (Robinson and Zee, 1981; Becker, 1989).

When electric fish investigate novel objects or hunt for prey, they swim in a scanning motion and bend their trunks (Lannoo and Lannoo, 1992; Nelson and MacIver, 1999; Nanjappa et al., 2000) as well as their tail (Heligenberg, 1975; Toerring and Moller, 1984; Nelson and MacIver, 1999; MacIver et al., 2001). Indeed, these behaviors increase the sensory volume over the movement time interval (Snyder et al., 2007; MacIver et al., 2010), but that may not be the most important role of such movements. To examine the

sensory function of these movements, we manipulated modality-specific sensory feedback in a task in which increasing the sensory volume is irrelevant.

We measured the performance of *Eigenmannia virescens* in a refuge-tracking task where we varied the availability of visual and electrosensory information *via* changes in illumination and conductivity, respectively. In the tracking task, a fish swims forwards and backwards to maintain its position within a longitudinally moving refuge (the 'shuttle'; Fig. 1B) (Blake, 1983; Lannoo and Lannoo, 1992). This behavior is mediated by at least two sensory modalities (Fig. 1A), vision and electroreception (Rose and Canfield, 1993a; Rose and Canfield, 1993b; Rojas and Moller, 2002). Importantly, although the fish's movements may increase the sensory volumes, the refuge-tracking task did not rely on this increase because the shuttle always remained within the sensing volumes of both the visual and electrosensory systems.

We found that despite categorical changes in the availability of sensory information, the animals maintained similar behavioral performance as measured by tracking gain. However, in the absence of visual information, fish produced costly movements, and as electrosensory information was degraded, these movements increased. In short, the animal controls its own movements, which in turn determines the pattern of feedback that the animal experiences as it moves through the environment. For example, if a fish swims faster past an object, the frequency of stimulation at a single electroreceptor is increased as the object passes in and out of the receptive field. Our data suggests that the fish may use active movements to shape the spatiotemporal dynamics of the electrosensory feedback.

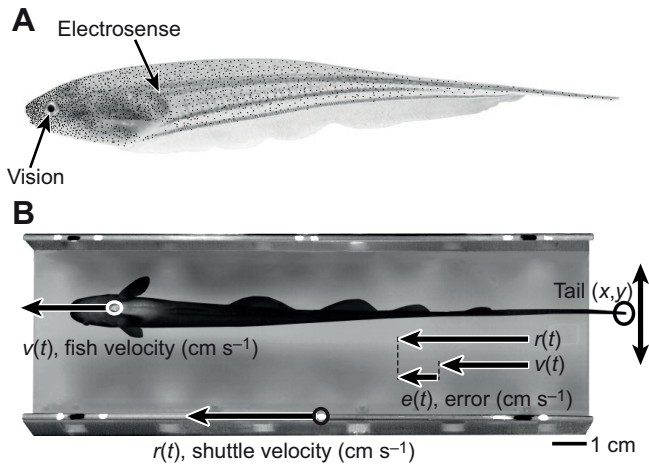


Fig. 1. Schematics of the fish and the experimental setup. (A) Weakly electric fish have both visual and electrosensory systems. (B) The experimental setup shows the velocities of the fish, $v(t)$, and the shuttle (refuge), $r(t)$, as well as the tracking error, $e(t)$, that were digitized for each trial. These velocities were used to calculate gain and phase of tracking, tracking error, swim path length and locomotor cost. For 60 trials, we also digitized the position of the tail.

MATERIALS AND METHODS

Adult *Eigenmannia virescens* (Valenciennes 1836) (10–15 cm in length) were obtained through a commercial vendor and housed according to published guidelines (Hitschfeld et al., 2009). Tanks were maintained with a water temperature of $\sim 27^{\circ}\text{C}$ and a conductivity in the range of $150\text{--}250\ \mu\text{S cm}^{-1}$. All experimental procedures were approved by the Johns Hopkins Animal Care and Use Committee and followed guidelines established by the National Research Council and the Society for Neuroscience.

For each experiment, an individual fish was transferred to a testing tank equipped with a computer-controlled moving refuge and a high-speed video camera [see Fig. 1 in Roth et al. (Roth et al., 2011)]. Animals were allowed to acclimate to the test tank and refuge for 2–24 h prior to any experimental trials. If the fish left the refuge during testing and did not return within approximately 1 min, the overhead lights were turned on and the fish was gently guided back into the refuge using an aquarium net (Rose and Canfield, 1993a). Subsequently, animals often returned to the refuge when the overhead light was turned on.

Experimental apparatus

The experimental setup was similar to that used in previous reports (Fig. 1B) (Cowan and Fortune, 2007; Roth et al., 2011). For these experiments, the refuge (or ‘shuttle’) was machined from a 15 cm segment of 2×2 inch gray rectangular PVC tubing. The bottom face of the refuge was removed and a series of six windows (0.625 cm in width and spaced 2.0 cm apart) were machined into each side to provide visual and electrosensory cues. The shuttle was suspended 0.3 cm from the bottom of the tank to allow the fish to be video recorded from below. Video was obtained using a high-speed camera (pco.1200s, Cooke Corp., Romulus, MI, USA) with a Micro-Nikkor 60 mm f/2.8D lens (Nikon Inc., Melville, NY, USA). Video was captured at $30\ \text{frames s}^{-1}$ with 1280×1024 pixel resolution using Camware software (Cooke Corp.). For each trial, the shuttle was moved forwards and backwards according to specified sine wave trajectories by a linear stepper motor (IntelliDrives, Inc, Philadelphia,

PA, USA) driven by a Stepmotor controller (Copley Controls, Canton, MA, USA). The actuator trajectories and camera triggering were synchronized using a Multifunction DAQ (USB-6221, National Instruments, Austin, TX, USA) and controlled with custom MATLAB scripts (MathWorks, Natick, MA, USA).

Experimental procedure

Individual fish ($N=4$) were presented with shuttle movement trajectories consisting of single sine waves (frequencies: 0.05, 0.01, 0.25, 0.55, 0.85, 1.15 and $1.55\ \text{Hz}$) at a velocity amplitude of $1.2\ \text{cm s}^{-1}$. Each trial was a total of 60 s in duration. During a trial, the stimulus amplitude was gradually ramped up for the first 10 s to prevent abrupt onset movements and similarly attenuated for the last 10 s to prevent movements in response to an abrupt stop. Data from these ramping periods were excluded from analysis.

Trials were run using two illumination conditions, either white light (‘light’ trials) or infrared light (‘dark’ trials). Each illumination condition was paired with a conductivity range: ‘low’ ($25\pm 5\ \mu\text{S cm}^{-1}$), ‘medium’ ($200\pm 20\ \mu\text{S cm}^{-1}$) and ‘high’ ($570\pm 15\ \mu\text{S cm}^{-1}$). These conductivities result in behaviorally relevant changes in the distribution and density of the electric field (MacIver et al., 2001).

The sequence of sensory condition (the pairings of illumination and conductivity) presentation was randomized across fish. For each sensory condition, the fish completed four to eight trials of each shuttle trajectory. The trial order was randomized with the constraint that the fish completed one trial for each trajectory before repeating a trajectory. The data for each sensory condition were typically collected over several hours on 1–2 days of testing. The minimum inter-trial interval was 70 s. Analyzed data included fish ($N=4$) that completed at least one set of trials for all sensory conditions. An additional fish ($N=1$) completed one set of ‘light’ trials at medium conductivity before and after enucleation of both eyes as a control measure to completely eliminate visual input. Data obtained from the blinded fish were for comparison purposes only and are not included in the final data set except where noted.

Data analysis

For each trial ($n=876$), the x – y positions of the fish and shuttle were digitized (Fig. 1B) using custom code implemented in MATLAB. Raw x – y pixel coordinates were transformed to align the x -coordinate with the length (and motion) of the refuge. For each trial, we calculated the time trajectory of velocity for both the shuttle and the fish, $r(t)$ and $v(t)$, respectively. For a subset of trials ($n=60$), the x and y positions of the tail were digitized and the mean tail-beat frequency was calculated for each trial.

The Fourier transform (FT) represents these time-domain signals, $r(t)$ and $v(t)$, as complex-valued functions of frequency, $R(\omega)$ and $V(\omega)$. Representing these complex functions in polar coordinates, we can describe each value by its magnitude, $|V(\omega)|$, and angle $\angle V(\omega)$. For sinusoidal input trajectories, the FT of the input, $R(\omega)$, is represented as a discrete spike at the stimulus frequency and zero at all other frequencies. The FT of the fish movement, $V(\omega)$, has power over a broader range of frequencies (0.1 to 1.0 Hz) with concentrated peaks at frequencies corresponding to the spectrum of the input.

The Bode plot (Fig. 2A) describes the response of a system by comparing the output signal $X(\omega)$ with the input $R(\omega)$ using two measures, gain and phase. Gain is calculated as the ratio of the signal magnitudes, $|V(\omega)|/|R(\omega)|$, and phase is computed as the difference of the signal angles, $\angle V(\omega) - \angle R(\omega)$. The Bode plot is evaluated only for the set of discrete frequencies presented as stimuli; the Bode ratio is not defined elsewhere where the $R(\omega)=0$.

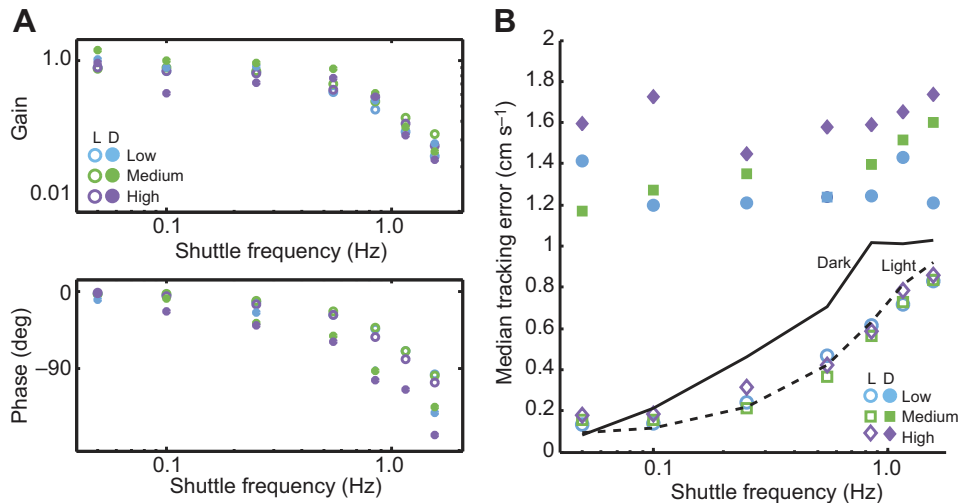


Fig. 2. Tracking gain is similar across sensory conditions despite increased tracking error in the dark. (A) The Bode plot indicates that tracking performance, measured by gain, is equivalent between trials completed in the light (L, open symbols) and those completed in the dark (D, filled symbols). The gain was similar across conductivities, low (blue), medium (green) and high (purple). We found a difference in phase for higher shuttle movement frequencies (0.55 Hz and above), where fish had an increased phase lag in the dark. (B) Median tracking error in the light matches the Bode-predicted error (dashed line) whereas median tracking error in the dark (black line) does not. There was a significant increase in error between light (L, open symbols) and dark (D, filled symbols) trials and when conductivity was increased from low (blue circles) to medium (green squares) to high (purple diamonds).

We further decompose the fish motion into two categories of movement: movements in response to the stimulus frequencies (the concentrated peaks of the FT) and broad-spectrum volitional motion (termed ‘whole-body oscillations’). To estimate the average volitional motion, we calculate the magnitude of the FT, $|V(\omega)|$, for each trial and omit the data corresponding to the input frequencies (the peaks in response to the stimulus). Because different trials have different points on the frequency spectrum omitted, we can reconstruct the entire spectrum by averaging across trials.

For each trial, we also calculate median tracking error, the median value of the time series $|v(t) - r(t)|$. We use the median tracking error to exclude occasional rapid shifts in the fish’s position and velocity. These excursions correspond to a behavior where the fish makes a full body reversal to correct for accumulated tracking error (e.g. the fish drifts to the edge of the shuttle and subsequently swims back to the center).

We calculate the total path length that the fish swam for each trial, $\int |v(t)| dt$. The values we report are normalized to the path length of the refuge trajectory, which was always 30.56 cm. As a conservative estimate of energy expenditure for locomotion (locomotor cost), we calculate the net positive mechanical work required to move the fish along its swimming trajectory. The net positive work is calculated as the integral of the positive power (those instances during which velocity and acceleration are in the same direction) excluding intervals where power is negative, $\int_{P>0} P(t) dt$. This estimate assumes that energy is expended for acceleration only and deceleration is achieved passively (i.e. *via* drag forces introduced through fluid–body interaction). The instantaneous power is $P(t) = F(t)v(t)$, where F represents the force and v is the fish velocity. Force is estimated by Newton’s law, $F = ma = m\dot{x}$, where m is the mass of the fish and \dot{x} is the acceleration.

This estimate of locomotor cost underestimates the mechanical work performed by the fish (e.g. using this estimate, constant velocity motion implies zero work, but fish clearly must inject work into the locomotor dynamics to overcome drag forces). Fish likely actively decelerate with ribbon fin actuation, so some of the neglected ‘negative’ work represents mechanical work performed

by the fish. Moreover, even stationary fish are observed moving their ribbon fin in counter-propagating waves, expending a baseline of mechanical work for no motion at all. Theoretically, there may be cases for which the net positive work exceeds the actual mechanical work contributed by the animal (i.e. through elastic storage of energy, as might happen in the tendons of terrestrial animals), but there is no evidence of these effects in swimming fish.

With these important caveats in mind, the net positive work estimate serves as a convenient lower bound to the mechanical work contributed by the fish; a true estimate of mechanical work contributed by the fish requires a more complete description of the ribbon-fin kinematics throughout the duration of the experiments. Still, such an estimate would not represent the metabolic cost. Additionally, there are other costs associated with increased movement, such as increased conspicuousness, which could result in higher predation rates, which we wholly ignore. Ultimately, the net positive work provides a consistent and convenient metric for comparing energetic costs of locomotion between different sensory conditions.

Dependent measures were analyzed using a factorial repeated-measures ANOVA with the Geisser–Greenhouse correction for non-sphericity. For each significant main effect we provide an effect size measure (η_p^2) to allow comparison across measures.

RESULTS

Fish use visual and electrosensory systems to control locomotor behavior

We computed Bode gain and phase, a measure of tracking performance (see Materials and methods), under different sensory conditions (Fig. 2A). In general, the tracking performance of these fish matched that of previous reports (Cowan and Fortune, 2007; Roth et al., 2011): fish had a tracking bandwidth of 0.05 to 1.55 Hz with phase lags up to 180 deg at the highest stimulus frequencies (1.15 and 1.55 Hz). Gains were strikingly similar across all visual and electrosensory conditions, which indicates that fish were able to match the velocities of the stimulus despite categorical changes in the availability of sensory information, which has not been

described previously (Rose and Canfield, 1993a; Rose and Canfield, 1993b). We observed a difference in the mean phase lag at higher frequencies (0.55, 0.85, 1.15 and 1.55 Hz) – fish responses lagged the shuttle input more in the dark than when visual cues were present by 31, 49, 42 and 48 deg, respectively. Despite this difference, the performance of the fish in light and dark and across conductivities was surprisingly consistent given the radical spatiotemporal differences between visual and electrosensory cues.

Next, we compared the error predicted by the Bode plot analysis with the measured median tracking error across all sensory conditions (Fig. 2B). If the tracking behavior were a linear system, the Bode plot could be used to accurately predict the median tracking error. Indeed, we found that the Bode-predicted error closely matched the fish's tracking performance when the fish had visual cues. However, the measured median tracking error increased dramatically from the Bode prediction when the fish performed the tracking behavior in the dark. There were significant main effects of illumination ($F_{1,3}=86.18$, $P=0.003$, $\eta_p^2=0.96$), conductivity ($F_{2,6}=36.41$, $P=0.008$, $\eta_p^2=0.93$) and shuttle movement frequency ($F_{6,18}=10.37$, $P=0.015$, $\eta_p^2=0.78$) on median tracking error. In particular, mean (\pm s.e.m.) tracking error increased from light (0.451 ± 0.013 cm s⁻¹) to dark (1.425 ± 0.027 cm s⁻¹) and as conductivity increased from low (0.875 ± 0.035 cm s⁻¹) to medium (0.931 ± 0.037 cm s⁻¹) to high (1.077 ± 0.044 cm s⁻¹; Fig. 2B).

Increased tracking error in the dark results from large whole-body oscillations

The source of the increase in tracking error can be seen directly in the raw tracking data: there was a categorical difference in swimming behavior when the lights were turned off. To illustrate this difference, Fig. 3A shows two trials in which the lights were switched on or off mid trial (30 s videos of illumination shift are shown in supplementary material Movies 1 and 2). These trials also show that the fish behavior switched immediately in response to changes in illumination. These two trials indicate a common feature across all of our data: the fish tracked the shuttle movement smoothly in the light, whereas in the dark the fish performed large back-and-forth movements that were superimposed on the underlying tracking trajectory.

In the frequency domain (Fig. 3B), the fish response in light trials appears as a single peak collocated with the input peak. For dark trials, the fish motion includes a peak at the input frequency (the response to the stimulus), and also shows power across a broader spectrum up to 1 Hz, which we call 'whole-body oscillations'. These whole-body oscillations were similar across stimulus frequencies and rarely occurred in the light. We also observed similar oscillations in a fish that was tracking in the light but was blind. Typically, the velocities of these oscillations were higher (1.2 to 15 cm s⁻¹) than the underlying shuttle velocity (0 to 1.2 cm s⁻¹).

In the light, the electrosensory feedback that the animal receives – which is the slip of the shuttle along the body surface – occurs roughly at the stimulus frequency. At night, however, the additional oscillations alter the frequency of the feedback, shifting it to higher frequencies. Our hypothesis is that these active movements increase the frequency range of feedback into a range that better matches the frequency filtering of the electrosensory system.

Fish swim significantly farther while tracking in the dark

We measured the distance that fish swam for each trial. The distance was normalized to the total distance moved by the shuttle, which was always 30.56 cm. We found that the fish swam an average of 3.35 times farther in the dark than in the light, and that swimming distance also increased with increased conductivity. There were

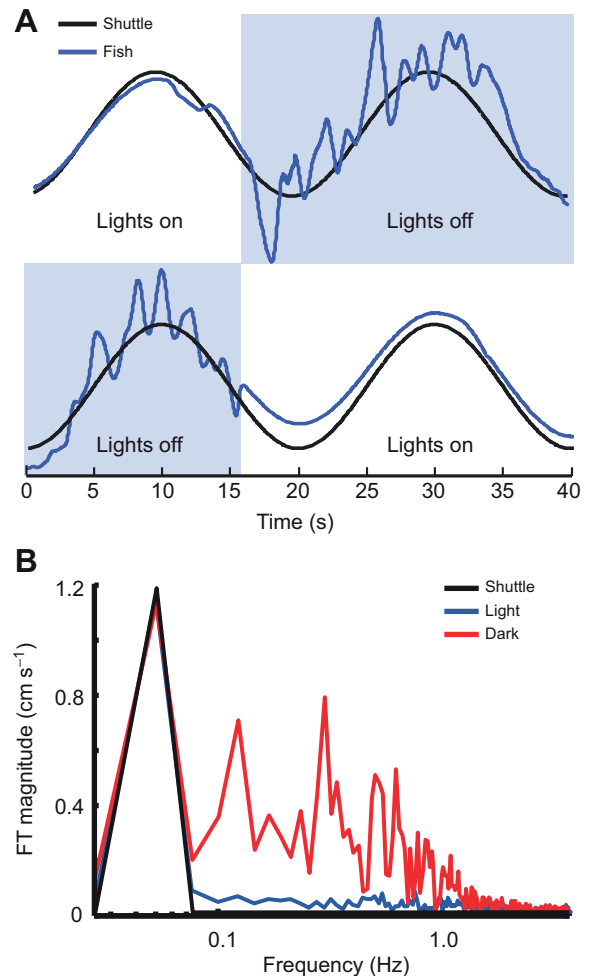


Fig. 3. Illumination and conductivity modulate the generation of active movements in *E. vireescens*. (A) Two sample trials are shown where the illumination was switched during tracking. The fish exhibited a dramatic difference in tracking behavior as a function of illumination. In the dark, fish swim back and forth with whole-body oscillations superimposed over the underlying tracking movement. (B) The magnitude of the Fourier transform (FT) computed from two trials of a fish tracking a shuttle moving at 0.05 Hz (black). The fish responded with nearly identical gain at the stimulus frequency, as indicated by the spectral peaks at 0.05 Hz for both the light (blue) and dark (red) trials. However, in dark trials fish motion had substantial spectral content at other frequencies (up to approximately 1 Hz).

significant main effects of illumination ($F_{1,3}=253.83$, $P=0.001$, $\eta_p^2=0.99$), conductivity ($F_{2,6}=20.30$, $P=0.012$, $\eta_p^2=0.87$) and shuttle movement frequency ($F_{6,18}=5.33$, $P=0.039$, $\eta_p^2=0.64$) on normalized swim path length (Fig. 4A). Mean (\pm s.e.m.) normalized swim path length increased substantially from light (0.789 ± 0.013) to dark (2.644 ± 0.041) and as conductivity increased from low (1.554 ± 0.059) to medium (1.744 ± 0.063) to high (1.979 ± 0.074 ; Fig. 4A).

Energetic costs of locomotion increase when tracking in the dark

The normalized swim path length does not differentiate between different categories of swimming. Positional drift (low velocity, low acceleration and low-frequency movements) and whole-body oscillations (high velocity, high acceleration and high-frequency movements) could result in similar path length measurements. However, oscillations represent greater mechanical work than do drifts of similar path length.

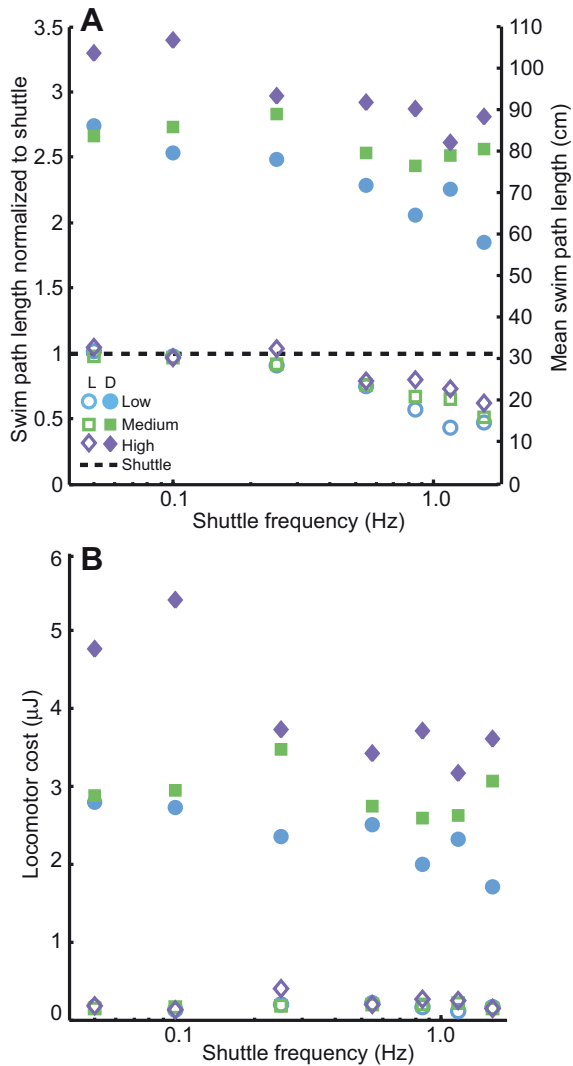


Fig. 4. Active movements incur increased locomotor cost in *E. virescens*. (A) The fish swam significantly less when tracking the shuttle in the light (L, open symbols) compared with in the dark (D, filled symbols). The fish's swim path also increased as a function of conductivity from low (blue circles) to medium (green squares) to high (purple diamonds). (B) Tracking in the dark (filled symbols) also incurred an increased locomotor cost compared with tracking in the light (open symbols).

We estimated a lower bound for the costs of locomotion associated with tracking a moving shuttle. This cost was estimated as the net positive mechanical work required to move the fish's mass along its experimentally measured trajectory (see Materials and methods). Fish performed significantly more net positive work in the dark (Fig. 4B). For each shuttle frequency, the cost of locomotion was highest for the highest conductivity, and lowest for the lowest conductivity. There was a significant main effect of illumination ($F_{1,3}=142.60$ $P=0.001$, $\eta_p^2=0.98$) on the locomotor cost, but the effect of conductivity was not statistically significant. Mean (\pm s.e.m.) locomotor cost increased from light (0.186 ± 0.011 μ J) to dark (3.087 ± 0.108 μ J; Fig. 4B).

Whole-body oscillations increase with increases in conductivity

To determine whether fish use these whole-body oscillations to facilitate electrosensory processing, we altered the conductivity of

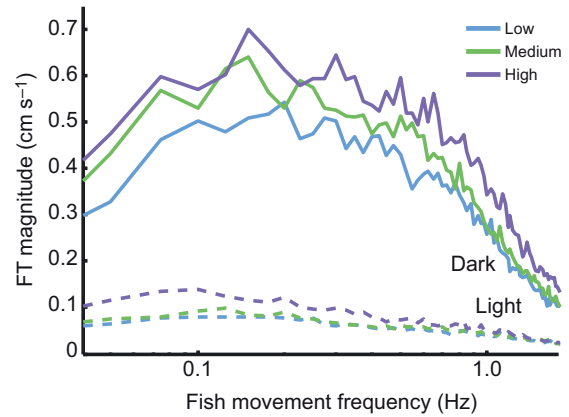


Fig. 5. Whole-body oscillations of *E. virescens* increase with increasing conductivity. The magnitude of these movements increased from light to dark and also as a function of increasing conductivity.

the water. Conductivity affects the spatial distribution of the electric field and consequently affects the feedback that results from movement. If the additional movements reported above were unrelated to active sensing, one would expect that conductivity would have little or no effect on the oscillations. Instead, we found a significant increase (Fig. 5) in the magnitude of these oscillations ($F_{2,6}=14.79$, $P=0.010$, $\eta_p^2=0.83$) as conductivity was increased from low (mean \pm s.e.m. = 12.43 ± 0.38 cm s^{-1}) to medium (14.19 ± 0.40 cm s^{-1}) to high (16.01 ± 0.39 cm s^{-1}). In addition, these oscillations persisted even after more than 24 h of continuous darkness and were also observed in a blind fish that was tracking in the light.

Spontaneous tail movements emerge during dark trials, but not light trials

We observed that the fish constantly move their tails when tracking in the dark but not in the light (Fig. 6A,B). Tail-beat frequency ranged from 1.5 to 2.35 Hz across four fish (Fish 1–4: mean \pm s.e.m. = 1.88 ± 0.025 Hz) and an additional fish that was blind (Fish 5: 1.76 ± 0.058 Hz; Fig. 6C). Previous modeling results indicate that electric fish might bend their tail in order to compute lateral distance to objects (Sim and Kim, 2011). Accordingly, we found that fish maintained a mean y -position (Fig. 6D) that is more tightly clustered in the middle of the shuttle walls (open bars; 4 cm width) in trials in the dark (black bars) than those in the light (grey bars).

We also found that the mean standard deviation of the y -position (averaged over each trial) increased as a function of illumination from light (s.d. \pm s.e.m. = 0.080 ± 0.004 cm) to dark (0.186 ± 0.004 cm). This indicates that fish have more active side-to-side movement of their head when tracking in the dark. However, it is possible that this head movement is confounded with tail bending, which might cause the body to have a slight lateral oscillation. We also found that the standard deviation for the mean y -position increased as a function of conductivity in the light (low, s.d. \pm s.e.m. = 0.054 ± 0.005 cm; medium, 0.077 ± 0.006 cm; high, 0.180 ± 0.007 cm) and dark (low, 0.152 ± 0.007 cm; medium, 0.189 ± 0.007 cm; high, 0.217 ± 0.006 cm). Overall, these lateral movements were small compared with the width of the refuge (approximately 2 to 10%).

DISCUSSION

We measured the ability of the fish *E. virescens* to track a moving refuge in the light and the dark (with and without visual cues) and

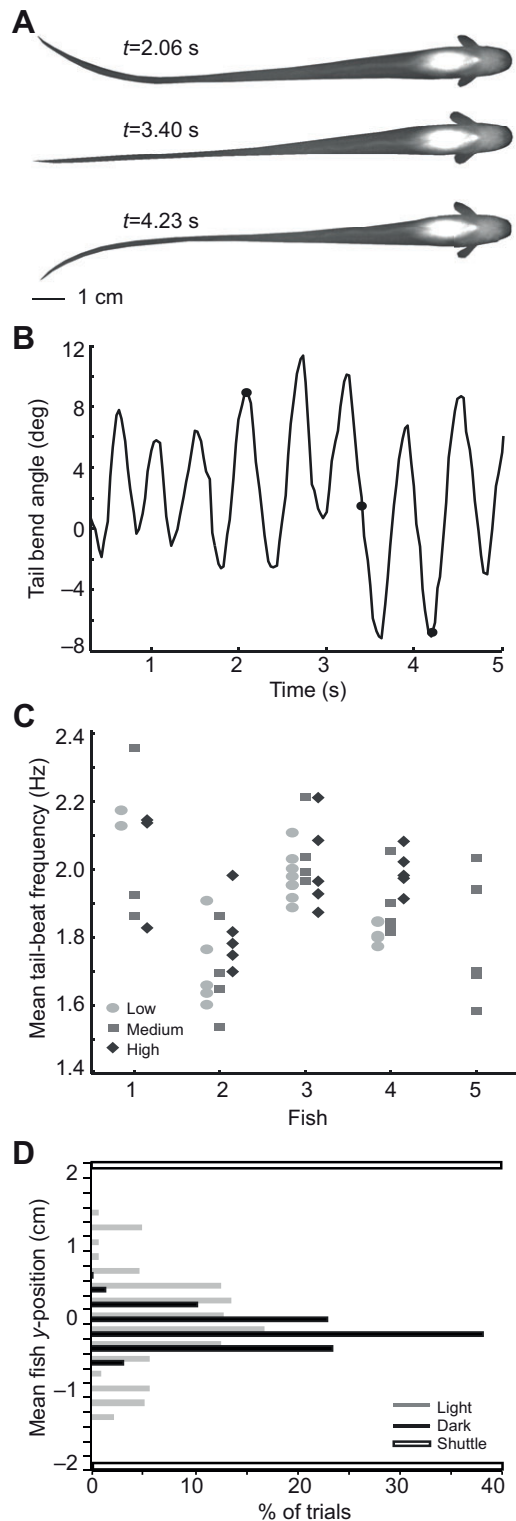


Fig. 6. Tail bending of *E. virescens* may facilitate maintenance of lateral position in the dark. (A) Three sample frames that show the fish bending its tail, a behavior observed almost exclusively during tracking in the dark. (B) A sample trace showing the angle from the tip of the tail to middle of the body, relative to head direction. The three sample frames from A are indicated with black dots. (C) The mean tail-beat frequency for tracking in the dark across the three conductivity levels (Fish 1–4) and a blind fish (Fish 5) tracking in the light at medium conductivity. (D) Histogram of lateral position in the light (grey bars) and the dark (black bars) relative to the shuttle walls (open bars at top and bottom).

in different water conductivities (which alters the pattern of electrosensory feedback). We found that *E. virescens* preferentially rely on the visual system when visual cues are present. This is consistent with their life history, as they hide in root systems, grasses and debris during daylight hours when visual cues are present (Tan et al., 2005; Stamper et al., 2010). Similarly, other nocturnal or crepuscular animals that can rely on non-visual sensory information for the control of behavior also preferentially rely on visual cues when they are present (Knudsen and Knudsen, 1989; Penteriani et al., 2007; Cummings et al., 2008).

We found that tracking performance, as measured by the Bode gain, was comparable across the sensory conditions that were tested, which included systematic changes in illumination and conductivity. However, there was a categorical difference between fish locomotion in light *versus* dark: fish in the dark make whole-body oscillations and bend their tails. These active movements in the dark dramatically increase the distance that the fish swim and subsequently the locomotor cost of tracking in the dark compared to the performance in the light. These active movements shape the electrosensory feedback. Indeed, these movements increased significantly in response to a degradation of the electrosensory feedback signal. To the best of our knowledge, these experimental results are the first to show a correlation between the degradation of modality-specific information and the active reshaping of the sensory feedback.

Active sensing incurs locomotor costs

Active movements are energetically costly and this cost must be balanced against other costs, such as the reward of obtaining sensory information (Shadmehr et al., 2010). Many studies have examined the cost of emitting signals for active sensing (e.g. electric field, echolocation chirp). This cost is tied to effective range of the signal and receptor system, i.e. the sensing volume (Nelson and MacIver, 2006; Snyder et al., 2007). For example, a modeling study by MacIver et al. indicates that doubling the electrosensory volume requires 16 times more energy (MacIver et al., 2010). The benefit of this increase in energy expenditure is an enlarged sensing volume, thereby increasing the probability of encountering prey items (Lannoo and Lannoo, 1992; Nelson and MacIver, 1999; Nanjappa et al., 2000; MacIver et al., 2001). In our tracking experiments, increased sensing volume is not a relevant parameter because the shuttle is within the sensing volume at all times.

So, what is the benefit of this significant increase in the locomotor cost during tracking in the dark? The spectrum of active movement is essentially unchanged across all sensory conditions and between fish; only the gain of these movements is modulated as a function of light and conductivity (Fig. 5). This is consistent with our hypothesis that active movements are tuned to the spatiotemporal filtering properties of the underlying neural circuits. For example, neurons in the torus semicircularis (Ts) respond strongly to amplitude modulations in the range of frequencies generated by both the whole-body oscillations and the tail bend (Fortune and Rose, 1997a; Rose and Fortune, 1999; Fortune and Rose, 2000). These movements may also reduce perceptual fading by increasing the stimulation frequency, which may better stimulate high-pass afferents (Nelson et al., 1997) and improve detectability in the ELL through its interaction with descending feedback (Chacron et al., 2003) (see below).

Tail bending contributes to sensory processing

We observed that fish actively bend their tails in the dark when they rely on electrosensory information for tracking. Tail bending produces

modulations of the strength of the electric field on the ipsilateral and contralateral sides with opposite signs (Chen et al., 2005). These amplitude modulations (AMs) are summed with the AMs that result from the movement of the animal across the inner surface of the shuttle, which includes both the tracking error (slip of the shuttle along the body surface) and the whole-body oscillations. Each of these signals occurs, roughly speaking, in a different frequency band, with tracking error equal to the stimulus frequency (e.g. 0.05 Hz), whole-body oscillations (0.1 to 1 Hz) and tail bending (1.5 to 2.35 Hz). Theoretically, each signal could be extracted using an appropriately designed linear filter implemented in the nervous system. Neurons that are selective for particular frequencies of AMs have been described in the midbrain (Fortune and Rose, 1997a; Fortune and Rose, 1997b).

For isolated fish, these three categories of movement (tracking error, body oscillations and tail bending) generate simple AMs, but in the presence of conspecifics they likely also produce ‘envelopes’, which are the second-order modulations of amplitude that can occur as a result of social interactions and locomotor behavior (Middleton et al., 2006; Savard et al., 2011). Unlike AMs, envelopes cannot be extracted using simple linear filters, but rather require nonlinear mechanisms, such as rectification (Savard et al., 2011).

The role of tail bending in information processing has been studied previously in the context of the cancellation of predictable signals in the electrosensory lateral line lobe (ELL), a cerebellum-like structure (Bastian, 1996a; Bastian, 1996b; Bastian, 1998). Information from P-type receptor afferents is transmitted to the three tuberous maps of the ELL (Metzner, 1999; Maler, 2009a; Maler, 2009b; Fortune and Chacron, 2011). Pyramidal cells in the ELL receive descending feedback and exhibit adaptation to predictable signals by producing a negative image (Bastian, 1996a). Cyclical tail bending can be cancelled by descending feedback (Bastian et al., 2004). However, it remains to be determined how this cancellation might affect information processing during tail bending, which may explain why *E. virescens* increases tail bending when relying on electrosensory information in tracking behavior.

One clue comes from the responses of ELL neurons to intermittent electrosensory social signals. When two fish are in close enough proximity so that their electric fields interact (within approximately 1 m), the interactions of the electric fields continuously produce amplitude and phase modulations (Heiligenberg, 1991; Tan et al., 2005; Stamper et al., 2010). In *Apteronotus*, fish can also produce rapid, intermittent transients in their electric field (Zupanc et al., 2006; Dunlap et al., 2010), especially during agonistic encounters (Hupé and Lewis, 2008; Hupé et al., 2008). In the ELL, the cancellation of the predictable amplitude modulations that result from the mixing of electric organ discharges (EODs) from nearby fish also induces a concomitant enhancement of the responses to unpredictable chirp signals (Marsat and Maler, 2011). One possibility is that tail bending results in the same effect where the tail bending itself is cancelled but unpredictable signals related to the movements of the refuge are enhanced.

Further, there is a diversity of pyramidal cell types (deep, intermediate and superficial) that differ in the amount of descending feedback that they receive (Chacron et al., 2003; Bastian et al., 2004; Krahe et al., 2008). These differences are correlated with the degree of cancellation that the neurons experience in response to continuous global stimuli (Chacron et al., 2003). The role of these differences is unclear but may be related to the detection of combinations of predictable and unpredictable stimuli, such as occurs when the animal actively bends its tail (predictable) to determine the location of the shuttle (unpredictable). The combination of tracking error and the

whole-body oscillations produced by fish when tracking in the dark may indeed ensure that the position of the tail relative to the shuttle (moving object) at each moment in time is not predictable.

Movements shape sensory feedback to match neural properties

The additional movements in the dark necessarily alter the spatiotemporal patterns of the electric field on the body surface. Our hypothesis is that these movements are a form of active sensing in which the animal self-stimulates its electroreceptors to match the demands of the nervous system. Examples may include the requirements of high-pass filtering in primary afferents (Nelson et al., 1997), the spatiotemporal demands of filters in the midbrain (Fortune and Rose, 1997a; Fortune and Rose, 1997b; Ramcharitar et al., 2005) or the time scales required to update a representation of the shuttle through working memory (Baddeley, 1992).

Alternatively, these movements may not contribute to tracking performance in the dark but may emerge for other unknown reasons that are not related to electrosensory perception. Our data strongly suggest that this behavior is indeed related to electrosensory perception because we show that: (1) the magnitude of these whole-body oscillations increases as a function of increasing conductivity, (2) whole-body oscillations were observed in fish that had been in darkness for extended periods of time (12 to 24 h) and (3) whole-body oscillations were observed in a blind fish when tracking in the light. As conductivity increases, contrast decreases (MacIver et al., 2001). Therefore, an increase in movements when the conductivity is high could be used to shape spatiotemporal patterns of neural activity to match those as when the conductivity is low.

Interestingly, spatiotemporal shaping appears even in tasks where the apparent goal is to increase volume. Animals can achieve an increase in sensory volume in many ways, for example by increasing the energy of emitted signals, or through any of a variety of movement strategies. MacIver et al. described stereotyped patterns of movement during prey capture that increase the sensory volume (defined as the minimum detection distance for prey items) to increase the probability of prey detection (MacIver et al., 2001). It has also been shown that bats will engage in active movements to increase the ‘field of view’ or sensory volume detected using echolocation (Yovel et al., 2011). This behavior is dependent on the complexity of the environment and the location of the target. In general, the sensory volume depends critically on the relative movement of the animal’s receptor array relative to its prey (or target), because the receptor properties depend not on a static flux of energy onto the receptors, but rather on the dynamic (temporal) properties and changes in energy flux over time.

Thus, increasing the effective sensory volume is inherently linked to reshaping sensory feedback *via* the details of the movement, and *vice versa*. In fact, previous studies have described neurons that are tuned to the specific frequencies of sensory feedback experienced during prey capture (Chacron et al., 2003; Oswald et al., 2004; Chacron et al., 2005; Ramcharitar et al., 2005; Chacron et al., 2009). But, such predatory movements may be tuned, at least in part, to the spatiotemporal receptive field properties of the nervous system, rather than the traditional view of the nervous system being tuned to behavioral demands.

ACKNOWLEDGEMENTS

The authors thank E. M. Edwards for assistance with data collection and E. D. Tytell for useful discussions and contributions to data analysis. We also thank S. Sefati and two anonymous reviewers for comments and suggestions that greatly improved the manuscript.

FUNDING

This material is based upon work supported by the National Science Foundation (NSF) under grants IOS-0817918, CMMI-0941674 and CISE- 0845749 and the Office of Naval Research (ONR) under grant N000140910531. S. A. S. and E. R. were supported by NSF Graduate Research Fellowships. E. R. was also supported by an Achievement Rewards for College Scientists (ARCS) Foundation Fellowship.

REFERENCES

- Assad, C., Rasnow, B. and Stoddard, P. K.** (1999). Electric organ discharges and electric images during electrolocation. *J. Exp. Biol.* **202**, 1185-1193.
- Babineau, D., Lewis, J. E. and Longtin, A.** (2007). Spatial acuity and prey detection in weakly electric fish. *PLoS Comput. Biol.* **3**, e38.
- Baddeley, A.** (1992). Working memory. *Science* **255**, 556-559.
- Bastian, J.** (1996a). Plasticity in an electrosensory system. I. General features of a dynamic sensory filter. *J. Neurophysiol.* **76**, 2483-2496.
- Bastian, J.** (1996b). Plasticity in an electrosensory system. II. Postsynaptic events associated with a dynamic sensory filter. *J. Neurophysiol.* **76**, 2497-2507.
- Bastian, J.** (1998). Plasticity in an electrosensory system. III. Contrasting properties of spatially segregated dendritic inputs. *J. Neurophysiol.* **79**, 1839-1857.
- Bastian, J., Chacron, M. J. and Maler, L.** (2004). Plastic and nonplastic pyramidal cells perform unique roles in a network capable of adaptive redundancy reduction. *Neuron* **41**, 767-779.
- Becker, W.** (1989). *The Neurobiology of Saccadic Eye Movements*. New York: Elsevier.
- Blake, R. W.** (1983). Swimming in the electric eels and knife-fishes. *Can. J. Zool.* **61**, 1432-1441.
- Chacron, M. J., Doiron, B., Maler, L., Longtin, A. and Bastian, J.** (2003). Non-classical receptive field mediates switch in a sensory neuron's frequency tuning. *Nature* **423**, 77-81.
- Chacron, M. J., Maler, L. and Bastian, J.** (2005). Feedback and feedforward control of frequency tuning to naturalistic stimuli. *J. Neurosci.* **25**, 5521-5532.
- Chacron, M. J., Toporikova, N. and Fortune, E. S.** (2009). Differences in the time course of short-term depression across receptive fields are correlated with directional selectivity in electrosensory neurons. *J. Neurophysiol.* **102**, 3270-3279.
- Chen, L., House, J. L., Krahe, R. and Nelson, M. E.** (2005). Modeling signal and background components of electrosensory scenes. *J. Comp. Physiol. A* **191**, 331-345.
- Cowan, N. J. and Fortune, E. S.** (2007). The critical role of locomotion mechanics in decoding sensory systems. *J. Neurosci.* **27**, 1123-1128.
- Cummings, M. E., Bernal, X. E., Reynaga, R., Rand, A. S. and Ryan, M. J.** (2008). Visual sensitivity to a conspicuous male cue varies by reproductive state in *Physalaemus pustulosus* females. *J. Exp. Biol.* **211**, 1203-1210.
- Ditchburn, R. W. and Ginsborg, B. L.** (1952). Vision with a stabilized retinal image. *Nature* **170**, 36-37.
- Dunlap, K. D., DiBenedictis, B. T. and Banever, S. R.** (2010). Chirping response of weakly electric knife fish (*Apteronotus leptorhynchus*) to low-frequency electric signals and to heterospecific electric fish. *J. Exp. Biol.* **213**, 2234-2242.
- Fortune, E. S. and Chacron, M. J.** (2011). Physiology of tuberous electrosensory systems. In *Encyclopedia of Fish Physiology: From Genome to Environment*, Vol. 1 (ed. A. P. Farrell), pp. 366-374. San Diego, CA: Academic Press.
- Fortune, E. S. and Rose, G. J.** (1997a). Passive and active membrane properties contribute to the temporal filtering properties of midbrain neurons *in vivo*. *J. Neurosci.* **17**, 3815-3825.
- Fortune, E. S. and Rose, G. J.** (1997b). Temporal filtering properties of ampullary electrosensory neurons in the torus semicircularis of *Eigenmannia*: evolutionary and computational implications. *Brain Behav. Evol.* **49**, 312-323.
- Fortune, E. S. and Rose, G. J.** (2000). Short-term synaptic plasticity contributes to the temporal filtering of electrosensory information. *J. Neurosci.* **20**, 7122-7130.
- Ghose, K. and Moss, C. F.** (2006). Steering by hearing: a bat's acoustic gaze is linked to its flight motor output by a delayed, adaptive linear law. *J. Neurosci.* **26**, 1704-1710.
- Grant, R. A., Mitchinson, B., Fox, C. W. and Prescott, T. J.** (2009). Active touch sensing in the rat: anticipatory and regulatory control of whisker movements during surface exploration. *J. Neurophysiol.* **101**, 862-874.
- Heiligenberg, W.** (1975). Theoretical and experimental approaches to spatial aspects of electrolocation. *J. Comp. Physiol.* **103**, 247-272.
- Heiligenberg, W.** (1991). *Neural Nets in Electric Fish*. Cambridge, MA: MIT Press.
- Hitschfeld, E. M., Stamper, S. A., Vonderschen, K., Fortune, E. S. and Chacron, M. J.** (2009). Effects of restraint and immobilization on electrosensory behaviors of weakly electric fish. *ILAR J.* **50**, 361-372.
- Hupé, G. J. and Lewis, J. E.** (2008). Electrocommunication signals in free swimming brown ghost knifefish, *Apteronotus leptorhynchus*. *J. Exp. Biol.* **211**, 1657-1667.
- Hupé, G. J., Lewis, J. E. and Benda, J.** (2008). The effect of difference frequency on electrocommunication: chirp production and encoding in a species of weakly electric fish, *Apteronotus leptorhynchus*. *J. Physiol. Paris* **102**, 164-172.
- Knudsen, E. I. and Knudsen, P. F.** (1989). Vision calibrates sound localization in developing barn owls. *J. Neurosci.* **9**, 3306-3313.
- Krahe, R., Bastian, J. and Chacron, M. J.** (2008). Temporal processing across multiple topographic maps in the electrosensory system. *J. Neurophysiol.* **100**, 852-867.
- Lannoo, M. J. and Lannoo, S. J.** (1992). Why do electric fish swim backwards? An hypothesis based on gymnotiform behavior, interpreted through sensory constraints. *Environ. Biol. Fish.* **36**, 157-165.
- MacIver, M. A., Sharabash, N. M. and Nelson, M. E.** (2001). Prey-capture behavior in gymnotid electric fish: motion analysis and effects of water conductivity. *J. Exp. Biol.* **204**, 543-557.
- MacIver, M. A., Patankar, N. A. and Shirgaonkar, A. A.** (2010). Energy-information trade-offs between movement and sensing. *PLoS Comput. Biol.* **6**, e1000769.
- Madsen, P. T., Kerr, I. and Payne, R.** (2004). Echolocation clicks of two free-ranging, oceanic dolphins with different food preferences: false killer whales *Pseudorca crassidens* and Risso's dolphins *Grampus griseus*. *J. Exp. Biol.* **207**, 1811-1823.
- Maler, L.** (2009a). Receptive field organization across multiple electrosensory maps. I. Columnar organization and estimation of receptive field size. *J. Comp. Neurol.* **516**, 376-393.
- Maler, L.** (2009b). Receptive field organization across multiple electrosensory maps. II. Computational analysis of the effects of receptive field size on prey localization. *J. Comp. Neurol.* **516**, 394-422.
- Marsat, G. and Maler, L.** (2011). Preparing for the unpredictable: adaptive feedback enhances the response to unexpected communication signals. *J. Neurophysiol.* **107**, 1241-1246.
- Metzner, W.** (1999). Neural circuitry for communication and jamming avoidance in gymnotiform electric fish. *J. Exp. Biol.* **202**, 1365-1375.
- Middleton, J. W., Longtin, A., Benda, J. and Maler, L.** (2006). The cellular basis for parallel neural transmission of a high-frequency stimulus and its low-frequency envelope. *Proc. Natl. Acad. Sci. USA* **103**, 14596-14601.
- Moss, C. F. and Surlykke, A.** (2001). Auditory scene analysis by echolocation in bats. *J. Acoust. Soc. Am.* **110**, 2207-2226.
- Nanjappa, P., Brand, L. and Lannoo, M.** (2000). Swimming patterns associated with foraging in phylogenetically and ecologically diverse American weakly electric teleosts (Gymnotiformes). *Environ. Biol. Fish.* **58**, 97-104.
- Nelson, M. E. and MacIver, M. A.** (1999). Prey capture in the weakly electric fish *Apteronotus albifrons*: sensory acquisition strategies and electrosensory consequences. *J. Exp. Biol.* **202**, 1195-1203.
- Nelson, M. E. and MacIver, M. A.** (2006). Sensory acquisition in active sensing systems. *J. Comp. Physiol. A* **192**, 573-586.
- Nelson, M. E., Xu, Z. and Payne, J. R.** (1997). Characterization and modeling of P-type electrosensory afferent responses to amplitude modulations in a wave-type electric fish. *J. Comp. Physiol. A* **181**, 532-544.
- Oswald, A. M., Chacron, M. J., Doiron, B., Bastian, J. and Maler, L.** (2004). Parallel processing of sensory input by bursts and isolated spikes. *J. Neurosci.* **24**, 4351-4362.
- Penteriani, V., del Mar Delgado, M., Alonso-Alvarez, C. and Sergio, F.** (2007). The importance of visual cues for nocturnal species: eagle owls signal by badge brightness. *Behav. Ecol.* **18**, 143-147.
- Peters, R. C., Loos, W. J. G., Bretschneider, F. and Baretta, A. B.** (1999). Electoreception in catfish: patterns from motion. *Belg. J. Zool.* **129**, 263-268.
- Ramcharitar, J. U., Tan, E. W. and Fortune, E. S.** (2005). Effects of global electrosensory signals on motion processing in the midbrain of *Eigenmannia*. *J. Comp. Physiol. A* **191**, 865-872.
- Robinson, D. and Zee, D.** (1981). Theoretical considerations of the function and circuitry of various rapid eye movements. In *Progress in Oculomotor Research* (ed. A. Fuchs and W. Becker), pp. 3-12. North Holland: Elsevier.
- Rojas, R. and Moller, P.** (2002). Multisensory contributions to the shelter-seeking behavior of a mormyrid fish, *Gnathonemus petersii* Gunther (Mormyridae, Teleostei): the role of vision, and the passive and active electrosenses. *Brain Behav. Evol.* **59**, 211-221.
- Rose, G. J. and Canfield, J. G.** (1993a). Longitudinal tracking responses of the weakly electric fish, *Sternopygus*. *J. Comp. Physiol. A* **171**, 791-798.
- Rose, G. J. and Canfield, J. G.** (1993b). Longitudinal tracking responses of *Eigenmannia* and *Sternopygus*. *J. Comp. Physiol. A* **173**, 698-700.
- Rose, G. J. and Fortune, E. S.** (1999). Frequency-dependent PSP depression contributes to low-pass temporal filtering in *Eigenmannia*. *J. Neurosci.* **19**, 7629-7639.
- Roth, E., Zhuang, K., Stamper, S. A., Fortune, E. S. and Cowan, N. J.** (2011). Stimulus predictability mediates a switch in locomotor smooth pursuit performance for *Eigenmannia virescens*. *J. Exp. Biol.* **214**, 1170-1180.
- Savard, M., Krahe, R. and Chacron, M. J.** (2011). Neural heterogeneities influence envelope and temporal coding at the sensory periphery. *Neuroscience* **172**, 270-284.
- Shadmehr, R., Orban de Xivry, J. J., Xu-Wilson, M. and Shih, T. Y.** (2010). Temporal discounting of reward and the cost of time in motor control. *J. Neurosci.* **30**, 10507-10516.
- Sim, M. and Kim, D.** (2011). Electrolocation based on tail-bending movements in weakly electric fish. *J. Exp. Biol.* **214**, 2443-2450.
- Snyder, J. B., Nelson, M. E., Burdick, J. W. and MacIver, M. A.** (2007). Omnidirectional sensory and motor volumes in electric fish. *PLoS Biol.* **5**, e301.
- Stamper, S. A., Carrera, G. E., Tan, E. W., Fugere, V., Krahe, R. and Fortune, E. S.** (2010). Species differences in group size and electrosensory interference in weakly electric fishes: implications for electrosensory processing. *Behav. Brain Res.* **207**, 368-376.
- Tan, E. W., Nizar, J. M., Carrera, G. E. and Fortune, E. S.** (2005). Electrosensory interference in naturally occurring aggregates of a species of weakly electric fish, *Eigenmannia virescens*. *Behav. Brain Res.* **164**, 83-92.
- Toerring, M. J. and Moller, P.** (1984). Locomotor and electric displays associated with electrolocation during exploratory behavior in mormyrid fish. *Behav. Brain Res.* **12**, 291-306.
- Ulanovsky, N. and Moss, C. F.** (2008). What the bat's voice tells the bat's brain. *Proc. Natl. Acad. Sci. USA* **105**, 8491-8498.
- Wachowiak, M.** (2010). Active sensing in olfaction. In *The Neurobiology of Olfaction* (ed. A. Menini). Boca Raton, FL: CRC Press.
- Yovel, Y., Falk, B., Moss, C. F. and Ulanovsky, N.** (2011). Active control of acoustic field-of-view in a biosonar system. *PLoS Biol.* **9**, e1001150.
- Zupanc, G. K., Sirbulescu, R. F., Nichols, A. and Iles, I.** (2006). Electric interactions through chirping behavior in the weakly electric fish, *Apteronotus leptorhynchus*. *J. Comp. Physiol. A* **192**, 159-173.