

Jörg Oestreich · Harold H. Zakon

## Species-specific differences in sensorimotor adaptation are correlated with differences in social structure

Received: 3 September 2004 / Revised: 23 March 2005 / Accepted: 9 April 2005 / Published online: 9 July 2005  
© Springer-Verlag 2005

**Abstract** Here, we report a species difference in the strength and duration of long-term sensorimotor adaptation in the electromotor output of weakly electric fish. The adaptation is produced by changes in intrinsic excitability in the electromotor pacemaker nucleus; this change is a form of memory that correlates with social structure. A weakly electric fish may be jammed by a similar electric organ discharge (EOD) frequency of another fish and prevents jamming by transiently raising its own emission frequency, a behavior called the jamming avoidance response (JAR). The JAR requires activation of NMDA receptors, and prolonged JAR performance results in long-term frequency elevation (LTFE) of a fish's EOD frequency for many hours after the jamming stimulus. We find that LTFE is stronger in a shoaling species (*Eigenmannia virescens*) with a higher probability of encountering jamming conspecifics, when compared to a solitary species (*Apteronotus leptorhynchus*). Additionally, LTFE persists in *Eigenmannia*, whereas, it decays over 5–9 h in *Apteronotus*.

**Keywords** Jamming avoidance response · Weakly electric fish · Sensorimotor adaptation · Memory · Species difference

**Abbreviations** JAR: Jamming avoidance response · EOD: Electric organ discharge · LTFE: Long-term frequency elevation · LTFD: Long-term frequency depression · PMn: Pacemaker nucleus · SPPn: Sublemniscal prepacemaker nucleus · PPn-G: Thalamic prepacemaker nucleus portion G · NMDA: *N*-methyl-D-aspartic acid · AMPA: alpha-amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid

### Introduction

A central focus of contemporary neuroscience is the study of long-term changes in the CNS underlying behavioral plasticity and memory (Malenka and Nicoll 1999). Despite this, to our knowledge mechanisms governing species differences in the long-term plasticity of behavior have been only described in marine snails of the order Opisthobranchia, where the comparison of homologous behaviors in related species offers the possibility for detection of unique mechanistic changes (Wright 2000). Further, with few exceptions, little is known about how these neurophysiological processes of plasticity vary with ecological or social factors (Bullock 1993; Katz and Harris-Warrick 1999; Wright 2000).

Most research on the cellular mechanisms of memory formation focuses on changes in the efficacy of chemical synapses as the substrate of change. Recently, evidence has been presented that the intrinsic excitability of neurons could also potentially serve as a target for synaptically driven signaling cascades leading to long-term memory (Alkon 1984; Marder et al. 1996; Aizenman and Linden 2000; Zhang and Linden 2003). However, so far these types of changes have not been linked to actual behavioral manifestations of memory formation.

Electric fish produce electric fields around their body by means of specialized organs in their tail (Bennett 1971). Weakly electric fish primarily use their electric organ discharge (EOD) for communication and location of objects in their environment (Hopkins 1988). In wave-type species, the EOD waveform is quasi-sinusoidal. The electrosensory system of each fish is tuned to its own, highly stable EOD frequency (Zakon 1986) and interference with this sensory channel perturbs the animal's ability for orientation (Heiligenberg 1991, 1973; Bastian 1987). Jamming of each other's electrosense happens when two conspecifics with closeby frequencies meet, but one or both of the individuals shift their EOD frequency away from the intruding frequency and, therefore, preserve their sensory capabilities (Watanabe

J. Oestreich (✉) · H. H. Zakon  
Section of Neurobiology, University of Texas at Austin,  
Austin, TX, 78712 USA

Present address: J. Oestreich  
Department of Neurobiology, Harvard Medical School,  
220 Longwood Ave, Boston, MA, 02115 USA

and Takeda 1963; Bullock et al. 1972a; Heiligenberg 1991). This response is called the jamming avoidance response (JAR), and exists in the gymnotid species *Eigenmannia virescens* and *Apteronotus leptorhynchus*.

We have recently identified a novel form of long-term plasticity in *Apteronotus* involving its JAR (Oestreich and Zakon 2002): mimicking the long-term presence of a conspecific with a lower frequency evokes a prolonged upward JAR and leads to an adaptive, long-lasting shift in the basic EOD frequency beyond the duration of the stimulus signal (Long-term frequency elevation LTFE). The frequency relaxes back to baseline over tens of minutes to hours depending on stimulus duration and amplitude. LTFE is an example of sensorimotor adaptation, which is used by the nervous system to fine tune motor responses to long-lasting changes in sensory inflow. A classic example occurs with the manipulation of visual inputs in humans or other animals by outfitting them with prism goggles (Held and Freedman 1963). The offset in the visual input by a constant angle leads to an initial disorientation of the subjects, but, in minutes to tens of minutes, they learn to compensate for it by adjusting their motor program. The adaptation becomes visible as a compensatory overshoot after taking off the prisms.

Structure–function relationships are difficult to describe in many model systems for motor learning (Striedter 1998). However, in weakly electric fish, the circuitry for the JAR is well understood and a clear structure–function relationship exists: a medullary pacemaker nucleus (PMn) controls the EOD frequency by eliciting one EOD for each of its own discharges. Therefore, behavioral modulations of the EOD are a direct reflection of the underlying neuronal changes.

Further, the sensory inputs to the nucleus are well described (Heiligenberg et al. 1996), and a neural correlate for the adaptation exists in a brain slice preparation of the *Apteronotus* PMn (Dye 1988; Dye et al. 1989; Oestreich and Zakon 2002). These experiments showed that LTFE is not maintained by continuing synaptic input, but results from a long-term increase in the firing frequency of the postsynaptic PMn neurons indicating a change in their intrinsic excitability. Moreover, the LTFE mechanism is induced by activation of NMDA receptors (Dye et al. 1989; Oestreich and Zakon 2002; Oestreich, unpublished observation).

In this study, we wanted to know if sensorimotor adaptation in response to long-lasting electrosensory stimulation also exists in *Eigenmannia virescens*.

We found that *Eigenmannia* expresses stronger LTFE than *Apteronotus* in response to stimulation over hours. Moreover, LTFE in *Eigenmannia* is persistent, whereas in *Apteronotus* it does not last longer than 5–9 h (Oestreich and Zakon 2002). We hypothesize that this difference is correlated with differences in the social structure of the animals. *Eigenmannia* is gregarious, and therefore has a higher propensity of being jammed by other group members, than the more solitary *Apteronotus*.

Unlike *Apteronotus*, *Eigenmannia* responds to a higher stimulus frequency with a downward JAR

(Watanabe and Takeda 1963; Bullock et al. 1972a). We also examined whether this JAR activated a reciprocal process of sensorimotor adaptation in form of long-term frequency depression (LTFD).

We observed LTFD, but in contrast to LTFE it only lasts for up to 1.2 h.

---

## Materials and methods

### Animals

Wild-caught *E. virescens* and *A. leptorhynchus* were obtained from Southern Tropical Fish Hatchery, Florida. For the purpose of convenience, we refer to them throughout the paper as *Eigenmannia* and *Apteronotus*. *Eigenmannia* were housed in a large community tank (width = 142 cm, height = 51 cm and depth = 72 cm) together with *Apteronotus*, or separately. *Apteronotus* was additionally housed in a smaller community tank (width = 122 cm, height = 51 cm, depth = 46 cm) in an environmentally controlled room at 26–28°C with circulating water system and 12 h/12 h light–dark cycle. To provide the fish with shelters, both tanks were outfitted with 22 plastic tubes each, which varied in length from 10 cm to 18 cm and from 2 cm to 5 cm in inner diameter. Fish were fed bloodworms, or brine shrimp every 2 days.

*Behavioral testing* was as previously described (Oestreich and Zakon 2002). In short, individual fish were picked from the storage tanks and then transferred to a separate setup tank for testing. There they were placed in an enclosed recording tube, and then allowed to acclimate overnight. The water temperature in the tank was accurately controlled at a few hundreds of a degree Celsius, and air stones aerated the water. In both species, a stable 1 mV/cm strong artificial sign wave signal 3 Hz below the fish's own baseline EOD frequency prior to the stimulation was delivered through a pair of carbon rod electrodes across the fish's body. Additionally, *Eigenmannia* was stimulated with a signal 3 Hz above its EOD frequency. From now on we refer to the stimulus frequency in relation to the EOD frequency as  $-3$  Hz and  $+3$  Hz.

Platinum wire electrodes at the ends of the tube recorded the fish's own EOD signal. Once a sufficient stability of the baseline frequency was observed, fish were presented with an initial 2-min long-stimulus signal, 30 min later then with a long signal of 3 or 6 h. The fish's EOD frequency was analyzed in real time by a computer, and stored for later offline analysis.

### Data analysis

For each group, the frequency traces were aligned along the time axis, so that the starts of the short stimulations were defined as point 0. The frequency for each fish was normalized to its own frequency at this time point and the mean of the frequency change was computed for each group every 10 min starting at 10 h prior to the

stimulation and for a total length of 26 h. Controls were aligned using mean values for the elapsed time between entering the setup arena and the begin of the stimulation in the stimulus groups.

In the text, LTFE persistence is defined as a stable LTFE magnitude for the duration of the experiment.

Unpaired, two-tailed *t* tests were used for statistical comparisons across groups. Within group comparisons were performed by paired, two-tailed *t* tests, e.g., in the case of comparing 2-min data with 3- and 6-h data. The JAR magnitudes for all groups were always significantly different from frequency changes in the control groups over a similar time period ( $P < 0.01$ ). All values are mean  $\pm$  SEM.

## Results

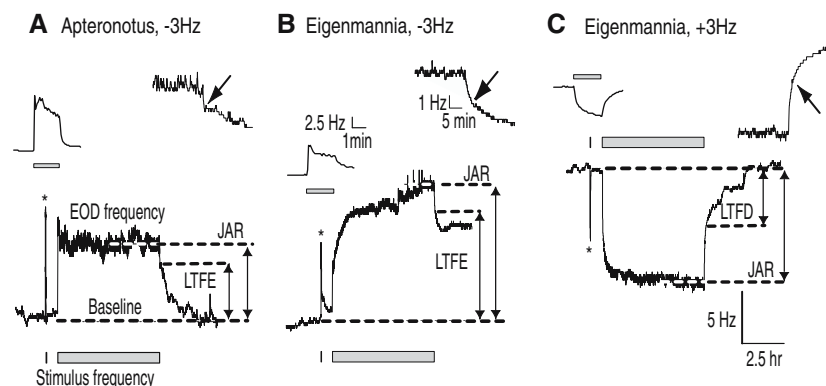
### Stimulus experiments: behavioral plasticity

In order to escape jamming by a stimulus signal slightly below their own EOD frequency both *Apteronotus* and *Eigenmannia* produce a JAR by shifting their EOD frequencies upwards. We tested if a species difference exists in the magnitudes of JAR and LTFE.

### Species differences in sensorimotor adaptation

**JAR magnitude** Each fish was given a 2-min long jamming stimulus ( $-3$  Hz, 1 mV/cm) to obtain a baseline measure of its JAR (Fig. 1a; asterisk, left inset).

**Fig. 1** Example EOD frequency traces of individual 6 h stimulation experiments defining JAR and initial LTFE/LTFD magnitude. Note that after upward JARs in *Apteronotus* the frequency returns to baseline, whereas in *Eigenmannia* LTFE is persistent. After a downward JAR in *Eigenmannia*, sensorimotor adaptation in form of LTFD is visible, but unlike LTFE in *Eigenmannia*, returns gradually to baseline. The left insets magnify the responses to the 2-min stimulations at the location marked by the asterisk. Note that practically no LTFE/LTFD is visible after short JARs. The right insets show a magnification of the EOD frequency trace around the end of the long stimulation highlighting a short, rapid drop in EOD frequency probably caused by a decrease in synaptic input to the PMn. Arrows point to the inflection point in slope, which defines the initial LTFE magnitude



Both species show JARs of similar magnitude ( $P = 0.32$ ; Fig. 2a; black bars) demonstrating that the initial effect of electrosensory jamming is the same in both species.

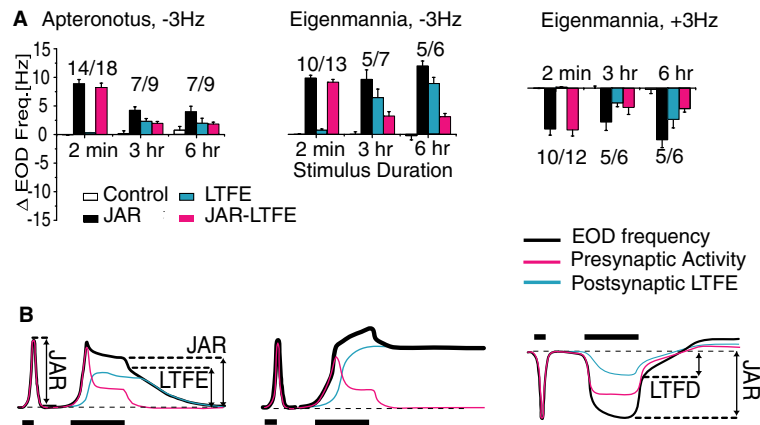
Unlike their responses to brief jamming signals, the JARs each species displays in response to prolonged electrosensory jamming are different from one another. When presented with the same jamming stimulus for 3 or 6 h, mean values for the JAR in the 3-h and the 6-h group are significantly less in *Apteronotus* than in *Eigenmannia* (55% and 54% of JAR in *Eigenmannia*;  $P = 0.0045$  and  $P < 0.0001$ , respectively; Fig. 2a). This is due to an initial decline in the JAR in *Apteronotus* (Oestreich and Zakon 2002; Fig. 3a) and a steady increase of the JAR in *Eigenmannia* (Fig. 3b).

The JAR magnitude in *Apteronotus* significantly declines by  $6.7 \pm 0.6$  Hz in the 3-h group ( $P = 0.0006$ ), and by  $6.8 \pm 0.8$  Hz in the 6-h group ( $P = 0.0008$ ; in both groups measured from 5 min after stimulus onset to offset). These values are not significantly different from each other, because the decline stabilizes by 3 h of jamming ( $P = 0.96$ ).

In contrast to *Apteronotus*, the JAR in *Eigenmannia* progressively increases in response to prolonged stimulation (3 h:  $4.3 \pm 0.9$  Hz,  $P = 0.002$ ; 6 h:  $8.4 \pm 1$  Hz;  $P = 0.0004$ ; comparing 3–6 h:  $P = 0.009$ ; measured as in *Apteronotus*). This suggests that the JAR in *Eigenmannia* is capable of increasing further with an even longer stimulus.

**LTFE magnitude** After the jamming stimulation ceases, sensorimotor adaptation (LTFE) is revealed as a lasting elevation in the EOD frequency. Right after the end of the stimulation, both species show an initial rapid drop in the EOD frequency, which is likely caused by a decrease in the synaptic input to the PMn. Shortly after, the frequency reaches a more stable value (Fig. 1a; right insets at arrow), which was used to define the initial LTFE magnitude (Oestreich and Zakon 2002).

Neither species shows appreciable LTFE following only 2 min of jamming in comparison to the much larger response to the long stimulus trials, although a small, but significant frequency increase in *Eigenmannia* in comparison to baseline changes in controls over a similar period is noticeable (*Apteronotus*:  $P = 0.09$ ; *Eigen-*



**Fig. 2 a** Summary data for JAR and LTFE in response to various stimulus durations. Note that for the upward JAR in *Aptereronotus* and *Eigenmannia*, synaptic activity (JAR–LTFE) is equal during 2 min and after the long stimulations in both species, whereas, LTFE is smaller in *Aptereronotus* than in *Eigenmannia* after long stimulations. Further note, that LTFD after 2 min stimulations is practically nonexistent, as it was the case with upward JARs. Data for the 2 min stimulation from different stimulus groups were pooled, because they are not significantly different ( $P > 0.05$ ; numbers reflect ns for control fish and stimulated fish; experiments are in different fish). **b** Model of how much presynaptic activity and postsynaptic LTFE contribute to the EOD frequency elevation during the JAR (not drawn to scale). Note that presynaptic activity (JAR–LTFE) is responsible for maintaining the JAR during short stimulations and the beginning phase of the long stimulation, whereas, the JAR in the late phase is mainly due to postsynaptic LTFE. In both species synaptic activity in both phases is of equal strength. In *Eigenmannia*, LTFE persists. A downward JAR is caused by a decrease in synaptic activity, which induces LTFD (see Discussion)

*mannia*:  $P = 0.01$ , respectively; Figs. 1a and 2a, blue bars). This indicates that LTFE is sensitive to stimulus duration.

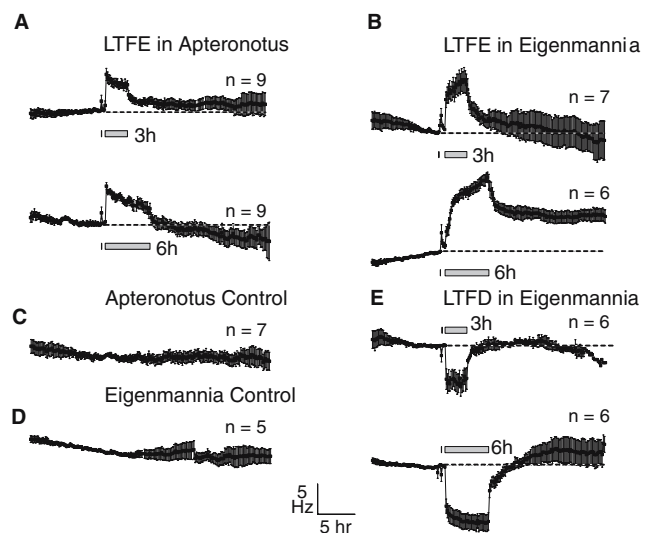
LTFE is present in *Aptereronotus* after 3 h and after 6 h of jamming (3 h:  $P = 0.0048$ , 6 h:  $P = 0.02$ ; Fig. 3a), but no further increase in LTFE magnitude is achieved with the 6-h stimulation ( $P = 0.74$ ; Fig. 2a). Similarly, mean LTFE magnitudes in *Eigenmannia* after 3- and 6-h stimulations are in both cases significantly different from controls (3 h:  $P = 0.0057$ , 6 h:  $P < 0.0001$ ), but not from each other ( $P = 0.22$ ; Fig. 2a).

LTFE after 3- and 6-h stimulations in *Aptereronotus* is only 36% and 22% of LTFE in *Eigenmannia* ( $P = 0.01$  and  $P = 0.0003$ , respectively; Fig. 2a), supporting our hypothesis that *Eigenmannia* shows stronger sensorimotor adaptation than *Aptereronotus*.

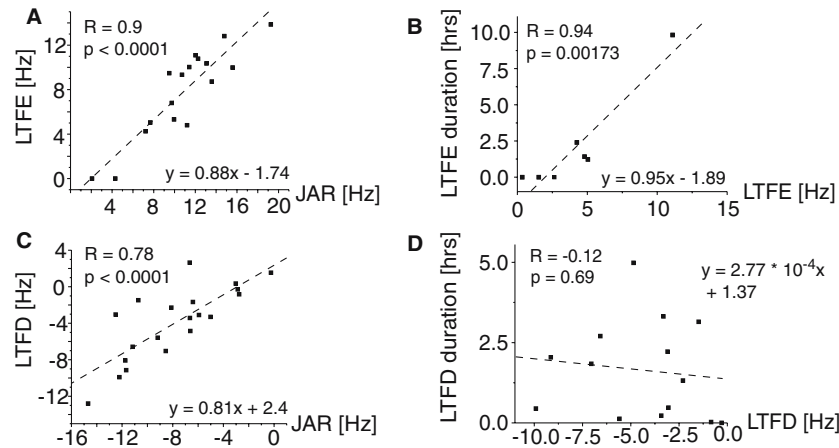
**Estimation of synaptic input to the PMn** The JAR is controlled by synaptic input from pacemaker nuclei to the PMn, which are in turn activated by descending sensory input (for details see Discussion, Fig. 6). Prolonged synaptic activity over time induces LTFE in the PMn (Oestreich and Zakon 2002). Therefore, the JAR is the sum of the contributions of synaptic drive and the gradual postsynaptic buildup of LTFE in the PMn. Each PMn cycle gives rise to one EOD cycle. Thus, the

EOD frequency is a direct readout of the PMn frequency. This fact allows us to estimate the strength of the synaptic drive to the PMn, by subtracting the LTFE from the JAR magnitude (JAR–LTFE).

During the short 2-min JAR or the initial phase of the long JAR, LTFE has not been activated yet and the JAR is exclusively caused by synaptic drive of the PMn (Fig. 2a, b; red bars and line). The JAR and, therefore,



**Fig. 3** Behavioral long-term plasticity in the mean EOD frequency (LTFE) of *Aptereronotus* and *Eigenmannia* after a jamming avoidance response. **a** LTFE in *Aptereronotus* after a 3- and 6-h long stimulus signal. Note that LTFE is visible in the 3 h, but hardly in the 6 h group. Further note that JAR and LTFE is weaker than in *Eigenmannia* and that the EOD frequency during the initial JAR progressively relaxes to a lower, but later stable value (**b**). **b** LTFE in *Eigenmannia* after 3- and 6-h stimulations. The JAR in *Eigenmannia* increases over time in both situations and LTFE becomes persistent after 6 h, but not after 3 h. **c + d**. Control traces of nonstimulated fish for *Aptereronotus* (**c**) and *Eigenmannia* (**d**) documenting baseline frequency stability. **e** LTFD in *Eigenmannia*. Presenting a stable stimulus signal at +3 Hz leads to a downward JAR, and after stimulation a depression in the EOD frequency is revealed, from which the frequency gradually relaxes back to baseline. Long stippled lines indicate baseline frequency, gray bars stimulation, all traces are mean EOD frequency values every 10 min with error bars reflecting SEM. All experiments are in different fish



**Fig. 4** Correlations between JAR and LTFE/LTFD, and LTFE/LTFD and its duration in *Eigenmannia* for pooled data from different fish with nonpersistent LTFE in response to 3- and 6-h stimulations. LTFE is linearly correlated with JAR magnitude (compare equation to  $y = 0.94x - 1.77$  in *Apteronotus* (Oestreich and Zakon 2002) (a), and LTFE duration also shows a linear relationship with its magnitude (b). The same relationships were described for *Apteronotus* (Oestreich and Zakon 2002). While LTFD also correlates with its JAR (c), in contrast to LTFE, LTFD duration is not connected to LTFD magnitude (d)

synaptic input strength is the same in both species after these short stimulations ( $P = 0.4$ ).

With longer jamming stimuli, LTFE is gradually induced in the PMn and contributes to the JAR (Fig. 2b, blue line). In *Apteronotus*, 54% and 49% of the JAR magnitude is due to LTFE after 3- and 6-h stimulations, respectively, whereas in *Eigenmannia*, LTFE contributes 67% and 74% to the JAR (Fig. 2a). The strong contribution of LTFE to the JAR in the later phase of the stimulation is also reflected in the linear relationship between initial LTFE magnitude after stimulus termination and the JAR magnitude in the end phase of the long stimulation in *Eigenmannia* (pooled data from 3-h to 6-h stimulations;  $r = 0.9$ ,  $P < 0.0001$ ; Fig. 4a). We previously described the same relationship in *Apteronotus* (Oestreich and Zakon 2002). As in *Apteronotus*, a minimum JAR is necessary in *Eigenmannia* to obtain LTFE, indicated by the fact that the linear fit does not intercept at the origin of the graph, but at 2 Hz (Fig. 4a). This value compares to 1.9 Hz in *Apteronotus* (Oestreich and Zakon 2002).

The contribution of the synaptic input to the JAR in *Apteronotus* or *Eigenmannia* does not significantly change after 3 h of jamming, when comparing 3- and 6-h groups (*Apteronotus*:  $P = 0.8$ ; *Eigenmannia*:  $P = 0.9$ ), and synaptic input strength is also roughly the same between both species (3 h:  $P = 0.1$ ; 6 h:  $P = 0.06$ ; Fig. 2a). Thus, the difference between the JAR responses of *Eigenmannia* and *Apteronotus* appears to be due to the differences in LTFE, not changes in synaptic input strength.

In summary, synaptic input strength to the PMn of *Apteronotus* and *Eigenmannia* appears similar in several features: magnitude, its contribution to the JAR, and

minimum amount needed to activate LTFE. Together these findings suggest that the stronger sensorimotor adaptation in *Eigenmannia* over *Apteronotus* is not likely due to the differences in synaptic input strength to the PMn.

**LTFE Duration** In *Apteronotus*, a 3-h long stimulation results in a slight elevation of the EOD frequency above baseline, lasting on average for 5 h ( $n = 9$ ; Fig. 3a) before it is no longer significantly different from the mean frequency change in controls at that time point ( $P = 0.07$ ). A 6-h long stimulation leads to a change, which only lasts for 0.3 h ( $P = 0.08$ ). In addition, in some fish after stimulus termination, the EOD frequency declines below baseline, resulting in a slight overall decline of the mean EOD frequency change below baseline for the group (Fig. 3a), which is however, not significantly different from controls. Similar to *Apteronotus*, a 3-h stimulation in *Eigenmannia* on average produces non-persistent LTFE, lasting 2 h ( $P = 0.07$ ; Fig. 3b). However, three of seven fish in this group responded with persistent LTFE suggesting that a 3-h stimulus period is close to the temporal threshold for eliciting persistent LTFE. Previously, we described in *Apteronotus* that the duration of LTFE after 0.5 and 3 h stimulation correlates positively with LTFE magnitude (Oestreich and Zakon 2002). To increase the number of data points and the range of LTFE magnitudes for a similar analysis, the *Eigenmannia* with nonpersistent LTFE in the 3-h group ( $n = 4$ ) were pooled with all available individuals outside of their group, which also responded to stimulation with nonpersistent LTFE. Two of these other fish were stimulated with a +3-Hz stimulus at 1 mV, which resulted in an erroneous positive JAR followed by low LTFE, and one stimulated at 15 mV/cm and -3 Hz, resulting in a regular JAR followed by high LTFE. Like in *Apteronotus*, for these fish, LTFE duration also correlates positively with LTFE magnitude ( $r = 0.94$ ,  $P = 0.00173$ ; Fig. 4b)

In *Eigenmannia*, with the 6-h long stimulation a persistent change in poststimulus EOD frequency can be achieved in all tested individuals ( $n = 6$ ), lasting longer than 16 h ( $P = 0.01$ ; Fig. 3b).

**Fig. 5** Social structure of *Eigenmannia virescens* and *Apteronotus leptorhynchus* in tanks. **a** A shoal of *Eigenmannia* during the day. **b** The same group at night. Fish are distributed over the entire extent of the tank. **c + d** *Apteronotus* during the day. All fish are hiding in plastic tubes (**d**). **e** Seconds after night fall, *Apteronotus* leave their tube and move around independently. **f + g** 'Predator avoidance' behavior in *Eigenmannia*. Before tapping the tank wall the shoal is more dispersed (**f**). After tapping the fish aggregate densely at the bottom of the tank (**g**). This demonstrates that *Eigenmannia* act together as a group. Night images were taken by flash photography, which did not seem to disturb the fish



In summary, these results lend further support to our hypothesis that sensorimotor adaptation is more strongly developed in *Eigenmannia* than in *Apteronotus*. Not only is LTFE of higher magnitude, but, in addition, a longer lasting change is achieved independently from the initial LTFE magnitude.

#### *Long-term frequency depression in Eigenmannia*

It is well known that *Apteronotus* cannot reduce its EOD frequency below the baseline level in response to stimulus frequencies above its EOD frequency (Watanabe and Takeda 1963; Bullock et al. 1972a; Heiligenberg et al. 1996). In contrast, *Eigenmannia* are capable of lowering their EOD frequencies in response to higher stimulus frequencies (Watanabe and Takeda 1963; Bullock et al. 1972a; Heiligenberg et al. 1996). The reasons for this difference are located in the different neural circuits for the electromotor system in both species (Heiligenberg et al. 1996) (see Discussion; Fig. 6).

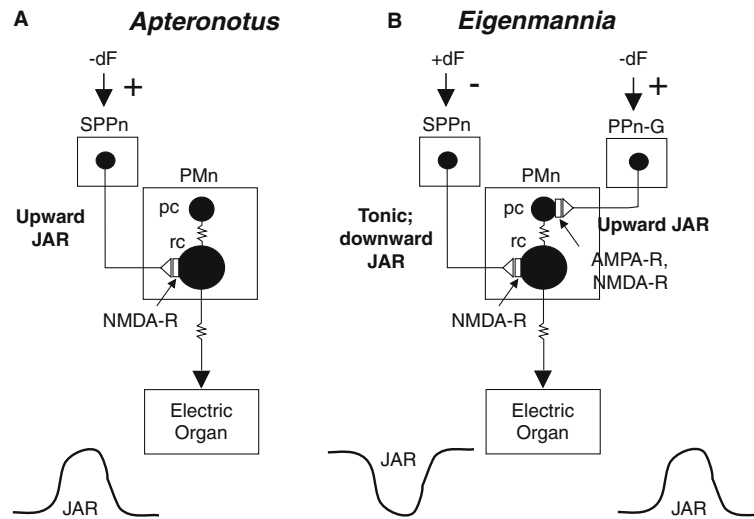
Presenting *Eigenmannia* with a 2-min long stimulus signal +3 Hz at 1 mV/cm causes a JAR, in which the fish reduces its EOD frequency (Fig. 1a). Similar to 2-min stimulus presentations at -3 Hz, 2-min presen-

tations at +3 Hz also do not lead to sensorimotor adaptation ( $P=0.29$ ; Fig. 2a). The downward JAR elicited during the long periods of electrosensory jamming progressively increases in magnitude until a stable frequency below baseline is achieved. This is especially noticeable in the 6-h stimulated group (Fig. 3e).

In both cases after stimulus termination, the frequency initially remains lower than the baseline frequency prior to stimulation (compared to baseline changes in controls; 3 h:  $P=0.02$ ; 6 h:  $P=0.02$ ; Fig. 3e). This LTFD of the EOD is shorter in duration than LTFE. LTFD remains below baseline until 0.5 h after a 3-h downward JAR ( $P=0.15$ ) and until 1.2 h after a 6-h downward JAR ( $P=0.13$ ). In comparison, LTFE lasts 2 h after 3 h of upward JAR and LTFE persists after 6 h of upward JAR. After a 6-h downward JAR, the EOD frequency slightly overshoots above the original baseline frequency by about 2.5 Hz (Fig. 3e), a change not significantly different from the control group.

The JAR magnitude is not significantly larger after 3 h of jamming than with 2 min stimulations within groups, but is significantly larger with 6 h of jamming (3 h:  $P=0.1$ ; 6 h:  $P=0.01$ ; Fig. 2a).

As it was the case with upward JAR and resulting LTFE, downward JAR and LTFD magnitudes are not



**Fig. 6** Neural circuitry of the electromotor system in *Aptereronotus* and *Eigenmannia* (Heiligenberg et al. 1996; Juranek and Metzner 1997). **a** In *Aptereronotus*, an upward JAR is activated by the presence of a stimulus signal with negative difference frequency ( $-dF$ ) via the SPPn and NMDA receptor activation on rcs in the PMn. This in turn drives the electric organ to fire faster. **b** In *Eigenmannia*, a  $-dF$  signal activates the PPn-G, which forms AMPA-R and NMDA-R carrying synapses with pcs in the PMn and the resulting PMn frequency acceleration drives the electric organ to fire faster. In contrast, a  $+dF$  signal inhibits the SPPn, which otherwise provides tonic input to the PMn via NMDA-R onto rcs. This will cause a downward JAR.  $-dF$ ,  $+dF$  stimulus frequency below or above EOD frequency, SPPn sublemniscal prepacemaker nucleus, PPn-G thalamic prepacemaker nucleus portion G, PMn pacemaker nucleus, pc pacemaker cell, rc relay cell

significantly increased after 3 h of stimulation (comparing 3- and 6-h group:  $P=0.15$  and  $P=0.11$ , respectively; Fig. 1b). LTFD after a downward JAR also correlates with JAR magnitude ( $r=0.78$ ,  $P<0.0001$ ; Fig. 4c). A minimum downward JAR of  $-3$  Hz is necessary for LTFD activation ( $r=0.78$ ,  $P<0.0001$ ). However, unlike LTFE, the duration of LTFD did not correlate with the magnitude of the LTFD, suggesting that a different mechanism may be involved ( $r=0.12$ ,  $P=0.69$ ; Fig. 4d).

#### Behavioral observations in the community tank: social structure

Weakly electric fish are nocturnally active and hide by day to avoid predators. At nightfall fish leave their cover and disperse (Lissmann 1961; Steinbach 1970; Kramer et al. 1981; Crampton 1998). Field observations indicate that *Eigenmannia* is gregarious (Lissmann 1961; Hagedorn and Heiligenberg 1985; Westby 1988; Taphorn, personal communication; Alves-Gomes, personal communication; Zakon, unpublished observation). In contrast, *Aptereronotus* is more solitary, living in loosely associated groups in rocky environments or along river banks, and tending to be bottom dwellers, and hiding in shelters (Schwassmann 1978; Hagedorn and Heiligenberg 1985; Taphorn, personal

communication; Alves-Gomes, personal communication). We hypothesized that differences in the social structure of both species might be responsible for the observed species-specific difference in long-term plasticity.

Being in a much larger group could increase the chance for an individual *Eigenmannia* to experience electrosensory jamming by increasing the likelihood to encounter another conspecific in the group with similar EOD frequency. Our hypothesis is that an *Eigenmannia* could avoid prolonged and repeated jamming from overlap with other group member's EOD frequencies by long-term adjustment of its own EOD frequency.

In an initial attempt, to characterize the social structure of the animals and to link it to differences in behavioral long-term plasticity, we wanted to confirm the sporadic field observations cited in the preceding paragraph. We followed groups of 80 *Eigenmannia* and roughly the same number of *Aptereronotus* together or in separate tanks in the lab. The observed behavior, as described as follows, was stereotypical in both species, whether or not both species were kept together. During the light hours, most of the *Eigenmannia* are aggregated together close to one of the smaller walls of the tank (Fig. 5a). Field observations also hint that in streams *Eigenmannia* often hides at the banks (Lissmann 1961; Crampton 1998). Only a few *Eigenmannia* actually use the provided plastic tubes, even when many tubes were available. In contrast, *Aptereronotus* readily hide in tubes (Fig. 5c, d; Dunlap and Oliveri 2002).

At the onset of darkness, the *Eigenmannia* shoal disperses and individuals move out over the entire extent of the tank (Fig. 5b). *Aptereronotus* leave their tubes (Fig. 5e). At onset of the light cycle, *Eigenmannia* again forms a shoal within a few minutes of lights on, and *Aptereronotus* return to their tubes. This behavior in *Eigenmannia* is also supported by field observations (Lissmann 1961).

That *Eigenmannia* behave as a group can also be demonstrated by evoking a typical predator avoidance behavior: if the tank wall is tapped, *Eigenmannia* do not

disperse randomly, but behave in a coordinated fashion by coalescing in a more compact group, which settles toward the bottom of the tank (Fig. 5f, g). This type of behavior can also be observed in other shoaling fish (Pitcher and Parrish 1993).

In summary, during the day *Eigenmannia* tend to be more closely spaced than *Apteronotus*, therefore potentially increasing the likelihood for an individual of *Eigenmannia* to experience electrosensory jamming.

## Discussion

Here, we report that *Eigenmannia*, like *Apteronotus* responds with long-term sensorimotor adaptation (LTFE in the EOD frequency) to a long-term stimulus signal. In *Eigenmannia*, LTFE in response to a 6-h long stimulus below the fish's own EOD frequency lasts much longer than in *Apteronotus*.

This result correlates with differences in the animal's social structure: *Eigenmannia* is a shoal-forming species, whereas, *Apteronotus* is not. Therefore, the probability that an individual *Eigenmannia* in its shoal is exposed to electrosensory jamming by a group member is greater than in *Apteronotus*. Such persistent shifts in EOD frequency may be used to avoid repeated jamming. *Eigenmannia* also shows sensorimotor adaptation in the opposite direction to stimulation above its own EOD frequency (LTFD), though it does not last as long as LTFE.

Differences in specific features of sensorimotor adaptation imply specific changes in neural mechanisms

Our findings demonstrate that three distinct processes lead to the expression of sensorimotor adaptation in the EOD frequency: the synaptic drive of the PMn, the coupling of synaptic input to the postsynaptic LTFE mechanism, which sets the LTFE magnitude, and regulation of LTFE duration. While there are no differences in the first process, the last two processes are different between *Eigenmannia* and *Apteronotus*.

First, in both species the amount of synaptic drive received by the PMn is similar (Fig. 2a). Further, in both species a minimum JAR of around 2 Hz is required for induction of LTFE, indicating a similar requirement for activating LTFE.

However, the second process, the coupling of synaptic input with the LTFE mechanism is stronger in *Eigenmannia*, suggested by the fact that the LTFE magnitude is twofold higher in *Eigenmannia*. The stronger coupling results in a progressive increase in the EOD frequency during the JAR in *Eigenmannia*, caused by a stronger increase in LTFE in the PMn (Heiligenberg et al. 1996; Oestreich and Zakon 2002).

Third, LTFE lasts much longer in *Eigenmannia*. In *Apteronotus*, LTFE duration is linearly correlated with

LTFE magnitude. In *Eigenmannia*, this is only true for fish with nonpersistent LTFE in the group stimulated at  $-3$  Hz for 3 h. In this group, a 5-Hz increase in LTFE would increase LTFE duration by 2.9 h, which compares to 3.2 h in *Apteronotus* (Oestreich and Zakon 2002), suggesting that the same mechanism for nonpersistent LTFE is in place in both species. With 6-h long stimuli, a lasting upward shift in EOD frequency in *Eigenmannia* can be evoked, whereas in *Apteronotus*, LTFE duration actually decreases with 6-h stimulations. This finding suggests that an additional mechanism exists in *Eigenmannia*, one that is not found in *Apteronotus*. The argument could be made that *Apteronotus* also possess such a mechanism, but that it is not activated because of the weaker LTFE magnitude in the later phase of the stimulation. This would imply that with stronger LTFE, its persistence could also be achieved in *Apteronotus*. However, even though 100 mV/cm stimuli evoke *Eigenmannia*-like JAR and LTFE magnitudes in *Apteronotus*, the EOD frequency in *Apteronotus* still declines back to baseline within 9 h (Oestreich and Zakon 2002). This finding suggests that LTFE duration is only linearly correlated with LTFE amplitude for fish with nonpersistent LTFE, as it is the case in *Apteronotus*, but that LTFE persistence is the result of a mechanism unique to *Eigenmannia* and this mechanism on average requires stimulus durations in excess of 3 h to be activated.

Neural mechanisms for sensorimotor adaptation in the brain

The neural circuitry underlying the JAR in *Apteronotus* and *Eigenmannia* is well described (Heiligenberg 1991; Heiligenberg et al. 1996; Juranek and Metzner 1997)(Fig. 6). A medullary pacemaker nucleus (PMn) controls the EOD frequency in one-for-one fashion by connecting electrotonically to electromotor neurons in the tail region of the fish. The PMn in turn receives input from an upstream nucleus, the sublemniscal prepacemaker nucleus (SPPn), which controls the upward JAR in *Apteronotus*. This nucleus is normally quiescent in *Apteronotus*, but is activated by electrosensory input during a jamming signal, and then increases the PMn frequency. Subsequently, the increase in PMn firing frequency will be relayed to the electromotor neurons and with that the EOD frequency will be raised accordingly.

The neural circuitry for the control of the JAR in *Eigenmannia* is different. Unlike in *Apteronotus*, the SPPn in *Eigenmannia* is tonically active and does not underlie the upward JAR. Instead, activation of a subportion of the thalamic prepacemaker nucleus (PPn-G) produces the upward JAR.

In *Apteronotus*, a neural correlate for the JAR exists in a brain slice preparation and LTFE is expressed in the PMn (Oestreich and Zakon 2002) as an increase in intrinsic neuronal excitability. There is no slice prepa-

ration of the *Eigenmannia* PMn yet, but it is likely that LTFE in *Eigenmannia* also resides in the PMn.

In both species, the PMn contains two electrotonically coupled cell types, pacemaker and relay cells. The relay cells project to the electromotor neurons in the spinal cord. The SPPn in *Apteronotus* and in *Eigenmannia* forms NMDA receptor-dependent synapses with relay cells in the PMn, whereas, afferent input from the PPn-G in *Eigenmannia* is received by pacemaker cells and mainly mediated by AMPA receptors, but NMDA receptors also contribute (Juranek and Metzner 1997). It is tempting to speculate that the stronger coupling of synaptic input to the LTFE mechanism in *Eigenmannia* is caused by the synaptic input onto pacemaker instead of relay cells. Further, long-lasting LTFE in *Eigenmannia* could be the result of a signaling cascade, either unique to *Eigenmannia*, or present in both species, but coactivation of NMDA and AMPA receptors onto pacemaker cells would lead to its activation only in *Eigenmannia*. Alternatively, lower JAR and LTFE magnitude in *Apteronotus* following 6 h of stimulation could be the result of the activation of an inhibitory signaling cascade. This mechanism then could explain why the average EOD frequency after stimulation (Fig. 3a) undershoots the resting EOD frequency prior to stimulation.

#### A mechanistic reason for postsynaptic adaptation

The nervous system like most biological structures and systems is plastic and adaptation to persistent changes in sensory input is a known feature of the nervous system leading to rapid changes in activity patterns (Held and Freedman 1963; Lisberger 1988; Houde and Jordan 1998), or even structural changes (Donoghue 1995; Schlaug 2001; Knudsen 2002; Butefisch 2004). Therefore, it is not altogether surprising that both species adapt to prolonged jamming.

We do not yet know what the mechanistic reason behind the adaptation might be. For example, an alternative to adaptation in the PMn would be to maintain the EOD frequency increase during the JAR by continuing synaptic input to the PMn. Instead, LTFE is induced in the PMn and is responsible for much of the JAR magnitude in the latter phase of a prolonged JAR. However, one possible mechanistic reason for a long-lasting, postsynaptic adaptation rather than continuing presynaptic input could be the avoidance of excitotoxic effects by prolonged NMDA receptor activation (Choi 1988; Rothman and Olney 1995; Oestreich and Zakon 2002).

#### LTFE is a form of nonassociative memory

LTFE is essentially the expression of a relatively long-lasting memory ranging from minutes to at least tens of hours, and this memory underlies sensorimotor adaptation in the electromotor system.

“Nonassociative learning results when an animal is exposed once or repeatedly to a single type of stimulus”, whereas “in associative learning an organism learns about the relationship of one stimulus to another” (Kandel et al. 2000). Examples for nonassociative memory formation are habituation and sensitization in the gill withdrawal reflex of the marine mollusk *Aplysia*. LTFE is categorically similar to these forms of nonassociative plasticity, because it can be evoked by a specific quality of a single modality stimulus, i.e., a pure sine wave within a few Hertz of the fish’s own EOD frequency (Oestreich and Zakon 2002). As it is the case with associative forms of synaptic plasticity such as LTP, NMDA receptors are also potentially involved in mediating LTFE (Dye et al. 1989; Oestreich, unpublished observation). However, in the PMn, they do not lead to the associative strengthening of two or more simultaneously active synapses, as has been proposed in the LTP model (Bliss and Collingridge 1993), but rather induce a long-lasting change in postsynaptic spike frequency via changes in intrinsic excitability (Oestreich and Zakon 2002).

Besides in the brainstem of weakly electric fish, nonassociative plasticity could potentially be abundant in the reflex pathways of other vertebrates as well, as suggested by Squire (Squire and Zola 1996).

#### LTFD in *Eigenmannia*

In contrast to *Apteronotus*, the SPPn in *Eigenmannia* provides tonic input to relay cells in the PMn via NMDA receptors and is inhibited by positive stimulus frequencies, which then leads to a lowering of the PMn frequency (Juranek and Metzner 1997). Therefore, *Eigenmannia* can respond to stimulus frequencies above its own EOD frequency with a downward JAR, whereas *Apteronotus* is incapable of doing so (Watanabe and Takeda 1963; Bullock et al. 1972a; Heiligenberg et al. 1996). Instead, *Apteronotus* sometimes will respond with an upward JAR by either moving its EOD frequency closer to the higher stimulus frequency or surpassing it (Dye 1988; Heiligenberg et al. 1996; Oestreich, unpublished observations). This so-called ‘Nonspecific Response’ (Dye 1988) is also followed by LTFE if evoked by prolonged stimulation (Oestreich, unpublished observations).

Here, we demonstrate that a long-term downward JAR in *Eigenmannia* also leads to sensorimotor adaptation (LTFD), but it is not as long-lasting as sensorimotor adaptation after an upward JAR.

The downward JAR occurs, because tonic input to the PMn via NMDA receptors from the SPPn is removed. This input presumably kept nonpersistent LTFE at a certain level. Thus, the ongoing decline in EOD frequency during the initial phase of the downward JAR is due to the decay of LTFE from the absence of the SPPn input. Once the higher frequency-jamming signal is removed, the SPPn becomes active again and provides

NMDA receptor—dependent input to the PMn, returning the PMn frequency and thus, the EOD frequency to baseline. The increase in PMn frequency then is comprised of two active processes: synaptic input from the SPPn and the reintroduction of LTFE in the PMn, both of which determine the duration of LTFD. In contrast, the duration of LTFE appears to be due to a passive process, a wearing off of whatever molecular change has taken place in the cells of the PMn with the formation of LTFE.

Passive decay of this nature would cause the LTFE duration to correlate with its original magnitude, as is the case in LTFE. Therefore, the fact that there is no correlation between LTFD magnitude and its duration is not altogether surprising. An adjustment error then could account for the fact that only a gradual increase in EOD frequency back to baseline can be observed, instead of an immediate return to baseline caused by excitatory drive of the PMn.

That even a 6-h long downward JAR fails to show a persistent sensorimotor adaptation has implications as to which mechanism *Eigenmannia* uses to alter its EOD frequency for prolonged periods. Based on these data, it is reasonable to speculate that if an individual *Eigenmannia* needs to persistently change its frequency in a group it would have to use the upward JAR. Thus, to activate this long-term memory, input over AMPA and NMDA receptors must come from the PPN-G, and not the SPPn.

#### Differences in behavioral long-term plasticity correlate with differences in social structure

Traditionally, the JAR of weakly electric fish has been described from a mechanistic point of view. However, unfortunately little is known about weakly electric fish ecology and intra- and interspecific interactions of these fish in their natural habitat. We provide here one of the first attempts of relating physiological differences to the ecological niche the animals live in, and a potential explanation for the differences in long-term plasticity observed by us.

Electric fish are nocturnally active and move about while they forage or interact socially (Lissmann 1961; Hagedorn and Heiligenberg 1985; Crampton 1998). During the day, they hide (Lissmann 1961; Kramer et al. 1981). In the wild, *Apteronotus* are solitary or associate in small groups in vegetation (Schwassmann 1978; Hagedorn and Heiligenberg 1985; Taphorn, personal communication; Alves-Gomes, personal communication; Zakon, unpublished observation). In contrast, *Eigenmannia* are often found in large numbers in shoals (Lissmann 1961; Westby 1988; Taphorn, personal communication; Alves-Gomes, personal communication; Zakon, unpublished observation).

Our laboratory observations confirmed these field reports. In the tank, the differences in shoal-forming versus nonshoal-forming behavior are easily observed.

Weakly electric fish rely on their electrosensory system for orientation in their environment and the locating of food. In order to use their electrosensory capabilities, they need to have a private sensory channel. One possible solution to escape jamming is to simply swim away from other individuals with similar EOD frequency, because electric field strength falls off with the cube of the distance from its source (Knudsen 1975). However, leaving the safety of the shoal, or a shelter during the day could come with the cost of predation. Therefore, our hypothesis is that fish instead adjust their EOD frequency to avoid jamming, and therefore will produce a JAR if a conspecific with a close frequency is encountered (Heiligenberg 1991).

Knudsen estimated that *Eigenmannia* are still able to sense each other's EOD up to at least 1.4 m away (Knudsen 1975). The extent of shoals of *Eigenmannia* we observed in the laboratory is much less than that (often roughly 30–40 cm for a group of 80 fish in a 142-cm tank) suggesting that two or more fish with similar EOD frequencies at the opposite, outer perimeters of the shoal should still respond to each other's EODs with a JAR. Bullock demonstrated that *Eigenmannia* indeed still performs a JAR to weak jamming signals 1/1,000 the strength of its own EOD (Bullock et al. 1972a; b). Further, the probability of encountering a jamming neighbor should increase with larger group size and density in gregarious species.

We found that the difference in social structure between *Eigenmannia* and *Apteronotus* is matched by the longer LTFE duration in *Eigenmannia*. That LTFE remained stable for at least 16 h after an upward JAR in response to the 6 h long stimulus presentation suggests that sensory input in form of a conspecific with a close frequency leads to a persistent readjustment of the EOD frequency in *Eigenmannia*.

In support of the idea, that *Eigenmannia* responds with stronger adaptation to the presence of a frequency intruding into its sensory space, populations of *Eigenmannia* show a larger variation in EOD base frequencies than other nongregarious species (Lissmann 1961; Kramer et al. 1981), which is expected if a substantial number of fish in the population have to adjust their EOD frequency to avoid jamming by other group members. In detail, Lissmann notes: "It would be tempting to suggest that the great variation of frequencies found in individuals of gregarious species has developed so that each fish can receive sensory information on its own frequency range without interference from its neighbors." Though, he further says: "Since these fish are dispersed at night during the active phase of their life this problem of mutual interference may perhaps be more apparent than real." (Lissmann 1961). However, as mentioned above, Lissmann also reported that the shoal of *Eigenmannia* he had observed would return to the same hiding place at the end of each night (Lissmann 1961). Thus, another important factor for sensorimotor adaptation is territoriality and this could explain the paradox raised by Lissmann. If the same fish

come back to a particular hiding place, interference between fish of similar frequency would occur again. By activating LTFE fish could adjust their EOD frequencies according to the presence of interfering signals. LTFE in *Eigenmannia* lasts long enough to span the night and fish would still be at their personal EOD frequency. Therefore, perhaps LTFE could be the mechanism, which explains the greater variability of EOD frequencies in gregarious species over more solitary species and longer-term adjustments in EOD frequency in response to prolonged jamming then may be useful in cases, in which there is a high probability of future jamming from the same neighbors.

Based on our and previous observations (Lissmann 1961; Kramer et al. 1981), we propose that fish in a shoal will be jammed by multiple neighbors, either sequentially or simultaneously, that they optimize EOD differences to avoid jamming as much as possible from their nearest neighbors, and that LTFE essentially solidifies the jamming-induced change in each fish's EOD frequency so that when the school reconvenes each morning, a fish will seek out its previous neighbors and automatically be in a situation with minimal jamming.

We have not yet directly tested our hypothesis in large groups of newly introduced *Eigenmannia* in the laboratory or in studies of the group dynamics of the fish in their natural habitat. However, in support of our hypothesis, it has been reported that in small groups of *Eigenmannia* individuals maintain unique EOD frequencies and do not cross each other's EOD frequency, but maintain relative frequency positions to each other (Gaddis 1977; Fortune et al. 2003). In addition, if *Eigenmannia* are kept in isolation, the total range and variance of their EOD frequencies is less than if they are kept in under social conditions (Keeley 1995). Moreover, our observation of LTFE in *Eigenmannia* has recently been verified by another group in laboratory studies, which resulted in large frequency changes in *Eigenmannia* in response to long-term stimulation over weeks (Fortune et al. 2003).

**Acknowledgements** We thank Nikolai Dembrow, George Pollak, Wesley Thompson, and Frank Triefenbach for helpful comments. This work was supported by grant NIH MH56535 (to HZ). The experiments comply with the "Principles of animal care", publication No. 86–23, revised 1985 of the National Institute of Health.

## References

- Aizenman CD, Linden DJ (2000) Rapid, synaptically driven increases in the intrinsic excitability of cerebellar deep nuclear neurons. *Nat Neurosci* 3:109–111
- Alkon DL (1984) Changes of membrane currents during learning. *J Exp Biol* 112:95–112
- Bastian J (1987) Electrolocation in the presence of jamming signals: behavior. *J Comp Physiol A* 161:811–824
- Bennett MVL (1971) Electric organs. In: Hoar WS, Randall DJ (eds) *Fish physiology*. Academic, New York, pp 493–574
- Bliss TV, Collingridge GL (1993) A synaptic model of memory: long-term potentiation in the hippocampus. *Nature* 361:31–39
- Bullock TH (1993) How are more complex brains different? One view and an agenda for comparative neurobiology. *Brain Behav Evol* 41:88–96
- Bullock TH, Hamstra RH, Scheich H (1972a) The jamming avoidance response of high-frequency electric fish. I. General features. *J Comp Physiol* 77:1–22
- Bullock TH, Hamstra RH, Scheich H (1972b) The jamming avoidance response of high frequency electric fish. II. Quantitative aspects. *J Comp Physiol* 77:23–48
- Butefisch CM (2004) Plasticity in the human cerebral cortex: lessons from the normal brain and from stroke. *Neuroscientist* 10:163–173
- Choi DW (1988) Glutamate neurotoxicity and diseases of the nervous system. *Neuron* 1:623–634
- Crampton WGR (1998) Electric signal design and habitat preferences in a species rich assemblage of gymnotiform fishes from the Upper Amazon basin. *An Acad Bras Cienc* 70:805–847
- Donoghue JP (1995) Plasticity of adult sensorimotor representations. *Curr Opin Neurobiol* 5:749–754
- Dunlap KD, Oliveri LM (2002) Retreat site selection and social organization in captive electric fish, *Apteronotus leptorhynchus*. *J Comp Physiol A* 188:469–477
- Dye J (1988) An in vitro physiological preparation of a vertebrate communicatory behavior: chirping in the weakly electric fish, *Apteronotus*. *J Comp Physiol A* 163:445–458
- Dye J, Heiligenberg W, Keller CH, Kawasaki M (1989) Different classes of glutamate receptors mediate distinct behaviors in a single brainstem nucleus. *Proc Natl Acad Sci USA* 86:8993–8997
- Fortune, ES, Tan, EW, Nizar, J (2003) Relation of group size to the control of electric organ discharges in gymnotiform fish. In: Abstract viewer/itinerary planner. Washington, DC: Society for Neuroscience, 2003. Online.
- Gaddis P (1977) Communication by harmonization of electric organ discharge frequencies by *Eigenmannia virescens* (Sternopygidae, Pisces). *Rev Can Biol* 36:317–320
- Hagedorn M, Heiligenberg W (1985) Court and spark: electric signals in the courtship and mating of gymnotoid fish. *Anim Behav* 33:254–265
- Heiligenberg W (1991) *Neural nets in electric fish*. MIT Press, Cambridge
- Heiligenberg W (1973) Electrolocation of objects in the electric fish *Eigenmannia* (Rhamphichthyidae, Gymnotoidei). *J Comp Physiol* 87:137–164
- Heiligenberg W, Metzner W, Wong CJ, Keller CH (1996) Motor control of the jamming avoidance response of *Apteronotus leptorhynchus*: evolutionary changes of a behavior and its neuronal substrates. *J Comp Physiol A* 179:653–674
- Held R, Freedman SJ (1963) Plasticity in human sensorimotor control. *Science* 142:455–462
- Hopkins CD (1988) Neuroethology of electric communication. *Annu Rev Neurosci* 11:497–535
- Houde JF, Jordan MI (1998) Sensorimotor adaptation in speech production. *Science* 279:1213–1216
- Juranek J, Metzner W (1997) Cellular characterization of synaptic modulations of a neuronal oscillator in electric fish. *J Comp Physiol A* 181:393–414
- Kandel ER, Schwartz JH, Jessell TH (2000) *Principles of neural science*. McGraw-Hill, New York
- Katz PS, Harris-Warrick RM (1999) The evolution of neuronal circuits underlying species-specific behavior. *Curr Opin Neurobiol* 9:628–633
- Keeley BL (1995) Large, slow changes in electric organ discharge associated with social context in *Eigenmannia*. In: *Nervous systems and behaviour: proceedings of the 4th international congress of neuroethology*. Georg Thieme Verlag, Stuttgart, p 415
- Knudsen EI (1975) Spatial aspects of the electric fields generated by weakly electric fish. *J Comp Physiol* 99:103–118
- Knudsen EI (2002) Instructed learning in the auditory localization pathway of the barn owl. *Nature* 417:322–328

- Kramer B, Kirschbaum F, Markl H (1981) Species specificity of electric organ discharges in a sympatric group of gymnotid fishes from Manaus (Amazonas). Sensory physiology of aquatic lower vertebrates. *Akademiai Kiado, Pergamon*, pp 195–219
- Lisberger SG (1988) The neural basis for learning of simple motor skills. *Science* 242:728–735
- Lissmann HW (1961) Ecological studies on gymnotids. In: Chagas C, Paes de Carvalho A (eds) *Bioelectrogenesis*. Elsevier, Amsterdam, pp 215–226
- Malenka RC, Nicoll RA (1999) Long-term potentiation—a decade of progress? *Science* 285:1870–1874
- Marder E, Abbott LF, Turrigiano GG, Liu Z, Golowasch J (1996) Memory from the dynamics of intrinsic membrane currents. *Proc Natl Acad Sci USA* 93:13481–13486
- Oestreich J, Zakon HH (2002) The long-term resetting of a brainstem pacemaker nucleus by synaptic input: a model for sensorimotor adaptation. *J Neurosci* 22:8287–8296
- Pitcher TJ, Parrish JK (1993) Functions of shoaling behaviour in teleosts. In: Pitcher TJ (ed) *Behaviour of teleost fishes*. Chapman and Hall, London, pp 363–439
- Rothman SM, Olney JW (1995) Excitotoxicity and the NMDA receptor—still lethal after eight years. *Trends Neurosci* 18:57–58
- Schlaug G (2001) The brain of musicians. A model for functional and structural adaptation. *Ann N Y Acad Sci* 930:281–299
- Schwassmann HO (1978) Ecological aspects of electroreception. In: Ali M (ed) *Sensory ecology*. Plenum, New York, pp 521–533
- Squire LR, Zola SM (1996) Structure and function of declarative and nondeclarative memory systems. *PNAS* 93:13515–13522
- Steinbach AB (1970) Diurnal movements and discharge characteristics of electric gymnotid fishes in the Rio Negro, Brazil. *Biol Bull* 138:200–210
- Striedter GF (1998) A comparative perspective on motor learning. *Neurobiol Learn Mem* 70:189–196
- Watanabe A, Takeda K (1963) The change of discharge frequency by AC stimulus in a weakly electric fish. *J Exp Biol* 40:57–66
- Westby GWM (1988) The ecology discharge diversity and predatory behavior of gymnotiform electric fish in the coastal streams of French Guiana. *Behav Ecol Sociobiol* 22:341–354
- Wright WG (2000) Neuronal and behavioral plasticity in evolution: experiments in a model lineage. *Biosci* 50:883–894
- Zakon HH (1986) The electroreceptive periphery. In: Bullock TH, Heiligenberg W (eds) *Electroreception*. Wiley, New York, pp 103–156
- Zhang W, Linden DJ (2003) The other side of the engram: experience-driven changes in neuronal intrinsic excitability. *Nat Rev Neurosci* 4:885–900