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Effects of global electrosensory signals on motion processing in the midbrain of *Eigenmannia*

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Abstract Wave-type weakly electric fish such as *Eigenmannia* produce continuous sinusoidal electric fields. When conspecifics are in close proximity, interaction of these electric fields can produce deficits in electrosensory function. We examined a neural correlate of such jamming at the level of the midbrain. Previous results indicate that neurons in the dorsal layers of the torus semicircularis can (1) respond to jamming signals, (2) respond to moving electrosensory stimuli, and (3) receive convergent information from the four sensory maps of the electrosensory lateral line lobe (ELL). In this study we recorded the intracellular responses of both tuberous and ampullary neurons to moving objects. Robust Gaussian-shaped or sinusoidal responses with half-height durations between 55 ms and 581 ms were seen in both modalities. The addition of ongoing global signals with temporal-frequencies of 5 Hz attenuated the responses to the moving object by 5 dB or more. In contrast, the responses to the moving object were not attenuated by the addition of signals with temporal frequencies of 20 Hz or greater. This occurred in both the ampullary and tuberous systems, despite the fact that the ampullary afferents to the torus originate in a single ELL map whereas the tuberous afferents emerge from three maps.

Keywords Electrosensory jamming · Motion processing · Tuberous · Ampullary · Midbrain

Introduction

Sensory perception of salient signals is subject to interference by competing signals in many vertebrate modalities (e.g. auditory masking, Zwicker 1965; Moore 1978; visual masking, Schiller 1965; Dixon 1986). Weakly electric fish such as *Eigenmannia virescens* exhibit a classic example of the degradation of sensory function by naturally-occurring signals, and they are an excellent model for the study of neural mechanisms of this phenomenon.

Eigenmannia are Gymnotiform fish found in the Amazon basin. These animals produce continuous, nearly sinusoidal electric signals at frequencies that are between 200 Hz and 700 Hz: each fish maintains a steady electric organ discharge (EOD) frequency. When individual *Eigenmannia* are in close proximity to conspecifics, the electric fields interact which results in an emergent pattern of “beats” that occur at rates equal to the frequency difference between the two fish. Beats are composed of amplitude and phase modulations. Interestingly, the impact of these signals on sensory processing is a function of the temporal-frequency of beats: 3–8 Hz are most detrimental whereas modulations of 15 Hz or greater have little impact (Bullock et al. 1972; Heiligenberg 1973; Heiligenberg et al. 1978; Partridge et al. 1981). To avoid this interference, fish change their EOD frequencies to increase the frequency difference to values above about 15 Hz; these beat rates do not impair electrolocation (Bullock et al. 1972). This behavior is known as the jamming avoidance response, or JAR. In the JAR, the fish with the higher EOD frequency elevates its frequency and vice versa.

Previous neurophysiological investigations have examined neural correlates of electrolocation under jamming at different levels of the electrosensory pathway in several species of weakly electric fish (see Fig. 1). In the ELL of *Eigenmannia*, the performance of neurons that respond to moving objects was shown to be significantly degraded in the presence of low temporal-

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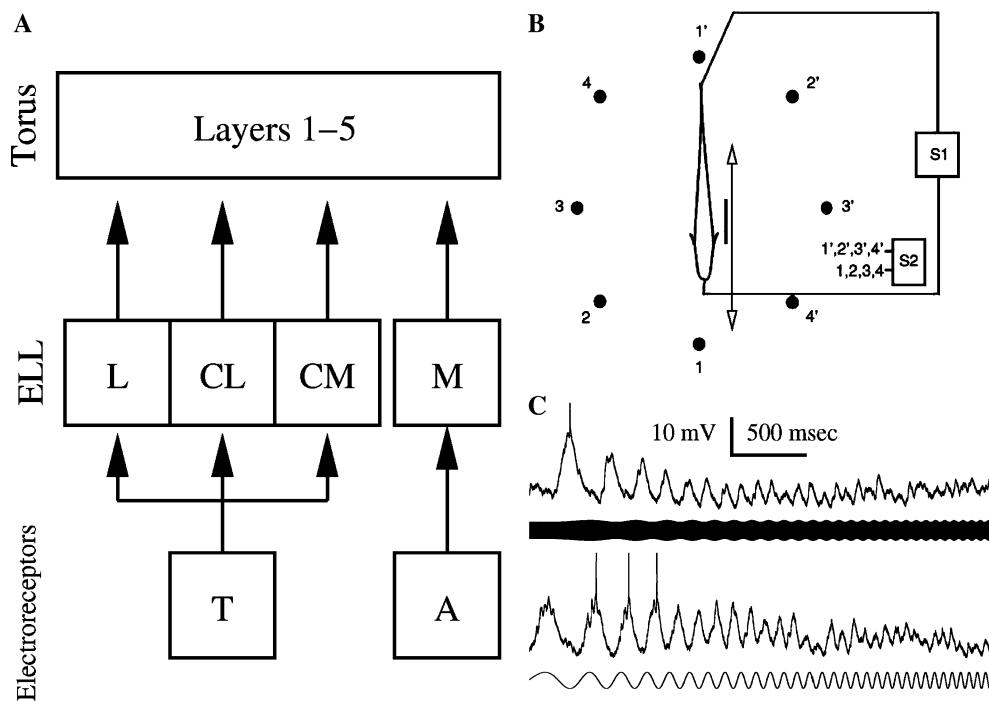


Fig. 1 **A** Schematic showing the ascending electrosensory system. Bottom boxes represent the Ampullary (*A*) and Tuberous (*T*) electroreceptors. Ampullary information terminates in the medial map (*M*) of the ELL, whereas tuberous afferents trifurcate and terminate in the centromedial (*CM*), centrolateral (*CL*), and lateral (*L*) maps of the ELL. Information from all four maps converges within the dorsal torus semicircularis (torus). **B** Stimulus layout. The S1, a replacement of the fish's EOD—was delivered through an electrode in the mouth and at the tail. S2 signals, including low-frequency sinusoids for ampullary neurons and sinusoids near the S1 frequency for tuberous neurons, were added to the S1 and presented through the electrodes in the mouth and at the tail. The moving object, line adjacent to fish, was moved 10 cm along the side of the fish. **C** Examples of low pass tuberous (*top*) and ampullary (*bottom*) responses from neurons in the torus semicircularis. Despite the fact that the tuberous neuron responded to an AM of a carrier signal and the ampullary neuron responded to sinusoids (stimuli for both were linear frequency sweep from ~1 Hz to 30 Hz over 5 s; 3 s shown), the frequencies and shapes of PSPs in these neurons are completely overlapping. For this reason we have used the term “temporal-frequency” as a method to describe the stimulation frequency for both ampullary and tuberous neurons

frequency beats (Matsubara 1982). In *Sternopygus macrurus*, a species that does not exhibit JAR behaviors, a unique cell type was described in the ELL (Type III) that responds to moving objects, but not to the global stimuli that impair electroreception in *Eigenmannia* (Matsubara 1981, 1982). Nevertheless, low temporal-frequency signals have been shown to degrade the responses of toral electrosensory units to moving objects in *Sternopygus* (Rose et al. 1987). In *Apteronotus leptorhynchus*, responses of electroreceptor afferents to moving electrolocation targets were shown to be attenuated by the addition of broad-band noise and low-frequency beat rates (Bastian 1987). Further, multi-unit recordings in the optic tectum of *A. albifrons* in response to moving electrosensory objects have revealed that the application

of a 4 Hz amplitude modulated stimulus significantly impaired electrolocation (Bastian 1982).

In *Eigenmannia*, the representation of moving electrosensory images under jamming has been previously examined at the level of the ELL (Matsubara 1982). In the present study, we quantified the effects of jamming signals on intracellularly recorded responses to moving electrosensory stimuli in the torus semicircularis of this species. This level for analysis is important for three reasons.

First, the torus is where selectivity for amplitude modulation rates of 3–8 Hz first emerges: these responses are a neural correlate of the JAR (Bullock et al. 1972; Heiligenberg et al. 1978; Partridge et al. 1981; Bastian and Yuthas 1984). Second, the torus is the site of convergence of inputs from the multiple electrosensory maps of the ELL. This convergence may be a mechanism underlying the generation of direction selectivity (see Fortune and Rose 2001; Rose and Fortune 2002; Chance et al. 1998). Third, this study compares data from two different electrosensory modalities; the tuberous system and the phylogenetically older ampullary system. The tuberous system mediates the JAR behavior exclusively, while the more primitive ampullary system is responsible for passive detection of signals generally below 100 Hz. Previous results suggest that the tuberous system evolved as an elaboration or duplication of the ampullary system (e.g. Fortune and Rose 1997).

Materials and methods

All of the procedures used in this work were approved by the institutional animal care and use committee of the Johns Hopkins University. Animal husbandry, anes-

thetia, and surgical procedures were performed under the guidelines established by the Society for Neuroscience and the National Research Council. Fish were obtained from several commercial suppliers. The general methods for preparing electric fish for neural recordings have been previously described in detail (Heiligenberg and Rose 1985; Rose and Call 1993; Rose and Fortune 1996). Intracellular recordings were made from 25 neurons in the dorsal five layers of the torus of 20 adult fish (*Eigenmannia virescens*).

The EOD of fish was measured and then attenuated (>1,000 fold) by intramuscular injection of Flaxedil (4 µg/g): Flaxedil immobilizes the fish. The tail, including most of the electric organ, was inserted into a plastic tube during the experiment. Because Flaxedil is not an anesthetic agent, topical 2% lidocaine gel was applied to the skin above the midbrain where incisions were made. The EOD was then replaced by a sinusoidal mimic (S1) applied through an electrode in the mouth and an external electrode at the tail (Fig. 1b). The amplitude and frequency of the S1 were adjusted to be within 50 Hz of the animal's EOD prior to Flaxedil treatment.

While searching for neurons, a linear frequency sweep (2–30 Hz, 5 s duration, 1–2 mV/cm at the fish's head) was added to S1, and an additional signal (S2) which was 4 Hz higher or lower than the S1 frequency, was either added to the S1 or delivered through one pair of an array of carbon electrodes surrounding the fish. Ampullary units were identified by the responses to sinusoidal stimuli, while tuberous units were identified by the responses to amplitude-modulated stimuli (Fig. 1c).

Borosilicate patch pipettes were constructed using a Sutter Instruments (Model P-97) puller. Electrodes were pulled in three stages to resistances between 15 MΩ and 40 MΩ. Electrode tips were filled with 1.5% w/v biocytin in a 285–290 mOsmol solution (pH 7.2) containing (units in mM) 100 potassium acetate, 2 KCl, 1 MgCl₂, 5 EGTA, 10 HEPES, 20 KOH and 43 biocytin. In the solution used to fill the electrode shanks, biocytin was replaced by mannitol. Electrodes were mounted in a Plexiglas holder with a pressure port for recording and were advanced in 1.5 µm steps (Burleigh microdrive) through the top five layers of the torus. The pressure port facilitated the application of either suction or pressure from a 30 cc syringe.

While the electrode was advanced through tissue, small positive pressure was applied (1–2 cc), and neurons were detected by an abrupt increase in resistance and the appearance of spikes and/or ripples in the recording trace. Suction was then applied until a seal resistance of 1–2 GΩ was achieved. The membrane patch was ruptured by manually applying negative current to the electrode while maintaining the suction. Recordings were made at several levels of holding current for removal of spikes and elimination of voltage-dependent active conductances. Neurons were filled with biocytin by applying 1–2 nA of positive DC for 1–3 min. All evidence is consistent with previous reports: the neurons under study have low-pass filtering properties

that are associated with large, spiny dendritic arborizations (Fortune and Rose 1997).

The moving stimulus was a 1.8 cm wide metal plate which was moved longitudinally approximately 1.5 cm lateral to the fish. At its most rostral extent, the trailing edge of the object was 3 cm past the tip of the fish's snout. The total distance covered by the object was 10 cm. The object was moved from tail to head, and then reversed direction to the original position near the tail of the fish. The rate of motion was constant (triangle wave), and three rates were used: 10, 15, and 20 cm/s. The moving object is similar to those used in several previous reports that involve moving electrosensory stimuli (see Rose et al. 1987; Rose and Canfield 1993; Green 1996; Bastian 1987a, b).

Intracellular recordings from electrosensory neurons in the dorsal layers of the torus in response to the moving object were made in the absence and presence of ongoing global signals. Per trial, the object stimulus was used for at least three complete cycles of movement (i.e. tail to head to tail) in each test case. Recordings were first obtained in the absence of jamming signals. Fish were subjected to competing global "jamming" signals for a minimum of 1 s prior to initiation of object movement. This duration is known to be sufficient to produce PSPs with stable amplitudes in toral electrosensory neurons (see Rose and Fortune 1999; Fortune and Rose 2000). For ampullary neurons the ongoing signal was one of a 5, 10, 20, 30, 40, or 50 Hz sinusoidal stimulus, whereas for tuberous neurons these were amplitude modulations at these same rates. The phase of ongoing global signals were rotated relative to the moving object from trial to trial. Mechanosensory inputs are unlikely to have contributed to the observed responses: (1) the dorsal torus is not known to receive mechanosensory inputs (see Carr et al. 1981); (2) responses to moving objects were modulated by electrosensory stimuli that are not known to activate mechanosensors.

Data were recorded (16 bit, 20 kHz) directly to a computer via a DaqBoard 2000 (IOtech, Cleveland). Matlab (MathWorks, Natick) and other custom software were used to in the measurement of PSPs and Fourier analysis of responses. Samples of both averaged and raw traces were analyzed using fast Fourier transforms (FFTs). Statistical analyses were performed using Statistica 5.5 (StatSoft, Tulsa).

Results

Intracellular recordings were maintained for up to 45 min and resting potentials were measured between –55 mV and –75 mV. Seals less than 1 GΩ were associated with lower values for resting potentials and smaller PSP amplitudes.

For the variety of stimuli used in this study, no qualitative or quantitative differences were observed between ampullary and tuberous neurons. In fact, in the

absence of stimulus traces, it was not possible to discriminate recordings made in ampullary and tuberous neurons in the torus. As a result, some of the descriptive measures of the data treat both neuron types as a single group. The specific measures that demonstrate the similarities between ampullary and tuberous response properties are indicated below.

Responses to moving objects

Most ampullary and tuberous neurons exhibited robust responses to the moving object. Moving stimuli presented alone elicited the greatest PSP amplitudes of any stimuli in 71% of all neurons. In those neurons where the moving object did not elicit the largest PSPs, the PSP amplitudes elicited by the moving stimulus were nevertheless within 4 dB (mean = -0.64 dB, SD = 1.21) of the maximum response elicited by any electrosensory stimulus. The moving object stimuli were effective and reliable superthreshold stimuli for both ampullary and tuberous neurons.

The location of the moving object relative to the fish affected the responses of toral electrosensory neurons. In most neurons the responses to the moving object occurred along the side of the fish (Fig. 3a). In five neurons however, best responses were observed when the object was rostral to the snout of the fish. Even though the trailing edge of the object was positioned so that it traveled 3 cm past the rostrum of the fish, these neurons nevertheless showed a single PSP indicating that the object had not traveled beyond the rostral extent of the receptive field (Fig. 2a).

The PSPs resulting from the moving object were predominantly excitatory and were sinusoidal or Gaussian in shape (Fig. 2). IPSPs may also have contributed to the responses, appearing adjacent to EPSPs. The shapes of PSPs reflected the sinusoidal change in local signal amplitude that was produced by the object. Nevertheless, several neurons showed asymmetric PSPs (Fig. 3) in response to this stimulus.

Three rates of motion were used: 10, 15, and 20 cm/s. The half-height durations of PSPs elicited by the moving object at these rates were between 55 ms and 581 ms. Durations of PSPs varied in relation to the rate of object motion (Fig. 4). At the 10 cm/s rate of movement, PSP durations were longest, ranging between 111 ms and 581 ms, and at 20 cm/s, durations were between 83 ms and 398 ms. The PSPs associated with moving object stimuli were similar to those elicited by the low temporal-frequency global stimuli in individual neurons.

Effects of ongoing global stimulation

For most neurons in this study, continuous 5 and 10 Hz global electrosensory signals elicited robust responses (Figs. 2b, 3b). The PSPs elicited by these global stimuli reflected the analog waveform of the electrosensory

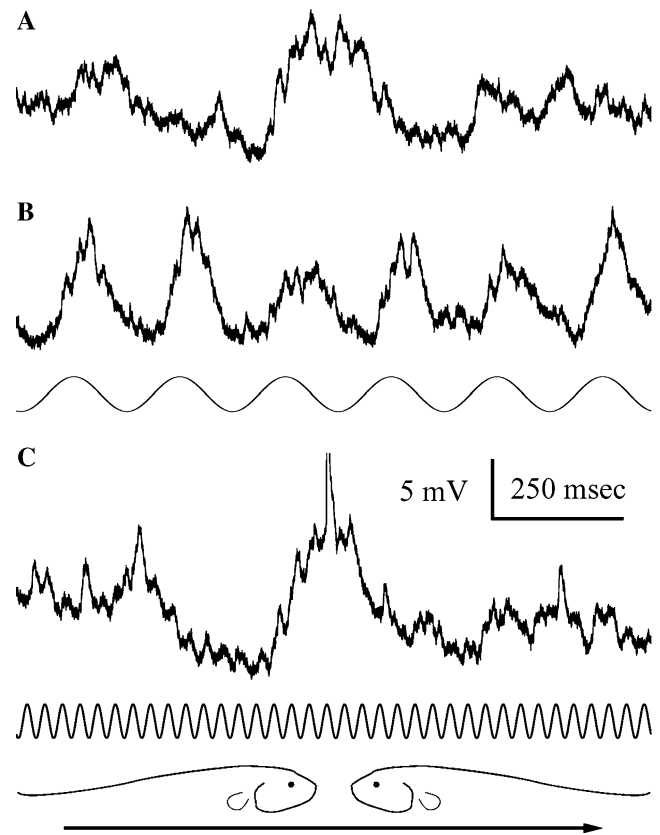


Fig. 2 Responses of a midbrain ampullary electrosensory neuron to a moving object (1 Hz). **A** Response with S1 alone. **B** Response in the presence of an ongoing 5 Hz sinusoidal signal. **C** Same as B with 30 Hz signal. Spikes are clipped -0.05 nA holding current. The *arrow* indicates the direction of movement of the object from tail to head to 3 cm past the snout and then back to tail

stimulus in the water (see Rose and Call 1993). These neurons exhibited low-pass temporal filtering of electrosensory stimuli: they responded with smaller sinusoidal PSPs to ongoing 20–50 Hz electrosensory stimuli than to low temporal-frequency stimuli or to moving objects.

Even though the responses to moving electrosensory stimuli were at the same magnitude or larger than the responses to the ongoing low temporal-frequency stimuli, responses to moving objects were greatly attenuated when these stimuli were presented simultaneously (Fig. 5). Figures 2b and 3b show raw (not averaged) responses to the combined stimuli. The responses to the moving object are not evident in either case, despite the different temporal relations of the responses to the moving object. Fourier analysis was used to determine the magnitude of responses to the stimuli.

Friedman ANOVAs of data obtained in the three conditions, moving object alone, moving object with ongoing 5 Hz temporal-frequency stimuli, and moving object with ongoing 20+ Hz temporal-frequency stimuli, revealed significant differences both in ampullary (Friedman ANOVA, Chi Sqr. ($N=9$, $df=2$) = 12.67, $P < 0.0018$) and tuberous (Friedman ANOVA, Chi Sqr.

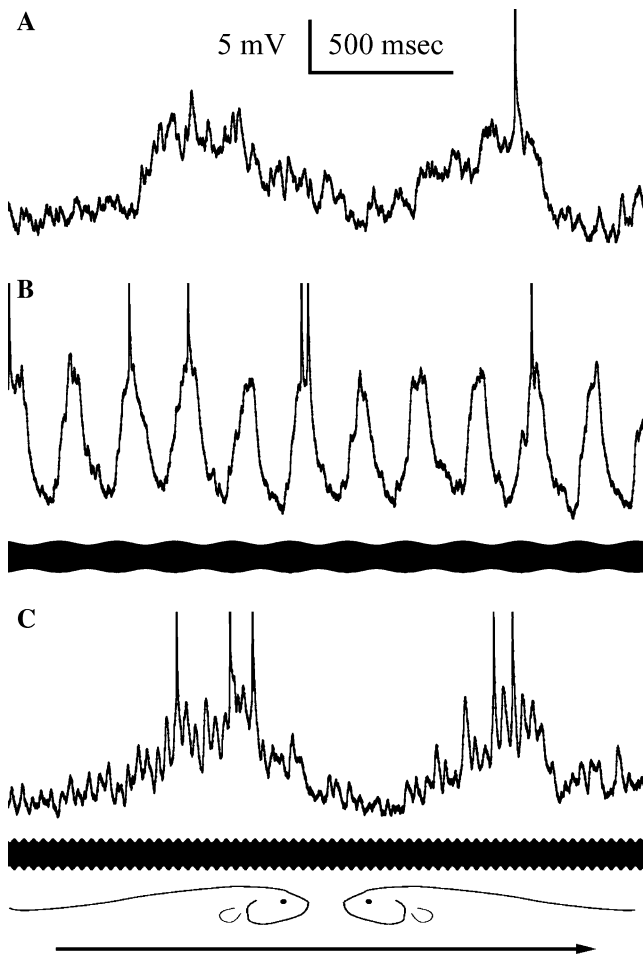


Fig. 3 Responses of a midbrain tuberous electrosensory neuron to a moving object (0.5 Hz). **A** Response with S1 alone. **B** Response in the presence of an ongoing 5 Hz sinusoidal AM of the S1. **C** Same as **(B)** with 30 Hz signal. Spikes are clipped -0.05 nA holding current. Notice that the time scale differs from that in Fig. 2. The arrow indicates the direction of movement of the object from tail to head to 3 cm past the snout and then back to tail. The pattern of spiking varied

($N=6$, $df=2$) = 8.33, $P < 0.0016$) neurons. In ampullary neurons the mean attenuation resulting from the addition of the ongoing 5 Hz stimulus was 5.9 dB (Fig. 5). A Wilcoxon matched-pair post-hoc test showed that the 5 Hz condition was significantly attenuated relative to the moving object alone condition ($Z=2.67$, $P < 0.008$). In tuberous neurons the mean attenuation due to the ongoing 5 Hz stimulus was 8.9 dB (Fig. 5), which was also significantly different (Wilcoxon matched-pair, $Z=2.20$, $P < 0.028$). There was no significant difference in the magnitude of attenuation resulting from the addition of ongoing 5 Hz temporal-frequency stimuli between ampullary and tuberous neurons (Mann Whitney U).

Both ampullary and tuberous neurons responded to moving stimuli in the presence of ongoing higher (20+ Hz) temporal-frequency stimuli (Figs. 2c, 3c). PSPs elicited by moving objects presented concomitantly with these stimuli were similar in amplitude and dura-

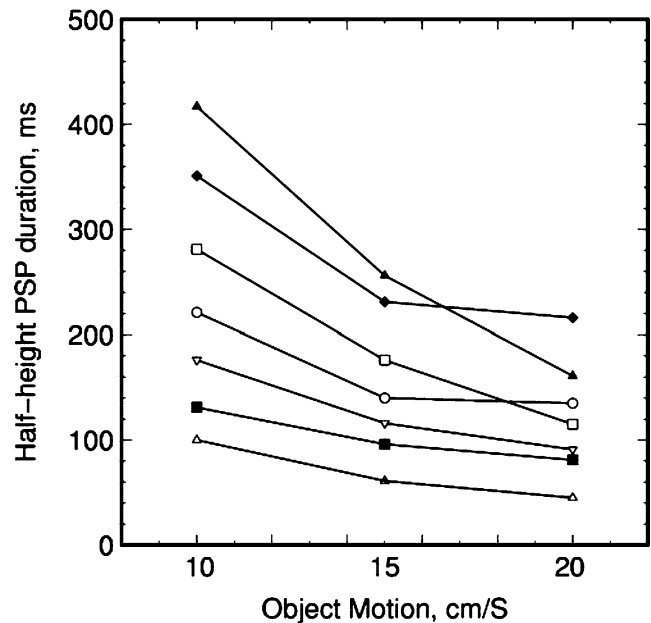


Fig. 4 Relation of response duration to rate of object motion. Each closed symbol is data from a single neuron. Closed symbols are tuberous and open symbols are ampullary data. PSP durations were largely correlated with rate of object motion

tion to those elicited by the moving object alone. The magnitudes of responses in the presence of ongoing 20+ Hz temporal-frequency stimuli were not significantly different from the moving object alone (see above, Wilcoxon matched-pair test) for both ampullary and tuberous neurons. A low-amplitude response to the ongoing 20+ Hz global stimuli could often be seen riding on the low temporal-frequency response associated with the moving object (Figs. 2c and 3c, easier to see in Fig. 3c). The primary result (i.e. impairment of electrosensory responses to moving objects under electrical jamming conditions) was consistent across all neurons investigated, notwithstanding variations in location of the object that best elicited responses.

Discussion

The addition of global, low temporal-frequency signals (5 Hz) reduced the magnitudes of responses to moving electrosensory images in both ampullary and tuberous midbrain electrosensory neurons. This impairment was statistically significant. Higher temporal-frequency stimuli, 20–50 Hz, however, did not significantly attenuate responses to the moving object.

Responses to the moving object stimulus

The moving object elicited PSPs with durations that were similar to those elicited by global low temporal-frequency stimuli. Further, the shapes of PSPs were similar to those elicited by the global stimuli, especially

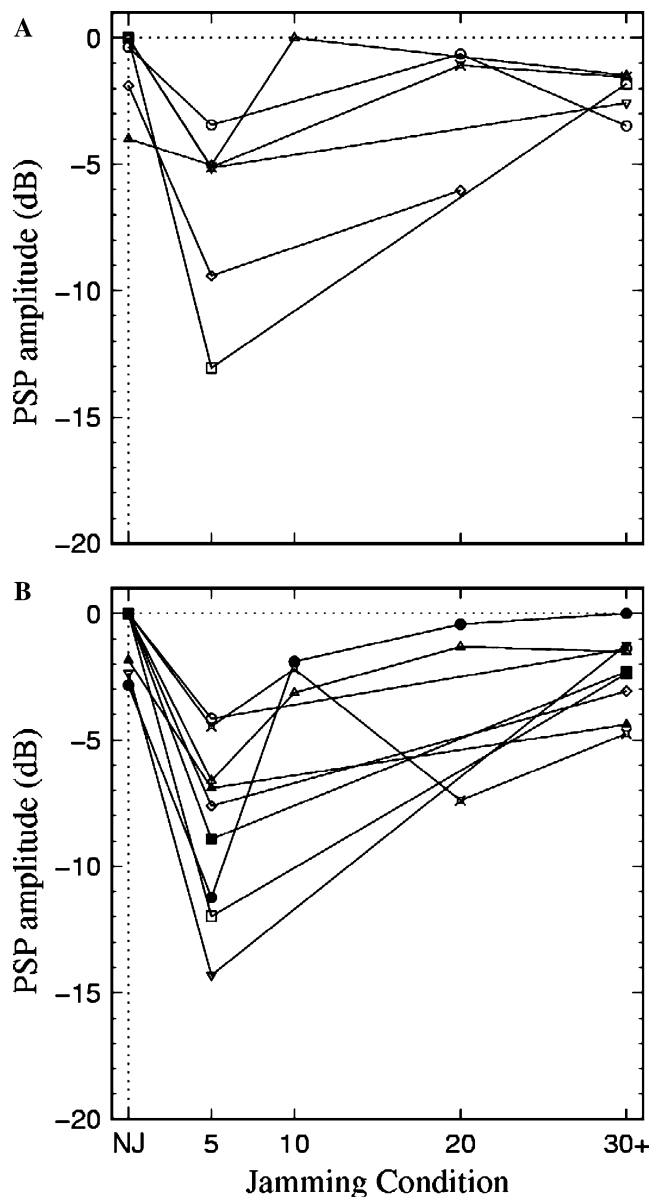


Fig. 5 Effects of global stimuli on responses to moving objects. **A** Tuberous neurons, **B** Ampullary neurons. Amplitudes were measured in the Fourier transform at the peak frequency of the response to the moving object, between 1 Hz and 2.5 Hz. Amplitudes are normalized to the peak response of the neuron to any electrosensory stimulus. *NJ* indicates “no jam”—the S1 alone. In tuberous neurons (**A**) jamming condition refers to the ongoing AM rate. In ampullary neurons (**B**) jamming condition refers to frequency of the ongoing sinusoid

those that result in an impairment of electrosensory function. The moving object used in this study was comparable to moving objects that were used in several previous studies (Matsubara 1982; Bastian 1987a, b; Rose et al. 1987).

Further, preliminary studies of the electromotor performance of *Eigenmannia* demonstrate that moving objects of the size and rates used in this study are effective stimuli for tracking behaviors (Tan et al. 2005). Bode plots generated from the movements of *Eigen-*

mannia in relation to a large sinusoidal moving grating demonstrate a tracking bandwidth of ~ 0.5 Hz. The stimuli used in this study are within the range of temporal-frequencies that can elicit tracking behaviors in these fish. Nevertheless, these stimuli differ considerably from those used by Nelson and MacIver (1999) where prey capture was under study.

Evolution of electrosensory processing in Gymnotiformes

Gymnotiform fishes have two parallel electrosensory systems, the phylogenetically older ampullary system and the novel tuberous system (Zakon 1986). The neural circuitry of the tuberous system, which is required for “active” electrolocation and the jamming avoidance response, may have been derived from the plesiomorphic circuitry of the ampullary system (Fortune and Rose 1997). *Sternopygus* do not exhibit a JAR behavior even though the tuberous circuitry is similar to other Gymnotiform fishes including *Eigenmannia* (Bullock et al. 1975). This genus is able to electrolocate effectively in the presence of low-frequency amplitude-modulated stimuli (Matsubara and Heiligenberg 1978). Matsubara (1982) demonstrated a potential neural mechanism for this immunity to jamming. A unique cell type found in the ELL of these fish, type III, responded to moving objects but not to the global stimuli that would impair electroreception in *Eigenmannia* (Matsubara 1982).

As *Sternopygus* and *Eigenmannia* solve the jamming problem using two different mechanisms, *Eigenmannia* use the JAR whereas *Sternopygus* rely on the activity of type III units in the ELL, it is unclear what the primitive condition of ELL processing was in the earliest Gymnotiform fishes. That is, were type III neurons present in the primitive ELL? The data presented here are a first step in resolving this issue. We found that the ongoing 5 Hz signal profoundly reduced responses to the moving object in the ampullary system. The fact that ampullary neurons were impaired by the addition of the ongoing 5 Hz stimulus suggests that type III-like neurons may not exist in the ampullary map of the ELL. If type III-like neurons were to exist in the ampullary map of the ELL, we might expect them to confer immunity to the ongoing 5 Hz global signal. Previous work suggests that the tuberous system may be an elaboration or duplication of the plesiomorphic ampullary system (Fortune and Rose 1997). If the ampullary system was indeed a precursor of the tuberous system, these data would support the hypothesis that the primitive tuberous system is more similar to that seen in *Eigenmannia* rather than in *Sternopygus*. Type III neurons in the ELL would therefore be an independent adaptation in *Sternopygus* that is used to avoid detrimental electrosensory jamming. Direct measurements in *Sternopygus* are necessary to resolve this issue.

Role of convergence

Interestingly, there are three somatotopic maps of tuberous information at the level of the ELL but only one ampullary ELL map (Carr et al. 1981; Heiligenberg and Dye 1982). All four of these maps in the ELL converge onto a single somatotopic map in the dorsal layers of the torus, where the recordings were made.

A common feature of ascending sensory systems is the emergence of multiple representations of the receptor sheet at particular levels in the CNS (see Young 1997; Metzner 1999). These representations are often associated with increased specialization in processing mechanisms (Young 1997). The function of the multiple topographic representations remains, however, unclear. This issue is confounded by the fact that these representations often converge onto a single target.

One possibility is that multiple maps are needed to support processing features associated with specific behaviors. Compelling evidence in support of this hypothesis has been obtained in Gymnotiform fishes. The CM map of the ELL exhibits low-pass temporal filtering properties (Shumway 1989), which is a correlate of the JAR. The L map, in contrast, exhibits high-pass temporal filtering (Shumway 1989). The range of frequencies preferred by neurons in this map is more similar to those that occur in the electric “chirps” used by these fish in social communication. The effects of lesions of individual maps in the ELL were studied using behavioral experiments. Lesions of the CM map impaired the control of the JAR whereas lesions of the L map impaired the reception and production of chirps (Metzner and Juranek 1997).

Another possibility is that parallel processing is a mechanism to avoid potentially detrimental consequences of stimulus filtering. To achieve greater stimulus-specificity, activity related to other stimuli must be filtered. If filtering is achieved too early in the hierarchy of neural processing, it could potentially prevent access to biologically-relevant information (Fortune and Rose 2001). One way to solve this problem is to implement parallel pathways with different filtering properties. Specific functions could be achieved independently within each channel. The filtered information in these channels would then converge at a higher station. The result would be a combination of greater stimulus specificity without potential loss of function.

An excellent example of this mechanism occurs in the activity of neurons in the torus of *Eigenmannia*. Many neurons in the torus employ short-term synaptic depression as a mechanism to enhance low-pass temporal filtering (Fortune and Rose 2000). A potentially detrimental consequence of this mechanism is that the depletion of readily releasable synaptic vesicles might preclude desired responses to salient electrosensory stimuli (Fortune and Rose 2001). Data from direct stimulation of afferents suggest that convergent information is a mechanism that is used to solve this problem (Fortune and Rose 2000). By combining ELL inputs

that are differentially activated, these neurons avoid a negative consequence of stimulus filtering by short-term synaptic depression.

If the addition of functionally specialized maps were related to the filtering issue described above, then tuberous processing, which involves three ELL maps, may be enhanced relative to ampullary processing, which involves only one map. The similarities among the data obtained in ampullary and tuberous neurons suggest that all processing types found in the three tuberous maps of the ELL are likely present within the single ampullary map of the ELL. Nevertheless, the data presented here do not necessarily support the hypothesis that increased specialization in the tuberous maps of the ELL and its convergence onto the single map of the torus is used for enhancing aspects of spatiotemporal processing. The contributions of multiple sensory maps to processing in the torus could be explored further using selective blockade of information at the level of the ELL, as has been effectively used by Metzner and Juranek (1997).

Information from the ELL

What do the results tell us about the information ascending from the ELL in *Eigenmannia*? ELL neurons in a related Gymnotiform species, *A. leptorhynchus*, exhibit marked changes in receptive field properties depending on the spatial organization of the stimulus (Chacron et al. 2003). When electrosensory stimuli are localized, neurons respond best to lower frequency stimuli, under 20 Hz, whereas global electrosensory stimuli elicit strongest responses at high frequencies, between 40 Hz and 60 Hz, from the same neurons. This shift in tuning matches two categories of electrosensory stimuli, local prey items and social communication signals, respectively (Chacron et al. 2003). The interactions between local and global stimulation were not explored.

At the level of the torus of *Eigenmannia*, the strongest responses of most neurons to local and global stimuli were within a few dB of each other, and exhibited similar time courses and PSP shapes. The majority of toral neurons in layers 1–5 exhibit low-pass temporal filtering properties to global electrosensory stimulation, with best response magnitudes to stimuli below ~ 8 Hz. The durations of responses to the moving objects, a form of localized stimulus, were in the same range of frequencies. Due to the nature of the localized stimulus, an actual moving object, it was not physically possible to generate stimuli at the rates above 2 Hz. Thus, in this study, both global and localized stimuli elicited strong responses at the lower range of temporal frequencies, although it must be noted that the stimulation regime in this study could not have revealed the properties observed by Chacron et al. (2003) in the ELL of *Apteronotus*.

The combination of local and global stimulation revealed a temporal-frequency dependent interaction be-

tween local and global stimulation. The responses to the local stimulus, as measured by Fourier transform, disappeared when low temporal-frequency global stimuli were presented concurrently, but not when high (> 20 Hz) temporal-frequency global stimuli were used. This phenomenon is not a form of masking, since the response to the moving object did not appear in the sub-threshold activity. In short, it appears that the low temporal-frequency global stimulation may have a non-linear effect that blocks the localized information. The computations that result in this phenomenon likely occur at the level of the ELL.

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