Global Electrosensory Oscillations Enhance Directional Responses of Midbrain Neurons in *Eigenmannia*

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Ramcharitar, J. U., E. W. Tan, and E. S. Fortune. Global electrosensory oscillations enhance directional responses of midbrain neurons in *Eigenmannia*. *J Neurophysiol* 96: 2319–2326, 2006. First published June 21, 2006; doi:10.1152/jn.00311.2006. *Eigenmannia*, a genus of weakly electric fish, exhibits a specialized behavior known as the jamming avoidance response (JAR). The JAR results in a categorical difference between *Eigenmannia* that are in groups of conspecifics and those that are alone. Fish in groups exhibit the JAR behavior and thereby experience ongoing, global synchronous 20- to 50-Hz electrosensory oscillations, whereas solitary fish do not. Although previous work has shown that these ongoing signals do not significantly degrade electrosensory behavior, these oscillations nevertheless elicit short-term synaptic depression in midbrain circuits. Because short-term synaptic depression can have profound effects on the transmission of information through synapses, we examined the differences in intracellularly recorded responses of midbrain neurons in awake, behaving fish to moving electrosensory images under electrosensory conditions that mimic solitary fish and fish in groups. In solitary conditions, moving objects elicited Gaussian or sinusoidal postsynaptic potentials (PSPs) that commonly exhibited preferential responses to a direction of motion. Surprisingly, when the same stimulus was presented in the presence of the global oscillations, directional selectivity was increased in all neurons tested. The magnitudes of the differences in PSP amplitude for preferred and nonpreferred directions were correlated with a measure of short-term synaptic depression in both conditions. The electrosensory consequences of the JAR appear to result in an enhancement of the representation of direction of motion in midbrain neurons. The data also support a role for short-term synaptic depression in the generation and modulation of directional responses.

INTRODUCTION

Animal behavior commonly requires the extraction of salient information in the presence of competing and interfering signals (Bregman 1990; Cherry 1953; Feng and Ratnam 2000; Julesz and Hirsh 1972; Ronacher et al. 2000; Schiller 1965). Sources of noise include environmental stimuli arising from nonbiological sources, heterospecific sources, and, importantly, conspecifics. Competing signals generated by conspecifics can be particularly detrimental because the stimulus parameters of these interfering signals closely match the sensory tuning of the individual (Appeliants et al. 2005; Narins 1995; Ulanozsky et al. 2004).

Evolutionary processes have resulted in an array of solutions to this problem. For example, in social situations, humans can isolate single conversations from competing background conversations (Cherry 1953). This phenomenon is known as the "cocktail party effect." Another solution to this problem is found in certain species of weakly electric fishes. These fish exhibit a robust behavioral adaptation, the "jamming avoidance response" or JAR, which dramatically reduces detrimental sensory interference from nearby conspecific signals. This behavior has been best studied in the glass knife fish, *Eigenmannia virescens* (Heiligenberg 1991).

Eigenmannia produce weak electric fields, on the order of tens of millivolts, which are used in electrolocation and communication (Heiligenberg 1991). The electric fields are quasi-sinusoidal, and each fish maintains a nearly constant frequency within the range 200–700 Hz. When *Eigenmannia* are within about 1 m of each other, the electric fields of the fish mix, which results in "global" (broad-field) oscillating interference patterns at a rate equal to the frequency difference between the fish. These oscillating interference patterns, more commonly known as "beats," include both amplitude and phase modulations of the electric signal (Heiligenberg 1991). Oscillation rates between 3 and 8 Hz maximally impair both fish's ability to electrolocate, whereas oscillation rates of ≥ 20 Hz do not (Bullock et al. 1972; Heiligenberg 1973). In the JAR, fish detect the detrimental oscillation rates, and the individual with the higher initial frequency raises its electrical frequency while the other fish lowers its frequency (Bullock et al. 1972; Watanbe and Takeda 1963). After the JAR has occurred, fish will experience ongoing global oscillations at rates typically between 20 and 50 Hz (Tan et al. 2005) as long as they remain in close proximity.

In the wild, *Eigenmannia* are most commonly found in close proximity to conspecifics (Tan et al. 2005). Given that alternate solutions to the electrosensory jamming problem exist, such as simply moving away from conspecifics or via other neural strategies (Matsubara 1981, 1982), we hypothesized that such oscillations in *Eigenmannia* might have specific computational consequences for electrosensory processing in the CNS. Indeed, previous studies demonstrated that global 20- to 50-Hz oscillations preferentially elicit short-term synaptic depression in midbrain electrosensory neurons (Fortune and Rose 2000; Rose and Fortune 1999). The dynamic responses of synapses that exhibit short-term synaptic depression, therefore, are expected to differ when fish are solitary versus when fish are in groups in which ongoing 20- to 50-Hz oscillations are generated as a result of the JAR. The changes in synaptic properties that are induced by the electrosensory signals that emerge as a result of the JAR behavior begs the question: how do these "background" signals affect the processing of salient signals, such as moving objects?

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To determine whether 20- to 50-Hz global oscillations affect the processing of sensory signals in the nervous system, we made intracellular recordings from midbrain electrosensory neurons in awake, behaving *Eigenmannia*. We recorded the responses to a moving object in conditions that mimic a solitary *Eigenmannia*, and in the presence of global 20- to 50-Hz oscillations that simulate the electrosensory signals that result from the JAR behavior.

Surprisingly, the global oscillations appear to enhance directional responses. This result suggests a possible new function of the JAR: to enhance electrosensory processing. The data also support the hypothesis that short-term synaptic depression may have a functional role in the generation of directional responses (Fortune and Rose 2002) and also in the enhancement of those responses by the global oscillations. Because the global synchronous 20- to 50-Hz electrosensory oscillations result in patterns of CNS activity that are similar to gamma-band oscillations seen in a wide variety of neural systems (Bullock and Achimowicz 1994), these data may indicate that gamma-band oscillations modulate short-term synaptic depression which results in enhanced processing of temporal information.

METHODS

The procedures used in this work were approved by the animal care and use committee of the Johns Hopkins University and performed under guidelines established by the Society for Neuroscience and the National Research Council. The general methods have been previously described in detail (Ramcharitar et al. 2005; Rose and Call 1993; Rose and Fortune 1996). Intracellular recordings were made in the dorsal 5 layers of the torus of adult *Eigenmannia virescens*. The method for intracellular recordings was whole cell patch under current clamp as described in Rose and Fortune (1996). Seal resistances were 1–2 GΩ and resting potentials were −55 to −75 mV. The response properties and mechanisms used in the processing of behaviorally relevant information have been well characterized in the ascending electrosensory systems of these fishes (Heiligenberg 1991; Rose 2004).

For experiments, the electric organ discharge was attenuated (>1,000-fold) and the fish immobilized by intramuscular injection of gallamine triethiodide (Flaxedil; 4 μg/g fish). The fish's electric field was replaced by a sinusoidal mimic, known as the "S1," applied through an electrode in the mouth and an external electrode at the tail (Fig. 1). The frequency of the S1 was adjusted to be within 50 Hz of the animal's natural electric field frequency, and its amplitude was set to ~20 mV/cm near the head. The moving stimulus was presented with combinations of global electrosensory stimuli (see following text). For solitary conditions, a continuous artificial mimic of the fish's own electric field was generated using a wire placed in the mouth and at the tail (Fig. 1*B*). The global oscillations were produced by adding a second sinusoidal electric field to the tank (Fig. 1, *B* and *C*).

Data were recorded (16 bit, 20 kHz) directly to a computer via a DaqBoard 2000 (IOtech, Cleveland, OH). Matlab (MathWorks, Natick, MA) and other software were used to in the measurement of PSPs (see following text).

Stimuli

The moving stimulus was a 1.8-cm-wide metal plate with an insulated backing that was moved at a constant velocity parallel to the fish from near the tail to 2 cm past the head and back again at rates between 10 and 20 cm/s (Ramcharitar et al. 2005) (Fig. 1*A*). Each trial
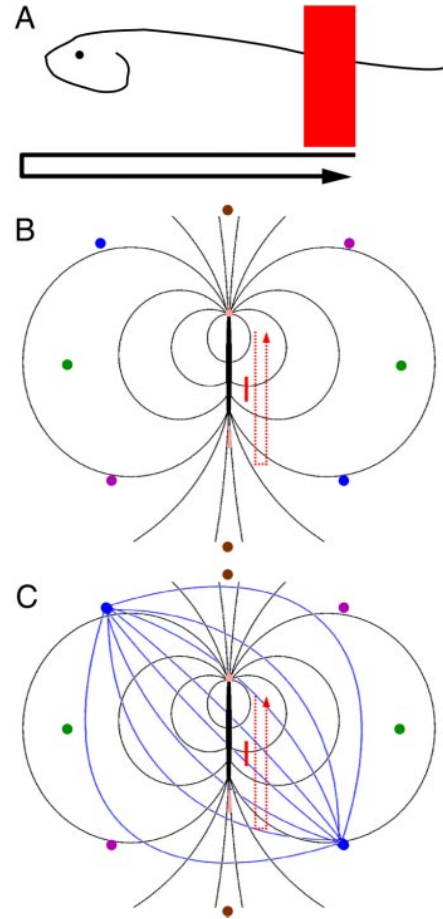

FIG. 1. Electrosensory stimuli. *A*: side view of object stimulus and fish. The moving object (red) is a 1.8-cm plate that is moved from the tail, beyond the head and back (arrow). *B* and *C*: top view of the immobilized fish. The fish's mouth is on a tube, electrodes (pink) are in the mouth and at the tail. Carbon electrodes surround the fish (colored dots). The object is indicated red. *B*: electric field lines for both solitary and identical geometry (IG) stimulation. In IG, the 2nd oscillatory field is added to the mimic of the fish's field, thus the field lines are identical. *C*: in differential geometry (DG), the second oscillatory field is added via pairs of carbon electrodes, example shown in blue. As occurs in nature, DG electric field lines differ from the mimic of the fish's electric field (see METHODS for details).

consisted of at least three complete cycles of object motion (i.e., tail to head to tail) (Ramcharitar et al. 2005).

Recordings of responses to the moving stimulus were first obtained with the sinusoidal mimic of the fish's own electric field in the absence of global oscillations. Next, fish were subjected to ongoing, constant frequency (20–50 Hz), global oscillations 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 Fortune and Rose 2000; Rose and Fortune 1999). That is, 1 s of stimulation is sufficient to fully induce the short-term synaptic depression in these neurons.

The global 20- to 50-Hz oscillations were presented using two methods: identical geometry (IG) and differential geometry (DG; Fig. 1, *B* and *C*, respectively). In DG, the second field was presented through a pair of electrodes adjacent to or across the fish. DG is a naturalistic method for generating socially derived oscillations as it mimics the orientation of the electric field of a nearby fish. DG, however, results in differences in combined electrical geometry of the field lines compared with the solitary electric field geometry. In IG, the second field was added to the artificial mimic and presented through the electrodes at the head and mouth. The IG stimulation

method is not naturalistic but has the advantage that there are no differences in the electric field geometries between solitary and IG stimulation (as shown in Fig. 1*B*). As a result, any effects of IG stimulation on motion processing are a direct result of the ongoing oscillations.

The range of global stimuli used in this study was defined on the basis of several studies of the physiological properties of toral neurons. Previous studies have demonstrated that both DG and IG can be effective methods to stimulate midbrain electrosensory neurons (Fortune and Rose 1997b, 2000; Rose and Fortune 1999). In many neurons, both IG and DG stimulation can elicit robust, reliable responses; a minority of neurons responds only to DG stimulation (Fortune and Rose 1997b, 2000; Rose and Fortune 1999). For this experiment, we preferentially used IG stimulation. Some neurons were tested with both IG and DG, and others with DG alone. For this study, the stimulation regime that elicited the most reliable and consistent responses from each neuron was used.

We recorded from midbrain neurons that received information from p-type tuberous electroreceptors and ampullary electroreceptors. p-type tuberous electroreceptors encode amplitude modulations of a carrier signal at frequencies within ~100 Hz of the fish's own electric field frequency, whereas ampullary electroreceptors detect low-frequency (less than ~80 Hz) electric signals (Zakon 1986). As described previously (Fortune and Rose 1997a,b, 2000; Rose and Fortune 1999), global oscillations for tuberous receptors were generated by adding a sinusoidal signal that differed in frequency from the electric field mimic by 20–50 Hz. Global oscillations for ampullary neurons were sinusoids of 20–50 Hz. The JAR produces tuberous but not ampullary oscillations in natural conditions. The p-type tuberous system appears to be an elaboration or duplication of the ampullary system (Fortune and Rose 1997a), and both exhibit identical responses and mechanisms to stimuli with identical temporal frequencies (Ramcharitar et al. 2005).

The specific frequency between 20 and 50 Hz that was used differed between neurons and was chosen on the basis of its frequency response to global stimuli. As has been reported previously, most neurons in the dorsal layers of the torus semicircularis exhibit low- or band-pass responses in the range of 2–50 Hz (Fortune and Rose 1997a). For the global stimulation, we typically used the highest stimulation frequency that elicited visible PSPs in the intracellular recording. This was done for two reasons. First, we were assured that the global stimulus was indeed driving synaptic input during the presentation of the moving object. Second, we measured the magnitude of short-term depression using similar stimuli—if a stimulus did not elicit PSPs, no measurement of short-term depression was possible.

Measurements of physiological data

The magnitudes of PSPs were determined by Fourier analysis of 50- to 750-ms segments of the intracellular responses and by measurements of peak PSP amplitudes (not including spikes) relative to baseline (Fig. 2*A*). Spikes, when present, were clipped, or, in some cases, low-pass filtering (153-Hz corner frequency) was used before analysis. For Fourier analyses, the peak of the power spectrum (in dB) near the stimulus frequency was used as a measure of the amplitude of stimulus-related PSPs. Measurements of peak PSP amplitudes were converted into dB as the ratio between PSP amplitudes: preferred versus nonpreferred direction for moving stimuli and initial versus steady state for the constant-frequency bursts.

The magnitude of short-term synaptic depression was measured using an established methodology (Fortune and Rose 2000; Rose and Fortune 1999). One-second-duration, constant stimulus frequency "bursts" were presented: stimulation frequencies were 5, 10, 20, 30, 40, 50 Hz. Bursts of 20 Hz and above can elicit strong PSP depression (Rose and Fortune 1999) that is caused by short-term synaptic depression (Fig. 2, *B* and *C*) (Fortune and Rose 2000). The details of
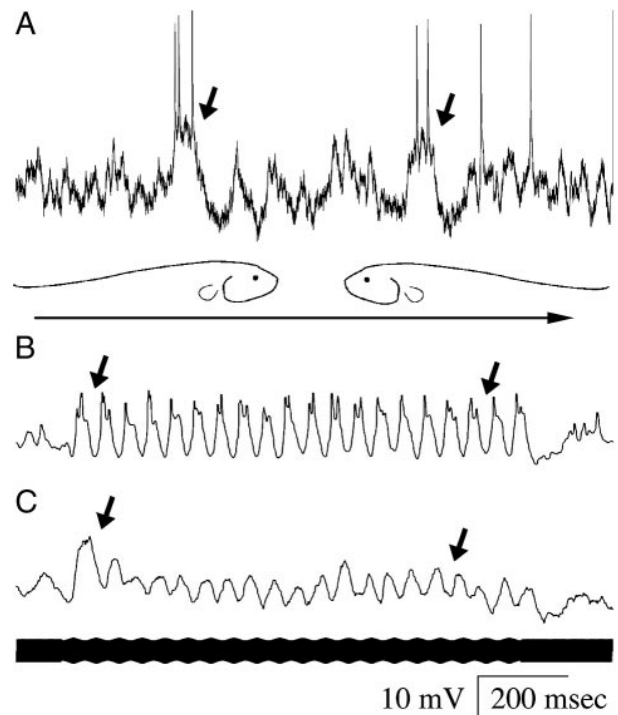

FIG. 2. Examples of intracellular responses to the moving stimulus (*A*) and to the burst stimui (*B* and *C*). *A*: unfiltered response (at resting membrane potential) to a moving object. →, movement of the object stimulus starting at the tail, moving beyond the head, and traveling back toward the tail. Measurements were made after the spikes were removed by clipping or low-pass filtering. ↓, excitatory postsynaptic potentials (EPSPSs) measured for direction selectivity. In this case, the responses for the head- to-tail and tail-to-head directions of object movement were similar. *B* and *C*: examples of responses to a 1-s-duration 20-Hz AM (*bottom*). ↓, area where measurements were made for the quantification of short-term depression. *B* shows response with <1 dB depression, and *C* shows a trace with >6 dB. Traces are averages of 3 repetitions that have been median filtered (MATLAB function ′medfilt1′) to remove spikes; −0.1-nA holding current.

these stimulus bursts are identical to the global stimulation used to simulate the addition of a conspecific during the presentation of the moving object, except that they are 1 s in duration and not continuous. This methodology for measuring short-term synaptic depression produces results that correspond to measures of short-term synaptic depression elicited by more traditional paired-pulse stimulation (Fortune and Rose 2000).

RESULTS

Intracellular recordings were achieved in 20 neurons in 14 fish: complete data sets were obtained for 16 electrosensory neurons of the torus semicircularis in *Eigenmannia*. Resting membrane potentials were measured between −55 and −75 mV. Seals <1 GΩ were associated with lower resting membrane potentials and smaller PSP amplitudes.

Responses to the moving object under solitary electrosensory conditions

Under solitary conditions, the moving object elicited complex PSPs with half-height durations between 55 and 581 ms (Figs. 2 and 3) (Ramcharitar et al. 2005). Peak excitatory responses in each neuron occurred when the object passed along specific areas along the head or trunk of fish. In many
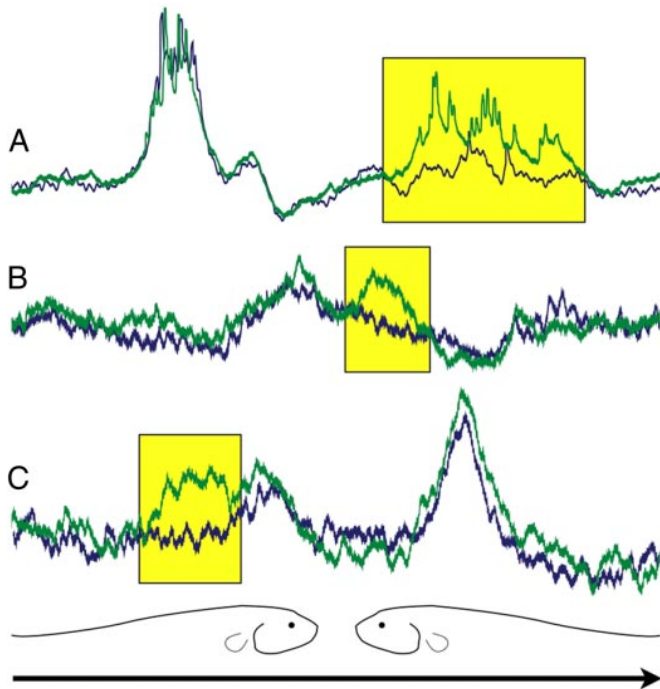
FIG. 3. Intracellularly recorded PSPs of 3 midbrain neurons. Arrow, movement of the object stimulus starting at the tail, moving beyond the head, and traveling back toward the tail. Green traces, responses to the object under solitary conditions. Blue traces, responses to the same stimulus with concomitant global 20- to 50-Hz oscillations. Changes in responses to the moving object under the 2 conditions are highlighted in the yellow boxes. In *A* and *B*, the change in response occurred in the head-to-tail direction, whereas in *C*, it occurred in the tail-to-head direction. In *A* and *C*, excitatory region of the receptive field was along the trunk of the fish, whereas in *B*, it was along the head of the fish. Holding current was −0.1 nA in the recordings. The height of the yellow box indicates 10 mV in *A* and *B* and 5 mV in *C*. The durations of the traces are *A,* 1,500 ms; *B,* 1,800 ms; *C,* 2,300 ms.

neurons, there were additional PSPs, including inhibitory PSPs (IPSPs) adjacent to the largest EPSPs. For this study, we nevertheless focused on measurements of the large EPSPs, as these generated the majority of spiking (which is the ultimate functional output of the neuron that is read by downstream targets) during moving-object stimulation. Responses to the moving object were generally symmetric in shape and timing, but all neurons exhibited some preference for directions of motion (Figs. 3). This preference was measured as differences in PSP amplitudes elicited by the head-to-tail versus tail-to-head stimulation (Fig. 2). Other differences were also seen, including differences in the slopes and durations of PSPs. In 11 neurons the preferred direction was tail to head, and in the opposite direction for 5 neurons. The magnitudes of direction selectivity observed in the solitary condition were between 0.25 and 5.4 dB (mean = 2.49, *n* = 16; Fig. 4).

Responses to the moving object in the presence of ongoing global 20- to 50-Hz oscillations

The responses of each neuron to the moving object were also recorded in the presence of ongoing 20- to 50-Hz oscillations. The most dramatic qualitative effects of the addition of the global oscillations were reductions in PSP amplitudes elicited by one direction of object motion (Fig. 3). This reduction in

amplitude in the response to one direction of movement results in a greater difference related to the direction of object motion. Indeed, for every neuron in this study, the magnitude of difference in responses to the two directions of object motion was increased with the addition of the global oscillations relative to the solitary conditions (paired *t*-test, *n* = 16, *P* < 0.0001). The magnitudes of direction selectivity in the presence of the global oscillations were between 1.60 and 11.80 dB (mean = 4.88, *n* = 16; Fig. 4). The magnitude of the change in directional responses associated with the addition of the global oscillations for individual neurons was between 0.18 and 6.4 dB (mean = 2.39, *n* = 16). We found no qualitative or quantitative differences between the responses to the moving objects in the presence of IG and DG stimulation across neurons.

Relation of short-term synaptic depression to directional responses

The magnitudes of short-term depression observed in this study were between 0.1 and 7.2 dB (mean = 2.79, *n* = 16), which is similar to previous reports (Fortune and Rose 2000; Rose and Fortune 1999). There was a significant correlation between the magnitude of direction selectivity observed in solitary conditions and the magnitude of short-term synaptic depression (linear regression, R^2 = 0.76, *P* < 0.0001; Fig. 4). Also we observed a significant relation between the magnitude of direction selectivity when the object was presented along with ongoing global 20- to 50-Hz oscillations and the magnitude of short-term synaptic depression (linear regression, R^2 = 0.82, *P* < 0.0001; Fig. 4). Finally, we observed a significant correlation between the magnitude of the enhancement of direction selectivity by the addition of the ongoing global oscillations and short-term synaptic depression (linear regression, R^2 = 0.56, *P* < 0.001).

DISCUSSION

We observed directional responses to a moving electrosensory object in the intracellularly recorded activity of midbrain
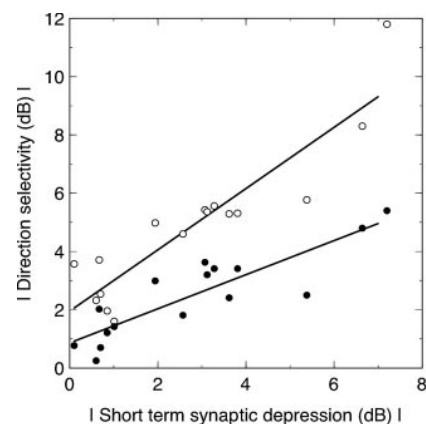

FIG. 4. *A*: relations between magnitudes of short-term depression and direction selectivity in solitary conditions (●) and with global 20- to 50-Hz oscillations (○, each above the corresponding filled dot from the same neuron). There is a statistically significant positive correlation between short-term depression and the direction selectivity in both conditions (regression lines).

neurons in *E. virescens*. Surprisingly, the addition of ongoing global 20- to 50-Hz oscillations increased the magnitude of the directionality of the neurons in this study. Such oscillations occur naturally as a result of the JAR behavior. Therefore post-JAR, background signals generated by nearby conspecifics appear to enhance rather than degrade sensory function, at least at the level of the electrosensory midbrain. The data also support a role for short-term synaptic depression in both the generation of directional responses and in the enhancement of those responses by the addition of the post-JAR global oscillations.

Function of the JAR

The name of the JAR is accurate: the behavior leads to a reduction of the emergent patterns of interference that degrade electrosensory function. Nevertheless, there are alternative solutions to the jamming problem. One solution is to simply move away from conspecifics. Recent data demonstrate that *Eigenmannia* are preferentially found in aggregates or shoals and as a result are continuously exposed to ongoing global oscillations (Oestreich and Zakon 2005; Tan et al. 2005). Another group, *Sternopygus*, solves the jamming problem using a sensory processing solution. These animals do not exhibit JAR behaviors and appear to be immune to electrosensory jamming (Bullock et al. 1975; Matsubara and Heiligenberg 1978; Rose and Canfield 1993). This immunity to jamming is conferred by a specialized class of neurons in the electrosensory lateral line lobe (ELL) (Matsubara 1981, 1982).

The JAR requires that fish simultaneously process information from two behaviorally-relevant sources. First, there is information from the global synchronous 20- to 50-Hz (gamma-band) oscillations that are produced by the combination of social behavior and the JAR. Second, there is information from more local, lower frequency stimuli. In a previous study, the magnitudes of midbrain responses to moving local stimuli were dramatically reduced by the addition of lower (<10 Hz) but not by higher-frequency (>15 Hz) global stimuli (Ramcharitar et al. 2005). Here we have shown that the higher-frequency global stimuli have an effect on direction selectivity: direction selectivity is enhanced.

Might the JAR, therefore be a mechanism that has two roles—first to avoid detrimental patterns of interference and, second, to create beneficial patterns of interference. Interestingly, the organization of the ascending electrosensory projections to the midbrain in electric fishes has dynamic features that appear to facilitate the propagation of low-frequency local stimuli and higher-frequency global stimuli like those that result from the JAR. The receptive field properties of neurons in the ELL are dynamic and differ with respect to the spatial extent of the stimulus. Local stimuli tend to elicit low-pass (<10 Hz) or all-pass responses, whereas responses to global stimuli are high-pass (>20 Hz) filtered; descending negative feedback is primarily activated by global stimulation and acts to suppress responses to slow modulations or steady-state levels of signal amplitude (Chacron et al. 2003, 2005; also see Oswald et al. 2004). A function of these dynamic receptive fields may be to allow the same afferent neuron to transmit both the ongoing 20- to 50-Hz global oscillations and lower-frequency local stimuli. In this way, the high-frequency global

oscillations elicit short-term synaptic depression at midbrain synapses that may also transmit the local, low-frequency information. The mechanism by which induction of short-term depression may contribute to the enhancement of directional responses in midbrain neurons is not yet known but may be similar to principles described in a model for visual processing of moving images (Chance et al. 1998).

Role of short-term synaptic depression in the generation of direction selectivity

In a model proposed by Chance et al. (1998), short-term synaptic depression limits the rise in PSP amplitude over time, which results in a phase-advance in peak amplitude (Fortune and Rose 2002). For the same pattern of inputs, the peaks of PSPs can be phase shifted by the activation of short-term depression relative to synapses that do not exhibit this depression (see Fortune and Rose 2001, 2002).

Direction selectivity can be achieved by systematic distribution of magnitudes of short-term synaptic depression among afferents with different receptive fields (Chance et al. 1998; Fortune and Rose 2002). Consider two receptive fields at adjacent locations in the receptor array with the same responses to a moving object. Information for one of the receptive fields passes through a synapse with short-term depression and the other does not. If the moving object passes first through the receptive field without depression and shortly thereafter through the receptive field with depression, the peak responses could occur at the same time. This would happen when the phase advance that results from short-term depression is equal to the time disparity between activation of the receptive fields. A neuron receiving these simultaneous inputs from the two receptive fields could respond strongly to the moving object. Movement in the opposite direction would reverse the order of stimulation of receptive fields. As a result, the peak responses would occur at different times. A neuron that received information from these two receptive fields would potentially not respond (Fortune and Rose 2002). This model can produce direction selectivity in circuits that use only excitatory synapses or in circuits that use a combination of excitatory and inhibitory synapses (Fortune and Rose 2002).

In this same manner, directionality could be further enhanced if information from one receptive field passed through a facilitating synapse, such that the response peak was delayed (Fortune and Rose 2001, 2002). Neurons in the torus can exhibit both short-term synaptic depression and facilitation (Fortune and Rose 2000). The depression and facilitation are differentially activated in such neurons: high-temporal frequency stimuli, like post-JAR global oscillations, maximally elicit depression and not facilitation, whereas low-temporal frequency stimuli can strongly drive facilitation.

The hypothesis that short-term synaptic plasticity is used as a form of delay line is difficult to test in intact systems. The pattern of afferent activity from moving stimuli will necessarily activate the synaptic plasticity and as a result, the plasticity and other mechanisms for processing of motion-related activity cannot be easily disassociated. Also, because the model requires the convergence of information through synapses that exhibit plasticity and others that do not, it is unclear what sort of measurements of depression one might expect from direct

afferent stimulation. Nevertheless, the electrosensory midbrain contains the processing units required by the model. First, neurons in the torus exhibit dramatic differences in the magnitude of short-term synaptic depression that are elicited by sensory stimuli and direct, paired-pulse stimulation of afferents (Fortune and Rose 2000). Second, moving stimuli elicit reliable responses in these neurons, and many neurons exhibit strongly directional responses.

What intrigued us initially was the possibility that we could use naturally occurring electrosensory stimuli in *Eigenmannia* to modulate the strength of short-term synaptic plasticity in the midbrain. If short-term synaptic depression has a role in the generation of directional responses, then the modulation of short-term plasticity by these stimuli should dramatically alter directionality. Specifically, if short-term synaptic depression is used as a form of delay line, alteration of the depression by the addition of the global stimulus should result in changes in the delays that result from depression and thus potentially degrade the directional responses. Indeed we expected that modulation of short-term plasticity by the addition of broad-field electrosensory stimulus would lead to a dramatic degradation of direction selectivity.

Remarkably, the opposite result occurred: the addition of the depressing broad-field stimulus led to an increase in direction selectivity. There are many possible substrates for this unexpected phenomenon. The most likely candidate at present is short-term synaptic plasticity, which is supported by our observation of a strong correlation between the magnitude of the enhancement of directionality and the magnitude of short-term depression. Such a mechanism might include the modulation of excitatory and inhibitory synapses (Fortune and Rose 2002). Other mechanisms are possible, however, and include short-term synaptic facilitation, descending inputs to the ELL (Bratton and Bastian 1990), and nonclassical receptive field properties in the ELL (Chacron et al. 2003), some form of gain modulation (Chance et al. 2002), among others.

Of particular interest are mechanisms present in the afferent system, the ELL, that may also contribute to the complex direction selectivity observed in toral neurons. The ELL receives descending inputs from the nucleus praeeminentialis (NPd) that enhance responses of ELL neurons to local stimuli such as prey (Bratton and Bastian 1990). These descending inputs must be delayed relative to incoming inputs and therefore may produce focal temporal disparities for motion processing. Other ELL mechanisms may also result in nonlinearities in the responses to moving objects including voltage-dependent EPSPs, dendritic Na^+ conductances, and nonlinearities associated with bursts (Berman et al. 1997).

Interestingly, the temporal filtering properties of ELL neurons in *Apteronotus* differ in relation to the spatial organization of the stimulus: ELL neurons exhibit high-pass responses to broad-field stimuli and low-pass responses to local stimuli (Chacron et al. 2003). The mechanisms for this spatially dependent change appear to result from descending feedback and differ among the classes of ELL pyramidal cells (Chacron et al. 2005). Although not tested, this circuitry likely results in nonlinear interactions during concomitant presentation of local and global stimuli. Analyses of data from concomitant presentation of beats and chirps, both of which are global signals,

demonstrated an interaction at the level of the receptor afferents that resulted from spike frequency adaptation (Benda et al. 2005). Finally, responses to moving objects in the presence of beat frequencies of 32 Hz in *Apteronotus leptorhynchus* are robust (Bratton and Bastian 1990) despite the fact that ELL neurons respond more strongly to higher AM rates (Bastian 1987) and may exhibit some directionality in the responses (see Fig. 5 of Bratton and Bastian 1990).

Relations of post-JAR global electrosensory stimuli to Gamma-band oscillations

Mammalian cortical systems commonly produce oscillations in a range of frequencies centered around 40 Hz (Csibra et al. 2000): these intrinsic cortical oscillations are known as gamma-band oscillations. Further, gamma-band oscillations appear to be generated during the processing of behaviorally-relevant, time-varying information in a phylogenetically diverse array of vertebrate species (Bullock and Achimowicz 1994). The functional role of gamma-band oscillations is a subject of great speculation.

Most species generate gamma-band oscillations using intrinsic mechanisms. Intrinsic gamma-band oscillations emerge at many levels in the nervous system among species (e.g., Csibra et al. 2000; Ishikane et al. 2005; Lutzenberger et al. 2002; Neiman and Russell 2004). In *Apteronotus,* a closely related species of electric fish, certain electrosensory stimuli can induce intrinsic oscillations in the gamma range using central mechanisms (Doiron et al. 2003). *Eigenmannia* appear to be unusual in that these animals generate gamma-band oscillations in CNS circuits using an external source: via electrosensory signals that result from social behavior and the JAR.
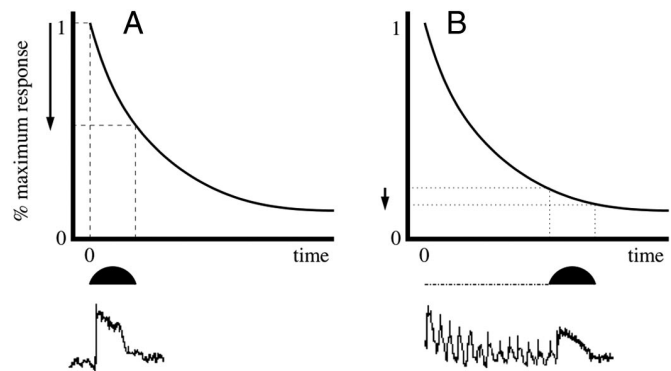

FIG. 5. Schematic plots show the response magnitude of a neuron that exhibits short-term synaptic depression as a function of ongoing stimulation. At the initiation of stimulation, the response of the neuron is at its peak, in this case, 1. As the stimulation is maintained, the response magnitude is depressed and eventually reaches an asymptote. If a salient stimulus, represented by the solid half circle, is presented alone (*A*), the neuron will respond initially at its maximum and rapidly depress. The dotted vertical lines indicate the beginning and end of the salient stimulus. A schematic PSP below the plot illustrates such a response. However, if the same stimulus is presented after a period of ongoing gamma-band activation of this neuron (*B*), the initial response magnitude will be smaller and will depress at a different rate and magnitude than without the prior stimulation. The schematic PSPs below the plot illustrate the response of the neuron to the gamma-band oscillation followed by the response to the salient stimulus. Again, the vertical lines indicate the beginning and end of the salient stimulus. Arrows at the left of each plot indicate the depression that occurs during the presentation of the salient stimuli in the 2 conditions.

Previous work has shown that there is a linkage between sensory-driven gamma-band oscillations and short-term synaptic depression in *Eigenmannia* (Fortune and Rose 2000). The sensory-driven gamma-band oscillations may therefore function to modulate synaptic weights for the purpose of enhancing the temporal processing of streams of information (Lutzenberger et al. 2002). The critical observation is that identical stimuli presented alone or simultaneously with a gamma-band oscillation can result in dramatic differences in stimulus-related information processing in the brain (Fig. 5). The specific mechanisms by which these changes in information processing lead to enhancement of temporal features remain unclear. Nevertheless, the key feature of this model is that the effect of global synchronous gamma-band spiking activity is measured by its affect on the processing of simultaneously occurring streams of information in single neurons.

This interaction between gamma-band oscillations and single neuron processing by the modulation of short-term synaptic plasticity may be a general mechanism for the enhancement of temporal processing in vertebrates. Short-term synaptic plasticity is ubiquitous in sensory systems of vertebrates (Abbott and Regehr 2004; Fortune and Rose 2001). The induction of global synchronous gamma-band oscillations associated with attention (Shibata et al. 1999), for example, may be used to enhance temporal processing of information from a specific region of the sensory array. Similarly, gamma-band oscillations associated with voluntary movements (Donoghue et al. 1998) may enhance the temporal processing of sensory feedback generated during motor behavior. These ideas can be tested in weakly electric fish using psychophysical tests under solitary and post-JAR social conditions.

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