Phantoms in the brain: Ambiguous representations of stimulus amplitude and timing in weakly electric fish

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ABSTRACT

In wave-type weakly electric fish, two distinct types of primary afferent fibers are specialized for separately encoding modulations in the amplitude and phase (timing) of electrosensory stimuli. Time-coding afferents phase lock to periodic stimuli and respond to changes in stimulus phase with shifts in spike timing. Amplitude-coding afferents fire sporadically to periodic stimuli. Their probability of firing in a given cycle, and therefore their firing rate, is proportional to stimulus amplitude. However, the spike times of time-coding afferents are also affected by changes in amplitude; similarly, the firing rates of amplitude-coding afferents are also affected by changes in phase. Because identical changes in the activity of an individual primary afferent can be caused by modulations in either the amplitude or phase of stimuli, there is ambiguity regarding the information content of primary afferent responses that can result in 'phantom' modulations not present in an actual stimulus. Central electrosensory neurons in the hindbrain and midbrain respond to these phantom modulations. Phantom modulations can also elicit behavioral responses, indicating that ambiguity in the encoding of amplitude and timing information ultimately distorts electrosensory perception. A lack of independence in the encoding of multiple stimulus attributes can therefore result in perceptual illusions. Similar effects may occur in other sensory systems as well. In particular, the vertebrate auditory system is thought to be phylogenetically related to the electrosensory system and it encodes information about amplitude and timing in similar ways. It has been well established that pitch perception and loudness perception are both affected by the frequency and intensity of sounds, raising the intriguing possibility that auditory perception may also be affected by ambiguity in the encoding of sound amplitude and timing.

1. Introduction

Sensory stimuli vary along several different dimensions. Often, these different dimensions are linked to distinct categories of perception. In the auditory system, for example, pitch perception is largely related to sound frequency, whereas the perception of loudness is largely related to sound intensity (Gelfand, 2004). Similarly, in the visual system, the perception of color largely corresponds to the wavelength of light, whereas brightness perception largely relates to the intensity of light (Marr, 1982). The existence of different perceptual categories that correspond to unique physical dimensions of stimuli suggest that these different dimensions are each encoded by separate, parallel neural pathways (Young, 1998). Indeed, mammalian and avian auditory systems have distinct central pathways that are specialized for processing sound amplitude, frequency, and timing (Oertel, 1999; Takahashi et al., 1984), and the primate visual system has separate pathways for processing information about form, color, movement, and depth (Livingstone and Hubel, 1987; Marr, 1982; Merigan and Maunsell, 1993).

Despite these specializations, however, the perception of different stimulus attributes is not always completely independent (Garner, 1974; Kemler-Nelson, 1993). In the auditory system, changes in sound intensity can result in perceived changes in pitch, and conversely, changes in sound frequency can result in perceived changes in loudness (Grau and Kemler-Nelson, 1988; Hartmann, 1978; Melara and Marks, 1990a,b; Neuhoff et al., 1999; Rossing and Houtsma, 1986; Stevens, 1935). The well known Doppler effect (Doppler, 1842), in which the perceived pitch of a sound rises as the sound source moves towards a receiver, and then falls as it passes the receiver, is widely believed to result solely from the effects of that motion on sound frequency (Neuhoff and McBeath, 1996). Contrary to popular belief, however, there is no increase in frequency as the sound source approaches the receiver, only a drop in frequency as the sound source passes the receiver. The perceived increase in pitch that occurs as the sound source moves towards the receiver actually results from the gradually increasing intensity of the sound (McBeath and Neuhoff, 2002; Neuhoff and McBeath, 1996).

Many perceptual interactions occur in the visual system as well. High contrast objects appear to move faster than low contrast objects that are moving at the same speed (Anstis, 2003,

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2004; Livingstone and Hubel, 1987). The phenomenon of color constancy refers to the perceived color of an object remaining constant despite changes in ambient illumination, revealing that color perception is a function of both wavelength and brightness (Land, 1959). Motion can influence form perception: a figure camouflaged against a background will suddenly become visible if it moves with respect to the background, a phenomenon known as coherent motion (Albright and Stoner, 1995).

Recent experiments in weakly electric fish demonstrate a similar lack of independence in the perception of the amplitude and timing of electrosensory stimuli (Carlson and Kawasaki, 2006a, 2007). Recordings from peripheral and central electrosensory neurons suggest that this lack of independence is directly related to ambiguity in the encoding of these two attributes by individual sensory neurons (Carlson and Kawasaki, 2006a, 2008). In this review, I describe how individual electrosensory neurons can respond similarly to changes in either stimulus amplitude or phase, and how these neuronal responses successfully predict behavioral responses to electrosensory stimuli. I then discuss the potential implications of these findings for stimulus encoding and sensory perception in general.

2. The importance of amplitude and timing information for electrosensory-mediated behavior

2.1. Weakly electric fish

The South American gymnotiform and the African mormyriform fishes generate weak electric fields using specialized electric organs (Caputi et al., 2005). They also sense these electric organ discharges (EODs) using an array of electroreceptors distributed throughout the body surface (Zakon, 1986). They are therefore able to use these EODs to communicate with each other (Carlson, 2006; Hopkins, 1988) and to actively sense their environment by detecting distortions in their own EOD caused by nearby objects, a process called active electrolocation (von der Emde, 1999). The ability to generate and receive these weak electric signals appears to have evolved independently in the two lineages of fishes (Lauder and Liem, 1983), providing a rare opportunity to study the convergent evolution of an entire sensorimotor system (Bullock et al., 1983; Bullock et al., 1982; Hopkins, 1995; Kawasaki, 1997).

2.2. Electric communication and the jamming avoidance response

Several species of gymnotiforms and a single species of mormyriform (*Gymnarchus niloticus*) generate continuous, quasi-sinusoidal electric fields at frequencies ranging from 60 to 2000 Hz (Fig. 1). The baseline EOD frequency plays a crucial role in electric communication behavior, as it exhibits characteristic species and sex differences and is generally very stable within individuals (Hopkins, 1972, 1974a,b, 1976, 1988; Kramer et al., 1980; Moortgat et al., 1998).

To determine the EOD frequency of a neighboring individual, a fish must perform a complex, spatiotemporal analysis of the electric field that results from the interaction between its own EOD (frequency = f_1) and its neighbor's EOD (frequency = f_2). When two periodic signals with different frequencies are added together, the effects of constructive and destructive interference result in a combined signal that is modulated in both amplitude and phase (timing) (Fig. 2A). The rates of amplitude modulation (AM) and phase modulation (PM) are both equal to the magnitude of the frequency difference between the two component signals, $Df = f_2 - f_1$. However, the temporal relationship between AM and PM is different for opposite signs of Df (Fig. 2A). Relative to the original, uncontaminated EOD, a neighboring fish with a higher EOD frequency ($+Df$) will give rise to a combined signal that is delayed in phase during
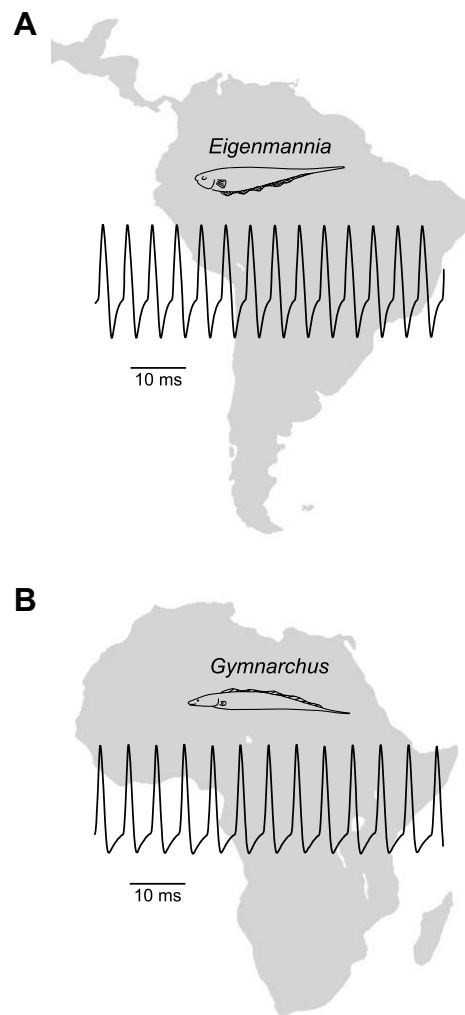
Fig. 1. Electrogenesis and electroreception evolved independently in the South American gymnotiforms and the African mormyriforms. The gymnotiform *Eigenmannia* (A) and the mormyriform *Gymnarchus* (B) both generate a quasi-sinusoidal electric organ discharge (EOD) ranging in frequency from about 250 to 600 Hz. Both species also perform the jamming avoidance response (JAR) using an identical computational algorithm (see text for details).

amplitude increases and advanced during amplitude decreases. When the neighboring fish has a lower EOD frequency ($-Df$), the exact opposite pattern occurs: amplitude increases during phase advances and amplitude decreases during phase delays. This difference can easily be seen if one plots amplitude vs. phase in a Lissajous graph that develops over time; for $+Df$, the result is a circle with a counterclockwise sense of rotation, while for $-Df$, the result is a circle with a clockwise sense of rotation (Fig. 2A).

In principle, fish could determine the magnitude and sign of Df by simply comparing the pattern of AM and PM over time. However, to detect phase advances or delays, the fish need a timing reference. They are unable to use their uncontaminated EOD for comparison, because that is no longer available. Instead, the fish take advantage of spatial variation in the electric field. Due to the different locations and orientations of two fish's electric organs, different portions of an individual's body surface are exposed to different amounts of interference from the neighboring fish's EOD. As a result, some regions of the body surface are subjected to strong modulation, while other regions are subjected to weak modulation, and the fish can measure differences in signal timing between these two regions to determine the pattern of PM. Combining this differential phase information with information about
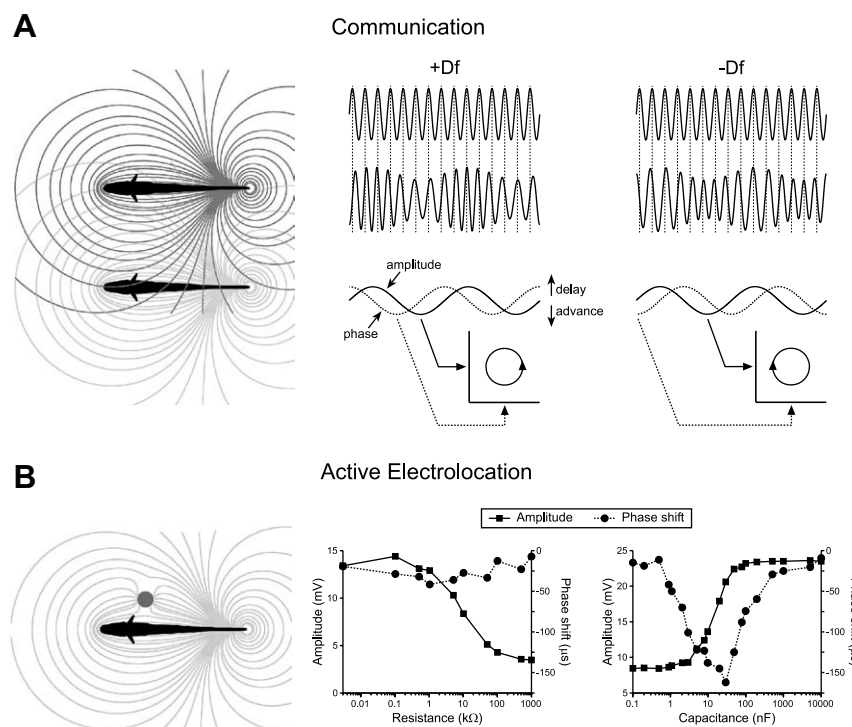
Fig. 2. Behaviorally-relevant information is transmitted via amplitude modulation (AM) and phase modulation (PM) of the EOD. Electric field images are modified after Krahe and Gabbiani (2004). (A) Electrical interference from the EOD of a neighboring fish results in AM and PM, which plays an important role in communication and the JAR. The temporal relationship between AM and PM differs depending on whether the fish has a lower EOD frequency than its neighbor (+*Df*) or a higher EOD frequency than its neighbor (−*Df*). For both cases, an unmodulated sine wave is plotted above a modulated sine wave, with vertical dashed lines marking the timing of peaks in the unmodulated sine wave. Below these plots, the pattern of AM (AM waveform) is shown as a solid line and the pattern of PM (PM waveform) is shown as a dashed line. Plotting AM against PM in a Lissajous graph that develops over time results in circles with a counterclockwise sense of rotation for +*Df* and a clockwise sense of rotation for −*Df*. (B) AM and PM can also result from the presence of nearby objects, which plays an important role in active electrolocation. The left graph shows the changes in amplitude and phase that result from purely resistive objects (simple impedances with no capacitance), whereas the right graph shows the changes in amplitude and phase that result from capacitive objects (complex impedances). Simple impedances affect amplitude only, whereas complex impedances affect both amplitude and phase. Both graphs are modified from von der Emde (1998).

changes in amplitude allow the fish to determine the sign of *Df* (Heiligenberg, 1991; Heiligenberg et al., 1978; Heiligenberg and Bastian, 1980; Kawasaki, 1993; Takizawa et al., 1999).

The ability to determine the sign of *Df* plays a crucial role in a behavior called the 'jamming avoidance response', or JAR. When two individuals with similar EOD frequencies meet (|*Df*| < 5 Hz), their active electrolocation abilities are impaired, or 'jammed', by mutual interference (Heiligenberg, 1973, 1975). Both fish actively avoid this jamming by shifting their EOD frequencies away from each other (Bullock et al., 1975; Bullock et al., 1972a,b; Watanabe and Takeda, 1963). Therefore, each fish needs to determine the sign of *Df* to decide whether to raise or lower its EOD frequency. The JAR and its underlying neural circuitry have been extensively studied in the gymnotiform *Eigenmannia* and the mormyriform *Gymnarchus* (Fig. 1), both of which use the same algorithm of comparing the pattern of AM with the pattern of differential PM to determine the sign of *Df* (Heiligenberg, 1991; Kawasaki, 1993, 1997; Takizawa et al., 1999). Both species are extremely sensitive to small changes in stimulus amplitude and phase. In *Eigenmannia*, JARs are elicited by stimuli with AM depths as small as 0.1% and PM depths as small as 400 ns (Carr et al., 1986; Rose and Heiligenberg, 1985). In *Gymnarchus*, JARs are reliably elicited by stimuli with AM depths of 0.2% and PM depths of 1 μs, and one particularly sensitive fish responded to a stimulus with an AM depth of 0.02% and a PM depth of 90 ns (Guo and Kawasaki, 1997).

2.3. Active electrolocation

Amplitude and phase information also play important roles in active electrolocation behavior (Bastian, 1986; von der Emde,

1999). A fish's electric field is distorted by objects within the field that have impedance which differs from the surrounding water (Fig. 2B). The fish use these distortions to obtain information about various characteristics of objects, such as size, shape, distance, and electrical properties (von der Emde, 1999). Purely resistive objects (simple impedances) cause changes in electric field amplitude, but not phase (Fig. 2B). By contrast, objects with capacitance (complex impedances) cause changes in both amplitude and phase (von der Emde, 1998). By using information about both AM and PM, weakly electric fish are able to distinguish the resistive and capacitive components of objects (von der Emde, 1990, 1998; von der Emde and Ringer, 1992). This ability is probably important for distinguishing living from non-living objects, because capacitance is a characteristic of living organisms (von der Emde, 1999).

3. Ambiguity in the encoding of amplitude and timing information

3.1. Separate electrosensory pathways are specialized for encoding and processing amplitude and timing information

In wave-type weakly electric fish, the tuberous electroreceptors that transduce EOD stimuli give rise to two distinct types of primary electrosensory afferent fibers, time-coding afferents and amplitude-coding afferents (Fig. 3) (Zakon, 1986). In the South American gymnotiforms, these are referred to as T-afferents (for *time*-coder) and P-afferents (for *probability*-coder), respectively (Scheich et al., 1973). In the African fish *Gymnarchus*, they are referred to as S- and O-afferents, respectively (Bullock et al., 1975). Within the natural range of stimulus intensities (1–3 mV/cm), time-coding afferents
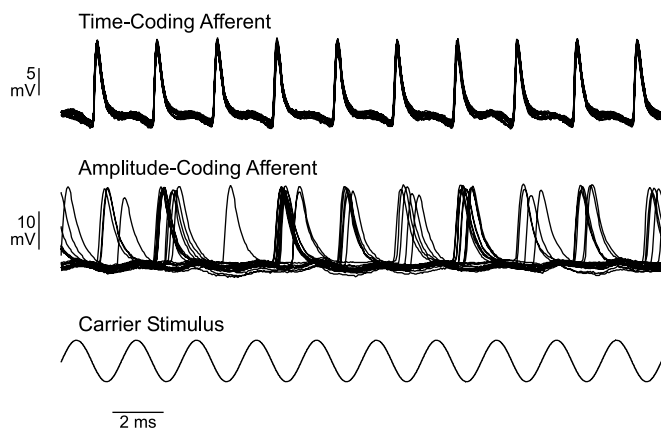
Fig. 3. Tuberous electroreceptors give rise to two distinct types of primary electrosensory afferents in *Eigenmannia* and *Gymnarchus*. Twenty sweeps of an intracellular recording from a time-coding afferent (S-afferent) and 20 sweeps of an intracellular recording from an amplitude-coding afferent (O-afferent) were obtained from a single *Gymnarchus* in response to an unmodulated sinusoidal electric carrier stimulus. For each afferent, the 20 sweeps are shown superimposed to illustrate the regularity of firing and the degree of phase-locking to the carrier stimulus.

fire a single spike in response to each cycle of a periodic stimulus. The timing of these spikes is very precise with respect to the stimulus (high degree of phase locking), so that the spike times of time-coding afferents serve as a fairly reliable indicator of stimulus timing, or phase (Fig. 3). By contrast, amplitude-coding afferents fire more sporadically and less tightly phase locked to the stimulus (Fig. 3). However, their probability of firing in a given cycle is directly proportional to stimulus amplitude. As a result, the firing rates of amplitude-coding afferents serve as a fairly reliable indicator of stimulus amplitude.

In both *Gymnarchus* and the gymnotiforms, the two different types of afferents give rise to separate, parallel electrosensory pathways within the hindbrain electrosensory lateral line lobe (ELL) and midbrain torus semicircularis that are specialized for processing either amplitude or timing information (Bell and Maler, 2005; Carr and Maler, 1986; Kawasaki, 2005). In both cases, these two pathways converge within the torus semicircularis, where there are many neurons that integrate information about AM and PM and thereby respond selectively to the magnitude and sign of *Df* (Carlson and Kawasaki, 2004, 2006b; Heiligenberg and Rose, 1986, 1985; Kawasaki and Guo, 2002; Rose and Heiligenberg, 1986).

3.2. Individual primary afferents encode both amplitude and timing information

In recent years, information theoretic techniques have been widely applied to study electrosensory encoding and processing in weakly electric fish (for reviews, see Fortune, 2006; Gabbiani and Metzner, 1999; Sawtell et al., 2005). The basic methodology of these studies involves presenting fish with sinusoidal electric fields subjected to random, low-pass filtered, Gaussian-distributed modulations, recording the responses of electrosensory neurons to these random modulations, and then determining the resulting rates of information transmission (Bialek et al., 1991; Borst and Theunissen, 1999; Rieke et al., 1997). One way to assess the stimulus encoding performance of a neuron is to use its response to a particular random modulation stimulus to reconstruct an optimal linear estimate of that stimulus (Bialek et al., 1991). The agreement between the actual and estimated stimulus provides a measure of how well that neuron encodes that particular stimulus, which can be quantified with a simple metric called the coding fraction, which ranges from 0 when estimation is at chance level to 1 when

the stimulus is perfectly estimated (Gabbiani and Koch, 1998; Gabbiani and Metzner, 1999; Wessel et al., 1996).

In weakly electric fish, this technique has been used extensively to study the encoding of AM by amplitude-coding afferents (P-afferents) in gymnotiforms. Coding fractions for low frequency random AM can be as high as 0.83, revealing that individual P-afferents can linearly encode as much as 83% of the information within a low frequency, random AM stimulus (Carlson and Kawasaki, 2006a; Gabbiani et al., 1996; Kreiman et al., 2000; Wessel et al., 1996). Similarly, O-afferents in *Gymnarchus* are able to encode up to 67% of low frequency random AM (Carlson and Kawasaki, 2008). Recently, we applied similar methods to study the encoding of PM by time-coding afferents: T-afferents in *Eigenmannia* are able to encode up to 80% of low frequency random PM (Carlson and Kawasaki, 2006a), and S-afferents in *Gymnarchus* are able to encode up to 77% of low frequency random PM (Carlson and Kawasaki, 2008).

We used this stimulus estimation method to test the hypothesis that amplitude and timing information are encoded independently by the two types of afferents (Carlson and Kawasaki, 2006a, 2008). When amplitude and phase are both randomly modulated simultaneously, time-coding afferents exhibit a clear preference for encoding random PM, whereas amplitude-coding afferents exhibit a clear preference for encoding random AM (Fig. 4A and B). Surprisingly, however, when low frequency random AM is presented alone (no PM), the coding fractions of T-afferents can be as high as 0.52, and the coding fractions for S-afferents can be as high as 0.57 (Fig. 4A and B). Similarly, when low frequency random PM is presented alone (no AM), P-afferent coding fractions can be as high as 0.83, and O-afferent coding fractions can be as high as 0.64 (Fig. 4A and B). Thus, even though there are two distinct types of afferents that preferentially encode information about either stimulus amplitude or timing, both types of afferents can also encode information about their nonpreferred attribute (AM for time-coding afferents and PM for amplitude-coding afferents).

The fact that we obtained similar results in two distantly related species from separate lineages that evolved their electrosensory systems independently suggests that a lack of independence in the encoding of amplitude and timing information may be an unavoidable feature of a sensory system that is specialized for encoding these two attributes. We addressed this issue by constructing simple model neurons with a preference for encoding either AM or PM (see Carlson and Kawasaki, 2006a for details). These model neurons exhibited a clear preference for encoding either amplitude or phase when both were modulated simultaneously (Fig. 4C). However, both types of model neurons also encoded significant amounts of information about their nonpreferred attribute when it was modulated separately (Fig. 4C), just like the actual primary afferents (Carlson and Kawasaki, 2006a). This supports the hypothesis that neurons that maximally encode information about either the amplitude or timing of sensory stimuli will inevitably also encode information about the other attribute.

3.3. Primary afferent responses result in phantom amplitude and phase modulations

If one considers the problem of sensory perception from the perspective of the organism (Bialek et al., 1991), then the lack of independence in the encoding of amplitude and timing information creates a problem. To appreciate this, assume that the organism obtains information about PM via time-coding afferent activity and information about AM via amplitude-coding afferent activity, a reasonable assumption given that both types of afferents preferentially encode those particular attributes. If a stimulus consists of modulations in both amplitude and phase, then this strategy allows the organism to obtain accurate information about both
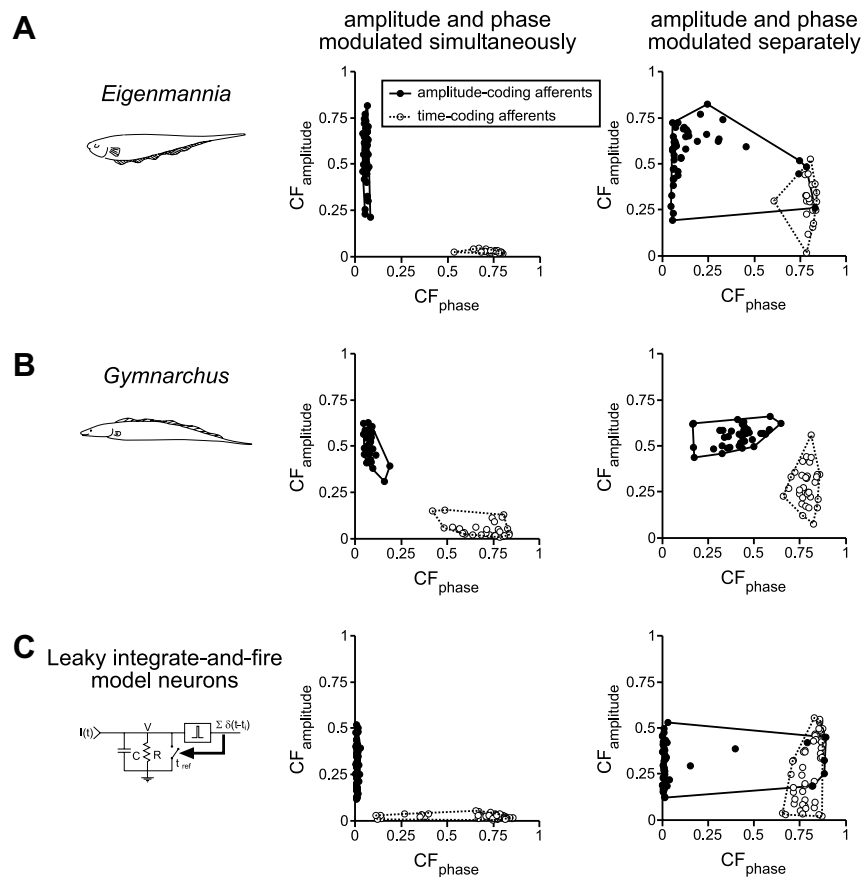
Fig. 4. Coding fractions for random AM ($CF_{amplitude}$) and random PM (CF_{phase}) for (A) amplitude- and time-coding afferents in *Eigenmannia* ($n=45$ P-afferents and $n=21$ T-afferents, respectively), (B) amplitude- and time-coding afferents in *Gymnarchus* ($n=40$ O-afferents and $n=38$ S-afferents, respectively), and (C) leaky integrate-and-fire model neurons that preferentially encode either AM (amplitude-coding afferents, $n=50$) or PM (time-coding afferents, $n=50$). In each case, the left graph shows the coding fractions when amplitude and phase were modulated simultaneously, whereas the right graph shows the coding fractions when amplitude and phase were modulated separately. Data in (A) are from Carlson and Kawasaki (2006a), using random AM with standard deviations ranging from 10% to 25% and random PM with standard deviations ranging from 10° to 30°, both with a low-pass cutoff frequency of 20 Hz. Data in (B) is from Carlson and Kawasaki (2008), using random AM with standard deviations ranging from 5% to 25% and random PM with standard deviations ranging from 5° to 30°, both with a low-pass cutoff frequency of either 10 or 20 Hz. Data in (C) are from Carlson and Kawasaki (2006a), using random AM with a standard deviation of 20% and random PM with a standard deviation of 15°, both with a low-pass cutoff frequency of 20 Hz.

attributes. However, time-coding afferents respond to AM when there is no PM. Continuing with our assumption that the organism obtains information about PM by way of time-coding afferent activity, those responses would cause the organism to perceive modulations in phase that are not actually occurring. Conversely, the responses of amplitude-coding afferents to a stimulus consisting solely of PM would cause the organism to perceive modulations in amplitude that are not actually occurring. These perceived modulations would represent 'phantom' modulations, since they are not present in the actual stimulus, but emerge internally within the animal's nervous system.

It is important to remember that the stimulus estimation method we used to determine information transmission uses a linear filter to yield an optimal estimate of the stimulus, which results in different filters for the same afferent when estimating either random AM or random PM. However, the postsynaptic neurons that receive input from primary afferents use one particular filter for decoding primary afferent activity that could, in principle, filter out the effects of the nonpreferred attribute on afferent activity. The postsynaptic neuron would thereby effectively "ignore" the information conveyed about the nonpreferred attribute. We tested this hypothesis by assuming that the postsynaptic targets of amplitude-coding afferents would use the optimal algorithm for estimating AM to decode afferent activity, and similarly, that the postsynaptic targets of time-coding afferents would use the optimal algorithm for estimating PM to decode afferent activity (Carl-
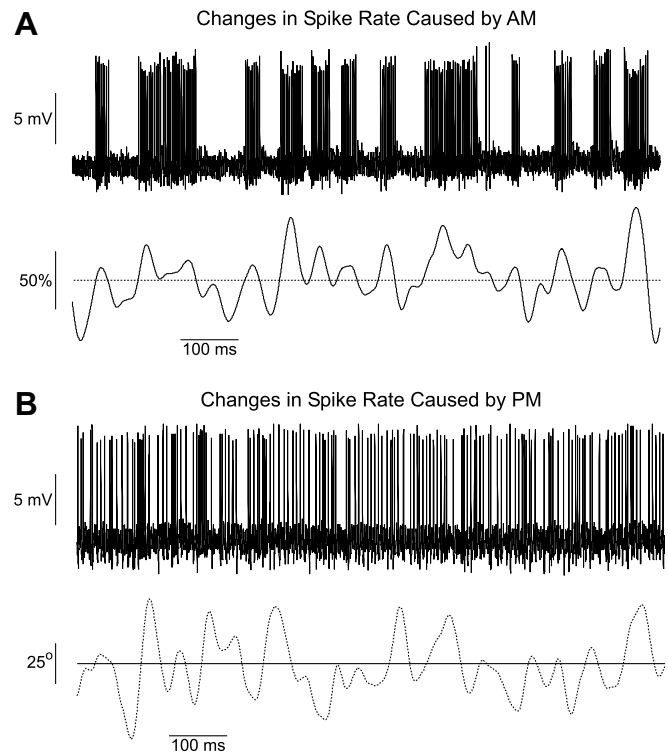
son and Kawasaki, 2006a). However, this approach did not solve the problem of phantom modulations: the responses of T-afferents in *Eigenmannia* to random AM with a standard deviation equal to 25% of the carrier amplitude resulted in an estimated standard deviation of PM equal to $2.54 \pm 0.25°$ (mean $\pm$ sem; $n=10$ units), and the responses of P-afferents to random PM with a standard deviation equal to 15° of the carrier phase resulted in an estimated standard deviation of AM equal to $6.83 \pm 0.68\%$ (mean $\pm$ sem; $n=43$ units). Both of these values (2.54° and 6.83%) are two orders of magnitude greater than the behavioral thresholds for actual modulations in phase and amplitude of 0.029° and 0.05%, respectively (Rose and Heiligenberg, 1985).

This finding suggests that both AM and PM have similar effects on the activity of individual primary afferents. Indeed, individual time-coding afferents precisely track changes in phase through shifts in spike timing (Fig. 5A), but also respond to changes in amplitude with shifts in spike timing: increases in amplitude lead to phase advances and decreases in amplitude lead to phase delays (Fig. 5B). In fact, this amplitude-dependent latency shift has been recognized for some time (Kawasaki and Guo, 1996; Scheich et al., 1973), and our recent results make it clear that it can play a significant role in encoding information about stimulus amplitude. Similarly, individual amplitude-coding afferents track changes in amplitude via changes in spike rate (Fig. 6A), but the spike rates of amplitude-coding afferents also change in response to PM, with spike rates typically increasing during phase delays and decreasing
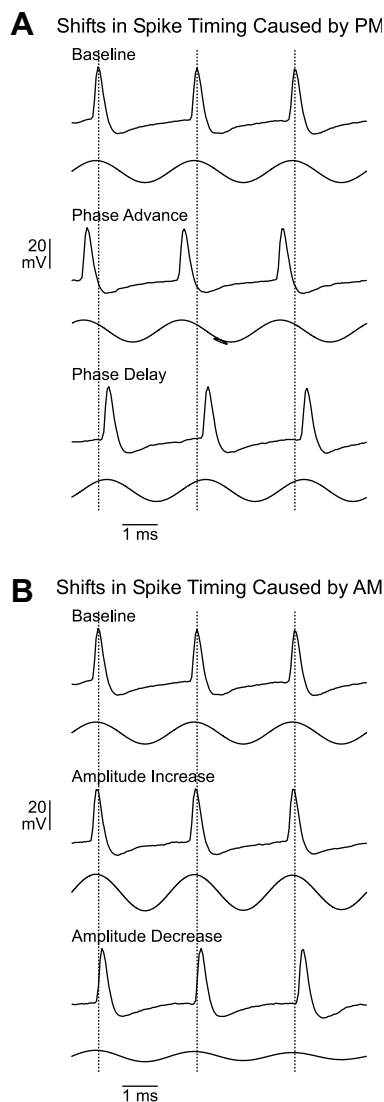
Fig. 5. Shifts in spike timing in a time-coding afferent (T-afferent) in *Eigenmannia* in response to random PM and random AM. (A) T-afferent spike times during PM. Three pairs of traces are shown. For each pair, the bottom trace shows the carrier stimulus and the top trace shows an intracellular recording of T-afferent activity. The vertical dashed lines mark the timing of action potential peaks in the top pair of traces. Note how the spikes are advanced when the carrier phase is advanced (middle pair of traces) and how the spikes are delayed when the carrier phase is delayed (bottom pair of traces). (B) Spike times of the same T-afferent during AM, presented as in (A). Note how the spikes are advanced when the carrier amplitude is increased (middle pair of traces) and how the spikes are delayed when the carrier amplitude is decreased (bottom pair of traces).

Fig. 6. Changes in spike rate in an amplitude-coding afferent (P-afferent) in *Eigenmannia* in response to random AM and random PM. (A) Changes in P-afferent spike rate during random AM. The bottom plot shows the AM waveform as a solid line and the PM waveform as a dashed line (no PM in this stimulus). The top trace shows an intracellular recording from a P-afferent. Note how the firing rate is tightly correlated with stimulus amplitude. (B) Changes in P-afferent spike rate during random PM, presented as in (A). Note how the firing rate tends to increase slightly during phase delays, and decrease slightly during phase advances.

during phase advances (Fig. 6B). I directly quantified the importance of spike timing (as opposed to spike rate) for stimulus encoding for 5 amplitude-coding afferents and 5 time-coding afferents in both *Eigenmannia* and *Gymnarchus*. This was achieved by adding various amounts of spike-timing jitter to the responses of each afferent (Jones et al., 2004; Sadeghi et al., 2007), and then quantifying encoding performance using the coding fraction. Spike-timing jitter was introduced by shifting the timing of each spike by a random amount drawn from a Gaussian distribution with zero mean and a standard deviation that represented the degree of jitter, which varied from 10 μs to 40 ms. The encoding of both AM and PM by time-coding afferents was slightly reduced by adding as little as 10 μs of jitter, and encoding performance dropped to chance levels with less than 1 ms of jitter (Fig. 7). By contrast, AM and PM encoding by amplitude-coding afferents was much more
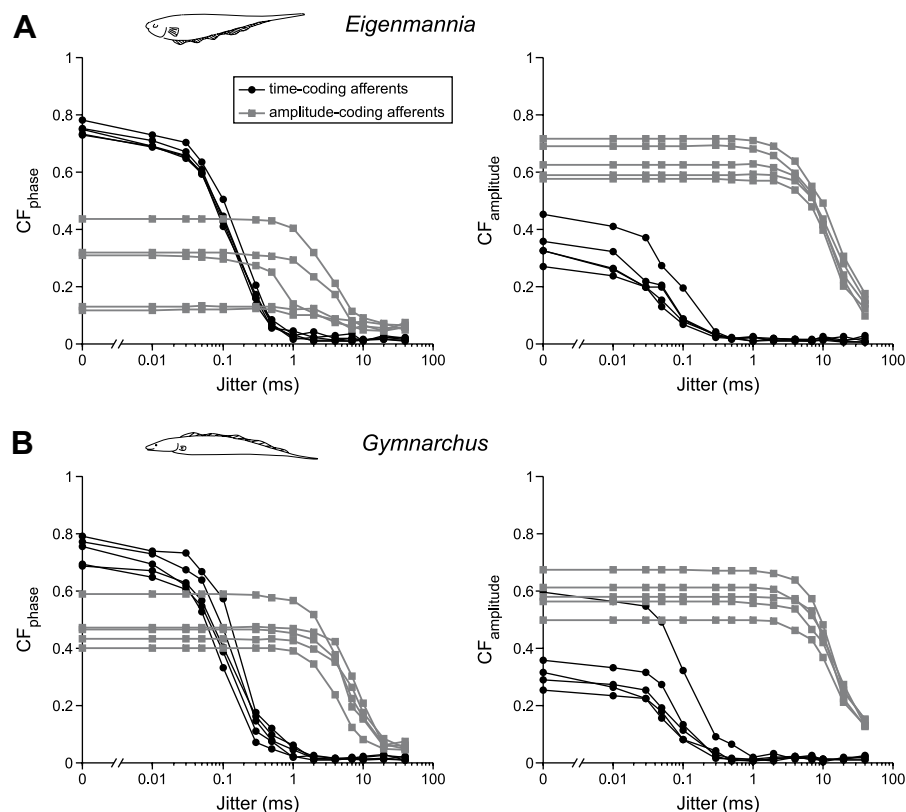
robust to the effects of spike-timing jitter, with encoding performance remaining relatively unaffected when adding as much as 1 ms of jitter in most cases, and not falling to chance levels until as much as 10 ms or even greater amounts of jitter were added (Fig. 7). These results clearly demonstrate that time-coding afferents encode both AM and PM via changes in spike timing, while amplitude-coding afferents encode both AM and PM via changes in spike rate.

4. Effects of ambiguity on central electrosensory processing and behavior

4.1. Central electrosensory neurons respond to the phantom modulations of primary afferents

Although primary afferent activity is clearly affected in similar ways by both AM and PM, the hypothesis that encoding ambiguity can give rise to phantom modulations still rests on the assumption that the amplitude- and time-coding pathways are dedicated to providing the organism with separate information about AM and PM, respectively. Given that both types of afferents are specialized for encoding one particular attribute, and that they give rise to anatomically and physiologically distinct central pathways, this seems a reasonable assumption, but it may not actually be true. It is possible that a population decoding algorithm is used to pool the information available from all primary afferents to extract unambiguous information about AM and PM.

We first addressed this issue by recording the responses of central electrosensory neurons in the hindbrain ELL and midbrain torus semicircularis of *Gymnarchus* to AM and PM. As described

A *Eigenmannia*

B *Gymnarchus*

Fig. 7. Effects of added spike-timing jitter on the encoding of AM and PM by amplitude- and time-coding afferents. (A) Coding fractions for random PM (CF$_{phase}$) and random AM (CF$_{amplitude}$) with varying amounts of spike-timing jitter for 5 time-coding afferents and 5 amplitude-coding afferents in *Eigenmannia* (T- and P-afferents, respectively). (B) Coding fractions for random PM (CF$_{phase}$) and random AM (CF$_{amplitude}$) with varying amounts of spike-timing jitter for 5 time-coding afferents and 5 amplitude-coding afferents in *Gymnarchus* (S- and O-afferents, respectively).

in Section 2.2, information about PM is extracted centrally by detecting differences in the spike times of different time-coding afferents. We therefore used a phase chamber to electrically separate the head and trunk of each fish so that we could independently generate AM and differential PM (Carlson and Kawasaki, 2004, 2006b). We stimulated fish with random AM and random PM, presented both separately and simultaneously, and then calculated spike-triggered average stimuli and used a feature extraction technique to quantitatively assess which features the central electrosensory neurons responded to (see Gabbiani and Metzner, 1999; Metzner et al., 1998). In response to AM and PM presented simultaneously, ELL neurons and many torus neurons responded primarily to changes in either amplitude (Fig. 8A and C) or differential phase (Fig. 8B) (Carlson and Kawasaki, 2008), reflecting the continued separation of amplitude- and time-coding pathways (Kawasaki and Guo, 1998). Just like the primary afferents, however, these neurons responded to both attributes when they were presented separately (Fig. 8).

This finding indicates that central electrosensory neurons respond to the phantom modulations of primary afferents. Indeed, the responses of AM- and PM-sensitive central electrosensory neurons are accurately predicted by the responses of amplitude- and time-coding afferents, respectively. As described in Section 3.3, advances in the spike times of time-coding afferents can be elicited by both phase advances and amplitude increases, whereas spike-timing delays can be elicited by both phase delays and amplitude decreases. Accordingly, ELL neurons within the time-coding pathway that respond to phase advances also respond to increases in amplitude, and ELL neurons that respond to phase delays also respond to decreases in amplitude (Carlson and Kawasaki, 2008). As also described in Section 3.3, increases in the firing

rate of amplitude-coding afferents can be elicited by both amplitude increases and phase delays, whereas decreases in firing rate can be elicited by both amplitude decreases and phase advances. Accordingly, ELL neurons within the amplitude-coding pathway that respond to amplitude increases also respond to phase delays, and ELL neurons that respond to amplitude decreases also respond to phase advances (Carlson and Kawasaki, 2008).

4.2. Phantom modulations elicit behavioral responses

Even though neurons in the ELL and torus respond to the phantom modulations of primary afferents, it is possible that neurons farther downstream in the electrosensory pathway manage to disambiguate primary afferent responses to obtain reliable information about AM and PM. Alternatively, it may be naïve to assume that accurate perception of particular stimulus features requires their independent encoding. Ultimately, the question of whether the phantom modulations of primary afferents have any affect on electrosensory perception depends on whether or not they influence behavior. We assessed the potential effects of phantom modulations on behavior using the jamming avoidance response (JAR) as a probe of electrosensory perception, since it is a robust behavior that relies on integrating information about amplitude and phase modulations (Heiligenberg, 1991; Kawasaki, 1993; Takizawa et al., 1999). As described in Section 2.2, both *Gymnarchus* and *Eigenmannia* respond to an electric field with a slightly higher frequency than their own (+*Df*) by lowering their EOD frequency and respond to an electric field with a slightly lower frequency (−*Df*) by raising their EOD frequency.

When plotted as a Lissajous graph of amplitude vs. phase that develops over time, +*Df* is characterized by a counterclockwise
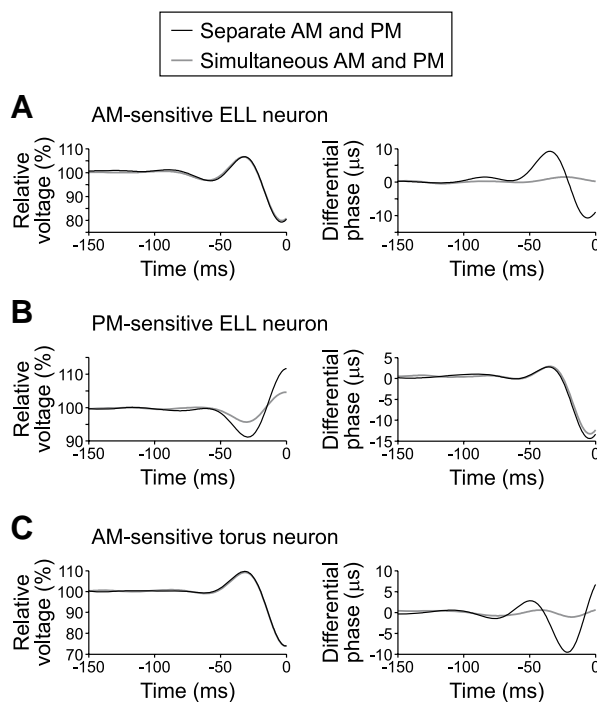
Fig. 8. Central electrosensory neurons respond to phantom modulations. Spike-triggered average AM and PM waveforms resulting from random AM and random PM presented separately and simultaneously are shown for (A) an AM-sensitive neuron in the ELL, (B) a PM-sensitive neuron in the ELL, and (C) an AM-sensitive neuron in the torus semicircularis. The graphs on the left show the spike-triggered average AM waveforms. The graphs on the right show the spike-triggered average PM waveforms, measured as the timing difference between the stimuli presented to the head and trunk (see text for details). Note how all three neurons respond to modulation of their nonpreferred attribute when it is modulated separately (the AM-sensitive neurons respond to PM presented separately, and the PM-sensitive neuron responds to AM presented separately).

sense of rotation whereas −*Df* is characterized by a clockwise sense of rotation (Figs. 2A and 9A). If, instead of plotting stimulus amplitude vs. stimulus phase, one plots the spike rates of amplitude-coding afferents against the spike times of time-coding afferents (Fig. 9B and C), the same difference in sense of rotation is observed (Heiligenberg, 1991; Heiligenberg and Partridge, 1981). It is this difference that the fish use to determine the sign of *Df*.

When sinusoidal AM is presented alone (i.e. vertical streaks in a Lissajous graph, as in Fig. 9A), the phantom modulations of time-coding afferents result in a neuronal representation with a counterclockwise sense of rotation (Fig. 9B and C). By contrast, when sinusoidal PM is presented alone (i.e. horizontal streaks in a Lissajous graph, as in Fig. 9A), the phantom modulations of amplitude-coding afferents result in a neuronal representation with a clockwise sense of rotation (Fig. 9B and C). This observation leads to specific predictions. If the fish accurately perceive AM and PM, then neither sinusoidal AM presented alone nor sinusoidal PM presented alone should elicit shifts in EOD frequency, because these stimuli do not exhibit any sense of rotation. If, however, the fish's perception is distorted by the phantom modulations of primary afferents, then sinusoidal AM should elicit decreases in EOD frequency, whereas sinusoidal PM should elicit increases in EOD frequency, due to the senses of rotation observed in Lissajous plots of the neuronal representations of these stimuli (Fig. 9B and C).

We tested these predictions using *Eigenmannia* because its JAR is stronger and more robust than that of *Gymnarchus* (Bullock et al., 1975; Kawasaki, 1993), and it is therefore better suited to detecting the potential effects of small phantom modulations

on behavior (Carlson and Kawasaki, 2006a, 2007). As with the recordings from central electrosensory neurons, the fish were placed in a phase chamber to electrically isolate the head from the trunk so that we could independently manipulate amplitude and differential phase. This required administering a drug that immobilizes the fish (gallamine triethiodide), which also has the effect of silencing the electric organ. However, we were able to assess the behavioral responses of fish by monitoring the electric organ pacemaker frequency using a small electrode placed directly next to the electric organ, where the synchronous activity of spinal electromotor neurons generates a large external potential.

As previously demonstrated in similar phase chamber experiments (Heiligenberg and Bastian, 1980; Takizawa et al., 1999), +*Df* evoked decreases in EOD frequency and −*Df* evoked increases in EOD frequency (Fig. 10A). Interestingly, sinusoidal AM evoked decreases in EOD frequency and sinusoidal PM evoked increases in EOD frequency (Fig. 10B) (Carlson and Kawasaki, 2006a, 2007; Takizawa et al., 1999), consistent with the hypothesis that the phantom modulations of primary afferents ultimately affect perception. Several additional observations support this hypothesis as well (see Carlson and Kawasaki, 2007). Firstly, in terms of tuning to modulation rate, sensitivity, and temporal dynamics, the behavioral responses to sinusoidal AM are correlated with JARs to +*Df*, but not JARs to −*Df*, whereas the behavioral responses to sinusoidal PM are correlated with JARs to −*Df*, but not JARs to +*Df* (Carlson and Kawasaki, 2007), suggesting that responses to +*Df* and sinusoidal AM are mediated by a common neural pathway, and that the responses to −*Df* and sinusoidal PM are likewise mediated by a common neural pathway. In addition, there is a smooth transition between the magnitude of JARs and responses to stimuli with variable relative depths of AM and PM, indicating that these responses represent different points along a continuum rather than categorically distinct behaviors (Carlson and Kawasaki, 2007). Finally, we directly tested the role that phantom modulations play in eliciting behavioral responses by performing experiments designed to eliminate the phantom modulations of primary afferents while preserving responses to their preferred stimulus attribute (see Carlson and Kawasaki, 2006a for details). This had the effect of significantly reducing behavioral responses to both sinusoidal AM and sinusoidal PM (Carlson and Kawasaki, 2006a).

Although we have not performed the equivalent behavioral experiments in *Gymnarchus*, we have made recordings from midbrain neurons in *Gymnarchus* that integrate information from the amplitude- and time-coding pathways and are thought to be involved in the JAR (Carlson and Kawasaki, 2004, 2006b, 2008; Kawasaki and Guo, 2002). Interestingly, the responses of midbrain neurons to sinusoidal AM are more similar to their responses to +*Df* than to −*Df*, whereas their responses to sinusoidal PM are more similar to their responses to −*Df* than to +*Df* (Carlson and Kawasaki, 2008).

4.3. Phantom modulations can influence behavior in natural contexts

Although phantom jamming stimuli can clearly elicit behavioral responses, an important question is whether phantom modulations have any effect on behavior in a natural context. We therefore performed experiments that were designed to emulate stimuli that the fish may encounter in their natural environment (Carlson and Kawasaki, 2007). In these experiments, we immobilized fish and silenced their electric organs as before, but rather than placing the fish in a phase chamber, we used a pair of electrodes placed at the head and tail of the fish to provide an electric field that mimicked the fish's own EOD ('EOD replacement'
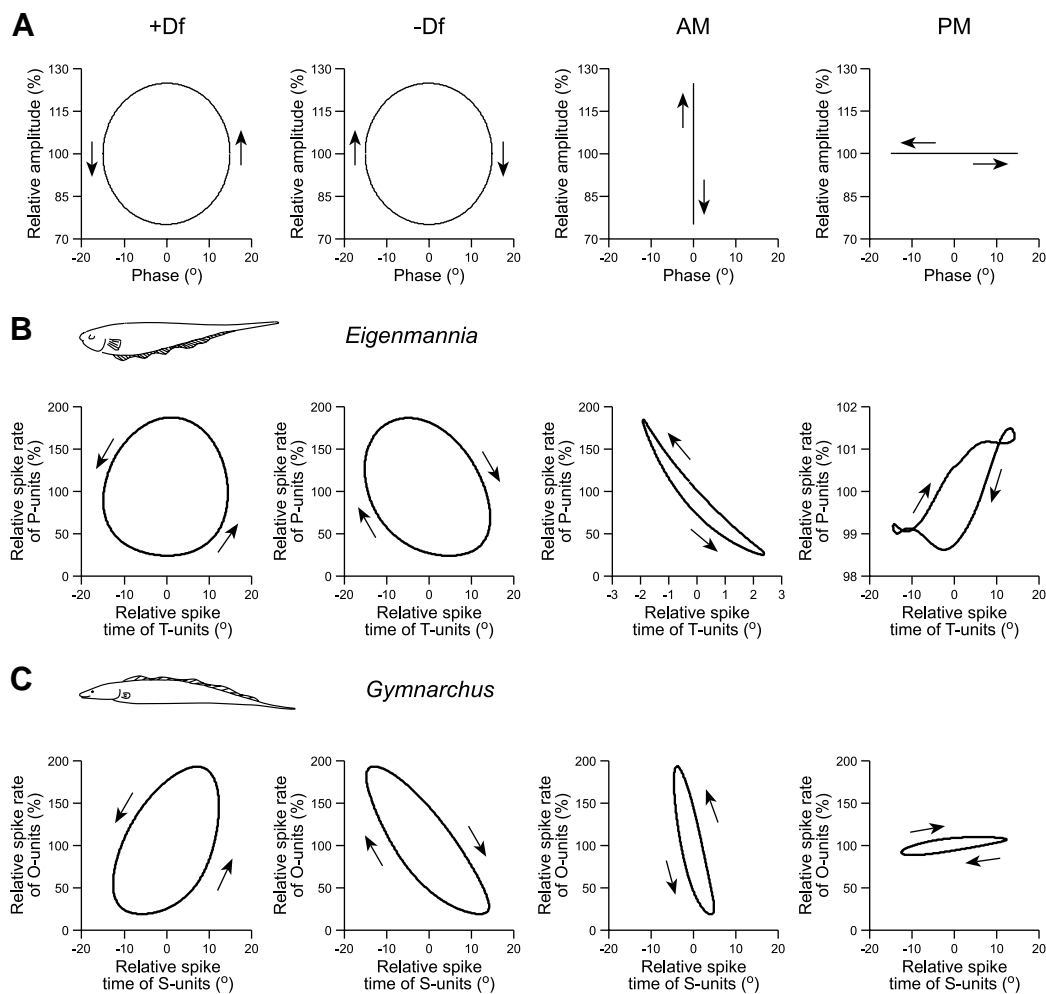
Fig. 9. Primary afferent representations of sinusoidal stimulus modulations in *Eigenmannia* and *Gymnarchus*. (A) Sinusoidal stimulus modulations, plotted as Lissajous graphs of relative amplitude vs. phase. (B) Primary afferent representations in *Eigenmannia* of the stimuli in (A), plotted as Lissajous graphs of the mean relative spike rate of P-afferents ($n=33$) vs. the mean relative spike time of T-afferents ($n=16$). Note that the abscissa is expanded in the representation of AM, and the ordinate is expanded in the representation of PM for clarity. (C) Primary afferent representations in *Gymnarchus* of the stimuli in (A), plotted as Lissajous graphs of the mean relative spike rate of O-afferents ($n=34$) vs. the mean relative spike time of S-afferents ($n=21$). (B) Is modified after Carlson and Kawasaki (2006a) and (C) is modified after Carlson and Kawasaki (2008).

in Fig. 11). Unfortunately, this did not allow us to independently manipulate differential phase, but it was possible to modulate amplitude using semi-natural stimuli to determine whether they elicited decreases in EOD frequency (see Carlson and Kawasaki, 2007 for details).

These stimuli included: 'global' sinusoidal or random AM (Fig. 11A), which approximates what a fish would encounter if it were to swim through a dense, cluttered environment (Crampton, 1998); step increases or decreases in amplitude, similar to what a fish would experience if it crossed a boundary between two bodies of water with different conductivities, such as the confluence of two rivers or streams (Hopkins, 1999); 'local' sinusoidal or random AM restricted to a small part of the fish's body surface (Fig. 11B), which approximates the effect of a small prey item entering the fish's electric field (Chacron et al., 2003; Nelson and MacIver, 1999; Nelson et al., 2002); and finally, amplitude modulations induced by moving a small plastic rod along the flank of the fish (Fig. 11C). All of these stimuli reliably elicited decreases in EOD frequency (Carlson and Kawasaki, 2007). In the case of the moving object, response magnitude was significantly reduced when the EOD replacement signal was turned off (Fig. 11C), verifying that this response was primarily due to the effect of the object on the electric field (Carlson and Kawasaki, 2007). These results suggest that stimuli encountered in the fish's natural envi-
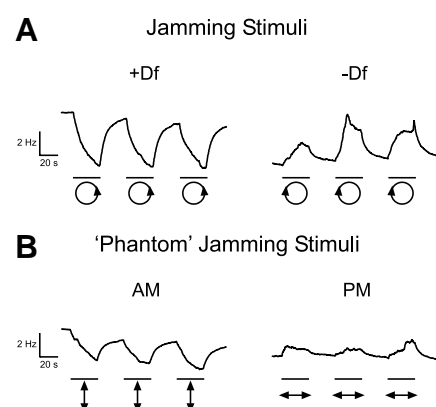
Fig. 10. Shifts in the EOD frequency of *Eigenmannia* in response to the sinusoidal stimulus modulations shown in Fig. 9. (A) EOD frequency shifts from a single individual in response to +Df and −Df. The bars beneath each trace delimit the periods of stimulus modulation, and the icons below each bar show Lissajous plots of the stimulus modulations (AM plotted against PM, after Fig. 9). (B) EOD frequency shifts from the same individual in response to sinusoidal AM and sinusoidal PM, presented as in (A). Modified after Carlson and Kawasaki (2006a).

ronment could give rise to phantom jamming stimuli that elicit behavioral responses.
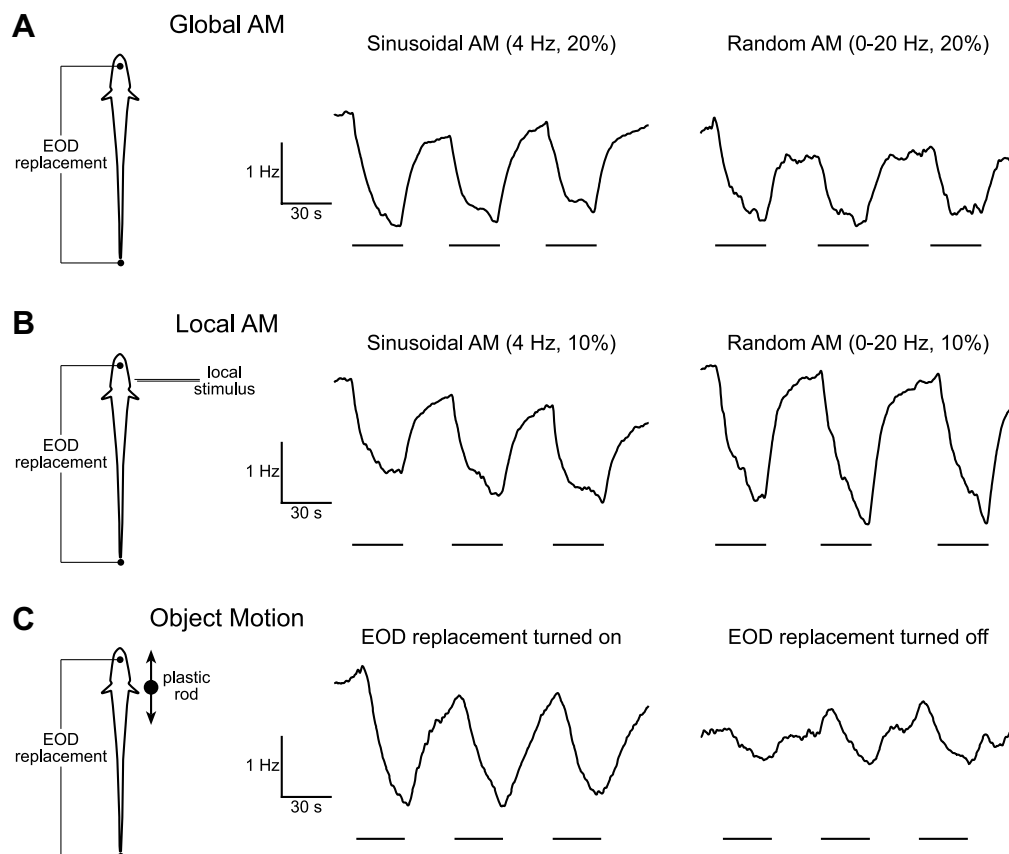
Fig. 11. Decreases in EOD frequency can be elicited by semi-natural stimuli that induce modulations in EOD amplitude. (A) For global stimulation, a pair of electrodes, one in the mouth and one directly behind the tail, is used to generate an EOD replacement signal. Modulations are presented through the EOD replacement electrodes. Both global sinusoidal AM and global random AM elicit EOD frequency decreases (horizontal bars beneath each trace delimit the periods of stimulus modulation). (B) For local stimulation, the same EOD replacement electrodes are used, but stimulus modulations are presented through a second electrode pair that produces modulations only over a small portion of the body surface. Both local sinusoidal AM and local random AM elicit EOD frequency decreases (horizontal bars beneath each trace delimit the periods of stimulus modulation). (C) For object motion, the same EOD replacement electrodes are used, but rather than providing a modulated electric field, a plastic rod is moved sinusoidally along the side of the fish to induce modulations in the amplitude of the EOD replacement. Movement of the rod elicits EOD frequency decreases when the EOD replacement signal is turned on, but these frequency shifts are largely absent when the EOD replacement signal is turned off (horizontal bars beneath each trace delimit the periods of object motion). Modified after Carlson and Kawasaki (2007).

5. Conclusions

5.1. Ambiguity and the jamming avoidance response

In the context of a natural jamming stimulus, the amplitude-coding afferents respond preferentially to AM, and the time-coding afferents respond preferentially to PM. As a result, the fish is able to reliably determine the relationship between amplitude and phase by analyzing the patterns of activity in these two populations of primary afferents, and shift its EOD frequency accordingly (Heiligenberg, 1991). Therefore, ambiguity in the encoding of amplitude and timing information does not affect normal execution of the JAR. However, the JAR proved to be a useful behavior for demonstrating that phantom modulations can influence electrosensory perception (Carlson and Kawasaki, 2006a).

In addition, we found that ambiguity in the encoding of amplitude and timing information can result in EOD frequency shifts in response to phantom jamming stimuli that may be encountered in the natural environment (Carlson and Kawasaki, 2007). It is unclear whether these behavioral responses themselves have any significant effect on behavior. The fish continually monitor their own EOD in the context of active electrolocation, and changes in the EOD carrier frequency could influence the responses of electrosensory neurons to object-induced modulations of this carrier signal (Carlson and Kawasaki, 2007). This effect could be due to

the intrinsic tuning of peripheral or central electrosensory neurons to carrier frequency (Hopkins and Heiligenberg, 1978). Alternatively, such an effect could be caused by the influence of carrier frequency on object impedance and/or capacitance-induced phase shifts. Capacitive impedance is inversely proportional to carrier frequency and capacitance (Horowitz and Hill, 1989). Therefore, for an object with fixed capacitance, changes in the carrier frequency will cause changes in capacitive impedance which in turn will affect the depth of amplitude modulation caused by the object. Over the natural range of EOD frequencies in *Gymnarchus* and *Eigenmannia* (250–600 Hz), a 3 Hz decrease in frequency in the presence of an object with 2 nF of capacitance will increase the object's impedance by approximately 0.67–3.9 kΩ. Similarly, the phase shift caused by an object with capacitance also varies as a function of carrier frequency (Horowitz and Hill, 1989). Shifting EOD frequency may therefore provide an animal with additional information about object capacitance. One intriguing possibility is that simple and complex impedances could be discriminated on the basis of whether or not shifts in EOD frequency result in any change in EOD phase or amplitude, since simple impedances are not affected by changes in carrier frequency.

Shifts in EOD frequency in response to phantom jamming stimuli could also play a role in electric communication behavior. If a fish's EOD frequency changes in response to its environment, such as when it swims through a densely cluttered area (i.e. Fig. 11A), or

when it encounters small objects (i.e. Fig. 11B and C), then a nearby fish could potentially detect those changes in frequency and glean information about the environment from them. Therefore, while the evidence strongly suggests that these frequency shifts result from activating JAR circuitry in the absence of actual jamming stimuli, these responses may actually serve a useful function. This would indicate that a particular neural circuit can mediate identical behavioral responses that serve entirely different functions. Alternatively, the behavioral responses to phantom jamming stimuli could have no significant effect on behavior, so that there was no selective pressure to disambiguate information about amplitude and phase through central processing. Lastly, the behavioral responses to phantom jamming stimuli could have a negative impact on behavior, but the benefits to be had by not shifting EOD frequency may not offset potential costs associated with resolving the ambiguity through central processing.

5.2. Ambiguity and active electrolocation

As discussed in Section 2.3, amplitude and timing information also play important roles in active electrolocation behavior (Bastian, 1986; von der Emde, 1999). The impedance of objects largely determines their effect on amplitude, whereas the capacitance of objects largely determines their effect on phase (von der Emde, 1998). As a result, purely resistive objects induce modulations in amplitude, whereas capacitive objects induce modulations in amplitude and phase (von der Emde, 1998). Early recordings from primary afferents in *Eigenmannia* indicated that amplitude-coding afferents change their firing rate primarily as a function of object impedance, regardless of whether the impedance is simple (purely resistive) or complex (capacitive) (Scheich et al., 1973). However, a follow-up study revealed that amplitude-coding afferents do actually respond differently to simple and complex impedances at a given impedance (Feng and Bullock, 1977), probably because of the effects of phase modulation on amplitude-coding afferent activity discussed in Section 3.3. The spike times of time-coding afferents are strongly affected by object capacitance due to the effects of capacitance on the phase of the electric field (Feng and Bullock, 1977; Scheich et al., 1973; von der Emde, 1998, 1999). However, time-coding afferent spike times are also affected by object impedance, due to the amplitude-dependent latency shift discussed in Section 3.3 (Feng and Bullock, 1977; Scheich et al., 1973). As a result, neither amplitude- nor time-coding afferents provide an unambiguous indicator of object resistance or capacitance. Extracting this information would therefore require a central comparison of amplitude- and time-coding afferent activity. The fact that *Eigenmannia* is able to distinguish purely resistive objects from capacitive objects (von der Emde, 1998, 1999) suggests that such a comparison does occur, most likely within the midbrain torus semicircularis, where the amplitude- and time-coding pathways converge (Heiligenberg and Rose, 1986, 1985; Rose and Heiligenberg, 1986). In this respect, it is interesting to note that the gymnotiform fish *Sternopygus* does not produce a JAR (Bullock et al., 1975), but nevertheless has midbrain neurons that respond to particular combinations of AM and PM (Rose et al., 1987), supporting the notion that integrating information across the amplitude- and time-coding pathways plays an important role in active electrolocation behavior.

Therefore, ambiguity regarding amplitude and timing information at the level of individual primary afferents may not be significant in the context of active electrolocation. If central electrosensory neurons are able to provide unambiguous information about object impedance (i.e. stimulus amplitude) and object capacitance (i.e. stimulus phase) by integrating information across the amplitude- and time-coding pathways, then it would be very interesting to determine the mechanisms underlying this disambiguation, as

the results are likely to prove broadly relevant in determining how ambiguity in the information content of individual neurons can be resolved by combining the information available from multiple neurons. The encoding of AM in the context of active electrolocation has been fairly well studied within the amplitude-coding pathway (Bastian, 1986; Nelson, 2005; Nelson and MacIver, 1999). Future studies should consider the importance of PM, and the role played by both the amplitude- and time-coding pathways in active electrolocation.

5.3. A comparative perspective on the encoding of multiple stimulus attributes and its relationship to sensory perception

The significance of ambiguity for sensory perception has long been appreciated, particularly with respect to visual illusions and multistable stimuli (Attneave, 1971; Eagleman, 2001; Rubin, 1951). Multistable stimuli are those that can be interpreted in more than one way, resulting in perceptual reversals between those interpretations (Leopold et al., 2002; Rubin, 1951). Well known examples include the Necker cube and face-vase illusion. Such stimuli represent 'conditional ambiguity', meaning that different conditions (e.g. two faces in profile vs. a vase) can give rise to the same stimulus, resulting in ambiguity as to which condition is occurring. This kind of ambiguity is widespread. For example, a large object at a distance can elicit the same pattern of retinal stimulation as a small object nearby. Similarly, a soft whisper can result in the same sound intensity at the ear as a loud noise occurring at a distance. In most cases, additional cues are available that allow this ambiguity to be resolved within the central nervous system. In other cases, such as with multistable stimuli, such cues are unavailable and sensory perception reflects this conditional ambiguity.

Our recent studies on the electrosensory system reveal that ambiguity can also occur when different stimuli elicit identical responses in sensory neurons, the phenomenon of 'encoding ambiguity'. Although encoding ambiguity and conditional ambiguity arise from distinct sources, they result in an identical problem: an inability to distinguish between different external conditions. It is likely that encoding ambiguity affects sensory processing in other modalities. In particular, the auditory system is thought to be phylogenetically related to the electrosensory system (New, 1997; Popper and Fay, 1997), and it encodes information about stimulus timing and amplitude in similar ways, namely through precise spike timing and spike rate, respectively (Ruggero, 1992). Like the electrosensory system, however, spike timing in primary auditory afferents is affected by an amplitude-dependent latency shift (Anderson et al., 1971). The lack of independence in the perception of pitch and loudness discussed in Section 1 may partly be due to the fact that spike timing can be affected by changes in both sound frequency and intensity. Peripheral mechanisms have previously been acknowledged as potential explanations for the perceptual interaction of pitch and loudness (Gulick, 1971; Moore, 1989; Stevens and Davis, 1938).

Sound source localization is another function of the auditory system that may be affected by encoding ambiguity, since spectral, temporal, and intensity cues can all play important roles (Hartmann, 1999). In barn owls, the unique structure of their ears has permitted sound source azimuth and elevation to be separately represented by interaural timing differences and interaural intensity differences, respectively (Knudsen and Konishi, 1979; Moiseff and Konishi, 1981; Takahashi et al., 1984). Although changing interaural intensity differences primarily causes shifts in the perceived elevation of sound sources, it also causes small shifts in the perceived azimuth of sound sources (Knudsen and Konishi, 1979; Moiseff, 1989). Furthermore, these errors are in the direction predicted by an amplitude-dependent latency shift: reducing the intensity at the left ear causes the owl to localize to the right of the

target and reducing the intensity at the right ear causes the owl to localize to the left of the target (Knudsen and Konishi, 1979; Moiseff, 1989). Similarly, changing interaural timing differences causes large shifts in the perceived azimuth of sound sources, but also small shifts in perceived elevation (Moiseff, 1989). Like the electrosensory system, the barn owl auditory system consists of two separate pathways that are specialized for encoding amplitude and timing information (Takahashi et al., 1984). However, the activity of neurons within the time-coding pathway is slightly affected by differences in stimulus intensity (Moiseff and Konishi, 1983; Sullivan and Konishi, 1984). Thus, it may be that encoding ambiguity is a problem for sound source localization; however, given the owl's extreme accuracy at localizing sounds (Knudsen et al., 1979), it seems likely that such ambiguity, if it actually exists, is resolved centrally, possibly in the midbrain where the amplitude- and time-coding pathways converge to create a two-dimensional map of auditory space (Knudsen and Konishi, 1978). Interestingly, a recent study in chickens reveals a clear influence of sound intensity on the processing of interaural timing differences within the sound localization pathway (Nishino et al., 2008).

Psychophysicists have long recognized that the perception of a particular stimulus attribute can be affected by interference from variation in a different attribute (Garner, 1974). Stimulus dimensions that interact perceptually in this way are referred to as 'integral dimensions' (Garner, 1974). Pitch and loudness are examples of integral dimensions in the auditory system (Grau and Kemler-Nelson, 1988; Melara and Marks, 1990b; Neuhoff and McBeath, 1996), as are brightness and saturation in the visual system (Garner and Felfoldy, 1970; Handel and Imai, 1972; Torgerson, 1958). By contrast, dimensions that do not exhibit perceptual interference, such as brightness and size in the visual system (Attneave, 1950; Gottwald and Gamer, 1975; Handel and Imai, 1972), are considered 'separable dimensions' (Garner, 1974). According to this distinction, amplitude and phase are clearly integral dimensions in weakly electric fish.

Several different hypotheses have been advanced to explain the underlying basis for integral dimensions. The traditional perspective maintains that the various dimensions within a stimulus are not initially perceived and stimuli are processed in a holistic manner (Garner, 1974; Lockhead, 1972, 1979; Shepard, 1964). According to this view, any dimensional structure to perception results from derived, secondary processes (Garner, 1974; Kemler-Nelson, 1993). However, stimuli do consist of physically distinct features, or orthogonal dimensions, with sound frequency and intensity being perfect examples. Although these physical attributes do not perfectly correspond to distinct perceptual dimensions, there is rough agreement between intensity and loudness on the one hand, and frequency and pitch on the other, suggesting that some independence in the perception of these two physically distinct attributes is a useful feature. It then seems unnecessary to posit that perceptually separating these attributes results from a central extraction of dimensions that are physically separate to begin with. This criticism is supported by the existence of separate neural pathways within early stages of the auditory system that are specialized for encoding distinct physical attributes (Oertel, 1999; Takahashi et al., 1984).

More recently, psychophysicists have recognized that there is immediate access to these separate dimensions, and have proposed that integral dimensions may influence each other by creating a context in which other dimensions are perceived (Melara and Marks, 1990b; Melara et al., 1993). Thus, if the perceived pitch of a sound is affected by whether that sound is loud or soft, then the sound volume is creating a context in which pitch perception occurs. An adaptive explanation for such context dependent perception is that stimuli that are identical in one respect (frequency) but different in another respect (intensity) may have very different meanings to the organism, such that perception of the former is altered in such a way as to make the stimulus more or less salient.

It has been suggested that the interacting perception of physically distinct stimulus attributes may relate to the fact that natural stimuli are often characterized by inherent correlations between different attributes (Neuhoff et al., 1999). According to this view, perceptual interactions have evolved to take advantage of these natural correlations. Electrosensory stimuli are clearly characterized by inherent correlations between amplitude and phase. As discussed in Section 2.2, interference from a conspecific EOD results in both amplitude modulation and phase modulation. The depth of modulation in both amplitude and phase is directly proportional to the relative amplitude of the two EODs, and the temporal relationship between the two can take only one of two forms, depending on the sign of the frequency difference (Fig. 2A). In the context of active electrolocation, it is likely that natural objects induce correlated modulations in amplitude and phase as well, considering that capacitive objects are characterized by an inverse relationship between capacitance and capacitive impedance (Horowitz and Hill, 1989).

Many perceptual interactions within the visual system result from central processing and serve clear adaptive functions (Spillman and Werner, 1996). For instance, coherent motion, the ability to detect the form of an object due solely to a shared direction of motion, serves to enhance the detection of objects against a camouflaged background. Similarly, color constancy ensures that objects are recognized consistently regardless of ambient light conditions.

As we have shown in our studies of weakly electric fish, perceptual interactions can also arise as a consequence of ambiguity in the peripheral encoding of multiple stimulus attributes. Regardless of whether perceptual interactions are the result of peripheral encoding or central processing, there is no reason to assume that physically distinct attributes should be independently perceived. The ultimate function of sensory processing is to provide an organism with information about the outside world so that it can use that information to guide and coordinate its behavior. We should only expect perceptual distinctions to occur when differences between stimuli are of biological significance. Furthermore, there is no a priori reason to expect that a multidimensional stimulus space is directly aligned with a corresponding multidimensional perceptual space. Such a view betrays the naïve assumption that sensory perception is simply a reflection of the outside world. Rather, sensory perception is a constructive process that generates an internal model for representing biologically relevant information (Rock, 1997). Model organisms such as weakly electric fish are ideally suited to establishing direct links between the physiology of individual neurons and quantitative characteristics of natural behaviors. For this reason, research on sensory processing in weakly electric fish has significantly advanced our understanding of the neuronal basis for these perceptual constructions, and there is every reason to expect that they will continue to provide fertile ground for research in this area.

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