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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 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

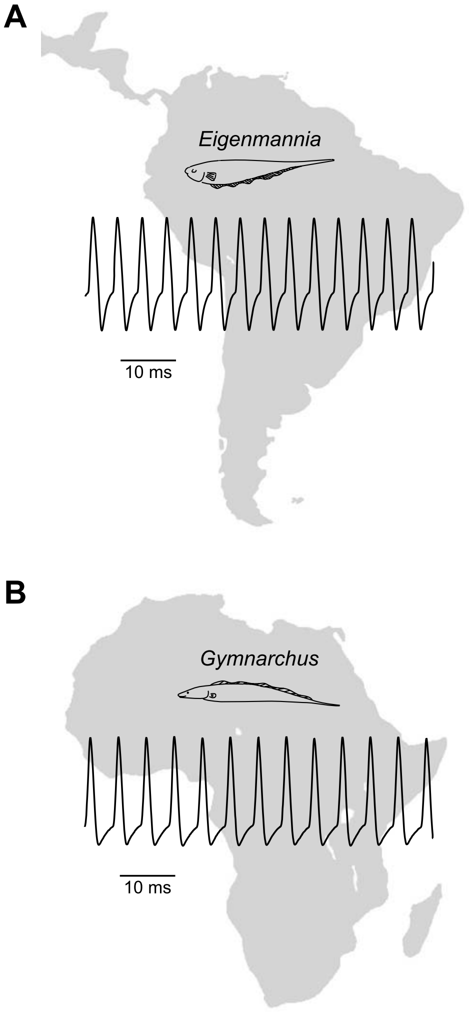

Fig. 1. Electrogenesis and electroreception evolved independently in the South American gymnotiforms and the African mormyriforms. The gymnotiform *Eigenmannia* (A) and the mormyriform *Gymnarchus* (B) both generate a quasi-sinusoidal electric organ discharge (EOD) ranging in frequency from about 250 to 600 Hz. Both species also perform the jamming avoidance response (JAR) using an identical computational algorithm (see text for details).