Gamma Oscillations, Synaptic Depression, and the Enhancement of Spatiotemporal Processing. Focus on "Global Electrosensory Oscillations Enhance Directional Responses of Midbrain Neurons in Eigenmannia"
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Oscillatory brain activity has been observed since the earliest EEG studies and classified by its frequency range. In particular, oscillations in the range of 20–60 Hz (gamma band) have been identified in numerous vertebrate species and brain regions (Bullock and Achimowicz 1994); in mammals, cortical gamma-band oscillations typically occur in activated brain states (Steriade et al. 1996) and they have in general been associated with processing behaviorally relevant information (Bullock and Achimowicz 1994; Csiba et al. 2000). The precise role of such oscillations and the mechanisms by which they might optimize information processing has remained controversial, in part because of the complexity of cortical circuits. In this issue of the Journal of Neurophysiology (p. 2319–2326) Ramcharitar and colleagues demonstrate that gamma-band oscillations, which occur naturally during social interactions of electric fish, enhance the directional selectivity of movement-responsive neurons (Ramcharitar et al. 2006). In addition this paper presents strong evidence that gamma-band oscillation-induced synaptic depression may be a biophysical mechanism that contributes to this enhancement of directional selectivity.

Eigenmannia virescens, the gymnnotiform species studied by Ramacharitar et al. (2006), produces a weak sinusoidal electric organ discharge (EOD) that creates an electric field around the animal. EOD frequencies in this species range from 200 to 700 Hz but isolated individual fish maintain near-constant frequencies. The EOD serves as a carrier that can be modulated by environmental objects such as prey (electrolocation) as well as by the EOD of conspecifics (electrocommunication). Prey—because its conductivity is greater than that of the ambient water—will increase the local EOD amplitude. Thus movement of the fish relative to prey will therefore produce a low-frequency amplitude modulation (AM, <20 Hz) moving across its skin. This AM is sensed by numerous specialized cutaneous electroreceptors (P-units) and the output used for prey capture (Nelson and MacIver 1999). Not surprisingly, many midbrain electrosensory neurons are responsive to moving electroreceptive images (in the torus semicircularis [TS] this region is analogous to the mammalian inferior colliculus).

When two fish are in proximity their EODs will interfere so as to produce a beat frequency (equal to the difference in the frequencies of their individual EODs). The beat AM is also a very effective stimulus for P-units and beat frequencies <20 Hz will interfere with the detection of prey. Eigenmannia, which are most commonly found in small groups (Tan et al. 2005), have developed a specialized electromotor behavior—the jamming avoidance response (JAR)—to prevent its neighbors’ EODs from interfering with electrolocation, including prey capture. The JAR shifts the EOD frequencies of neighboring fish away from each other so that the resulting beats increase to the 20- to 50-Hz (gamma-band) range and no longer overlap with the AM frequencies of prey; the JAR therefore permits electrolocation in the presence of conspecifics. The neural circuitry of the JAR has been thoroughly explicated by Heiligenberg and colleagues (Fortune and Rose 1997a,b, 2000, 2003; Heiligenberg 1991; Rose and Call 1992; Rose and Fortune 1999) who found many neurons in the TS responsive to beat frequencies (2–50 Hz).

Earlier studies from this group (Ramcharitar et al. 2005) established that low-frequency beats interfered with the electrosensory detection of moving objects by TS neurons, as might be expected from the earlier literature on the JAR. The paper in this issue reveals a surprising and far more interesting result: the gamma-band oscillations induced by the JAR can greatly enhance the directional selectivity of TS neurons to moving objects. The JAR thus serves not only to prevent the deleterious effect of low-frequency beats but actually enhances electrolocation by sharpening directionally selective responses to prey. There have been numerous studies that suggest that gamma-band oscillations are induced during perception and might be involved in attention to specific stimulus features (Cardin et al. 2005; Fries et al. 2002; Ishikane et al. 2005; Siegel and Konig 2003; Womelsdorf et al. 2006). Ramacharitar et al. (2006) are the first to convincingly demonstrate that behaviorally induced gamma-band oscillations can enhance “attention” to behaviorally relevant spatiotemporal signals. Furthermore, the generality of this effect across species and brain regions suggests that it may be a consequence of conserved neuronal biophysics.

The second major result of this paper is therefore also of general interest: the enhancement of directional selectivity is highly positively correlated with the previously demonstrated synaptic depression of TS input (Fortune and Rose 2000; Rose and Fortune 1999). Although the causal link between synaptic depression and directional selectivity was not established in this paper, the authors make a plausible connection to models of directional selectivity in visual cortex that use synaptic depression as a key biophysical element (Chance et al. 1998; Fortune and Rose 2002).

This conclusion is in some ways surprising because the literature on gamma-band oscillations typically emphasizes its role as enhancing perceptual processing by promoting neuronal synchrony (Cardin et al. 2005; Fries et al. 2002; Ishikane et al. 2005; Siegel and Konig 2003; Womelsdorf et al. 2006). More recently, Schaefer et al. (2006) suggested that neuronal oscillations enhance stimulus detection by promoting the temporal precision of action potentials. Perhaps these ideas are not as
disparate as first appears. Computational analysis has suggested that synaptic depression can allow a neuronal network to better detect synchronous input (Senn et al. 1998). There may thus be a deeper link between γ-band oscillations, synaptic depression, the detection of synchronous input, and the enhancement of specific types of time-varying signals. γ-Band oscillations might induce both synchrony (by an increase in spike precision across the oscillating neurons) and synaptic depression; these effects might then synergistically enhance the detection of more localized signals such as prey. Exploring this link experimentally and theoretically and across diverse sensory systems will likely prove a rewarding enterprise.

REFERENCES


