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Neural maps in the electrosensory system of weakly electric fish

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The active electrosense of weakly electric fish is evolutionarily and developmentally related to passive electrosensation and the lateral line system. It shows the most highly differentiated topographic maps of the receptor array of all these senses. It is organized into three maps in the hindbrain that are, in turn, composed of columns, each consisting of six pyramidal cell classes. The cells in each column have different spatiotemporal processing properties yielding a total of 18 topographic representations of the body surface. The differential filtering by the hindbrain maps is used by superimposed maps in the multi-layered midbrain electrosensory region to extract specific stimulus features related to communication and foraging. At levels beyond the midbrain, topographic mapping of the body surface appears to be lost.

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Introduction

Spatially organized sensory information is typically encoded by a spatial array of receptors and then conveyed to a topographically mapped central representation. This holds true not only for the familiar auditory, somatosensory and visual systems, but for the electrosensory system, where a cutaneous array of electroreceptors projects onto multiple hind-brain and mid-brain maps. A mapped representation is clearly advantageous for processing spatially localized sensory input, but it is likely that spatially independent features are also extracted from map representations.

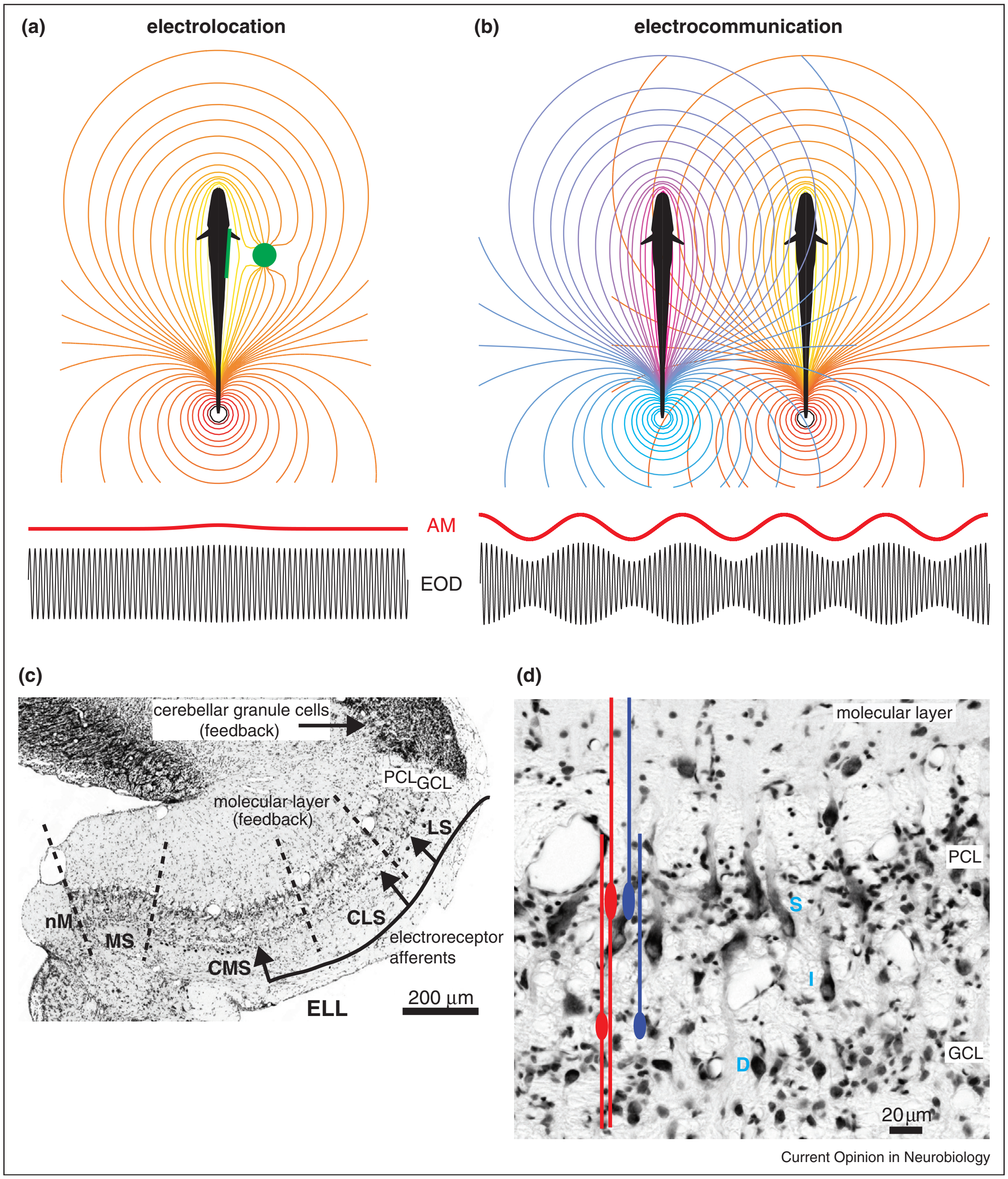
In this review we introduce the electrosensory system and survey the evolution of electrosensory maps and their structure. We specifically emphasize the modular composition of these maps as repeating columnar arrays, echoing a theme already known for decades in cortex [1]. We further emphasize the linked cellular and network properties that allow spatially organized maps to also extract nonspatial sensory attributes such as stimulus frequency.

Evolution of maps for electroreception

Electrosensory systems come in two flavors, passive and active. Passive electrosensory systems are sensitive to exogenous electric fields, for example, resulting from muscle activity related to respiration [2] or swimming and feeding movements of prey organisms [3]. The receptor organs of the passive electrosense (ampullary organs) share a common evolutionary origin with mechanosensory lateral line receptors [4•,5•]. Ampullary receptors were lost early in the teleost fish lineage but re-evolved several times independently within the clade [6]. Fish with an active electrosense possess a specialized electric organ whose discharges (electric organ discharge: EOD) generate an oscillating electric field in the water around the animal. The receptor organs of the active electrosense (tuberous organs) are tuned to the waveform of the species-specific and individual-specific EOD, and provide the fish with information on perturbations of its electric field. Perturbations of the electric field can result from the presence of nearby objects, such as small prey organisms or root masses that locally distort the flow of electric current in the water; the electric image of an object is defined as the region of skin where the object has perturbed (increased or decreased) the EOD amplitude (Figure 1a). The EOD can also be perturbed by interference with the EODs of conspecifics, leading to spatially extended modulations of current flow through the skin (Figure 1b) [7]. The electrosensory system thus serves the dual purposes of electrolocation of objects and communication. Active electrosensory systems evolved independently in South American gymnotiform fish (from a common ancestor with catfish equipped with ampullary receptors) and African mormyriform fish [6]. This review is restricted to the maps in the active electrosense of gymnotiform fish (but see [8]). The EOD of gymnotiform fish can consist of brief pulses (pulse species) or a continuous sinusoidal waveform (wave species; Figure 1a). We review detailed studies limited to two wave species (*Eigenmannia virescens*, discharge frequency ∼300–600 Hz; *Apteronotus leptorhynchus*, ∼700–1000 Hz).

The evolutionary sequence of lateral line to ampullary to tuberous electroreceptors is paralleled in their rhombencephalic target regions. Catfish ampullary receptors terminate in a topographic map — the electrosensory lateral line lobe (ELL) — laterally abutting the lateral line region (n. medialis) [9]. Tuberous electroreceptors terminate in three ELL segments lateral to the ampullary map

Figure 1



The active electrosense and its topographic maps of the electroreceptive body surface in the electrosensory lateral line lobe (ELL). **(a)** Weakly electric fish generate an oscillating dipole field around their body, the electric organ discharge (EOD), which creates an oscillating potential difference across the skin of the fish (EOD, bottom trace). The frequency of oscillation equals the frequency at which the electric organ is discharged. Top panel: Snapshot of the isopotential lines surrounding the fish. Objects (green sphere) near the fish perturb the electric field, creating local amplitude modulations (AM) of the potential difference across the skin — the electric image (green line on skin). When the fish swims by a conductive object, the EOD amplitude is transiently increased (bottom traces). Primary electrosensory afferents encode AMs with variations in firing rate. The evaluation of the patterns of AMs across the body constitutes the basis for the electrolocation of objects. **(b)** The summation of the sinusoidally oscillating dipole fields of two interacting weakly electric fish creates a periodic AM (red trace) of the EOD (black trace), whose beat frequency equals the difference between the EOD frequencies of the two fish. **(c)** A transverse cross section through the dorsal medulla of the *Apteronotus leptorhynchus* brain illustrating the structure of the ELL. The ELL is situated lateral to the nucleus medialis (nM), a small cell group receiving lateral line afferent input. The ELL is divided into four maps (segments): the medial segment (MS) receives ampullary electroreceptor input, while the centromedial (CMS), centrolateral (CLS) and lateral (LS) segments receive identical input from tuberous (P-unit) afferents. Each map is composed of several layers including a pyramidal cell layer (PCL), a granule cell layer (GCL) and a molecular layer receiving feedback input from an overlying mass of cerebellar granule cells. Each electroreceptor afferent (P-unit) trifurcates and terminates so as to form topographic maps of the cutaneous electroreceptors within all three ELL tuberous segments. **(d)** A higher magnification view of the cell layers of the CLS. The two major pyramidal cell types — E-cells (red) and I-cells