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
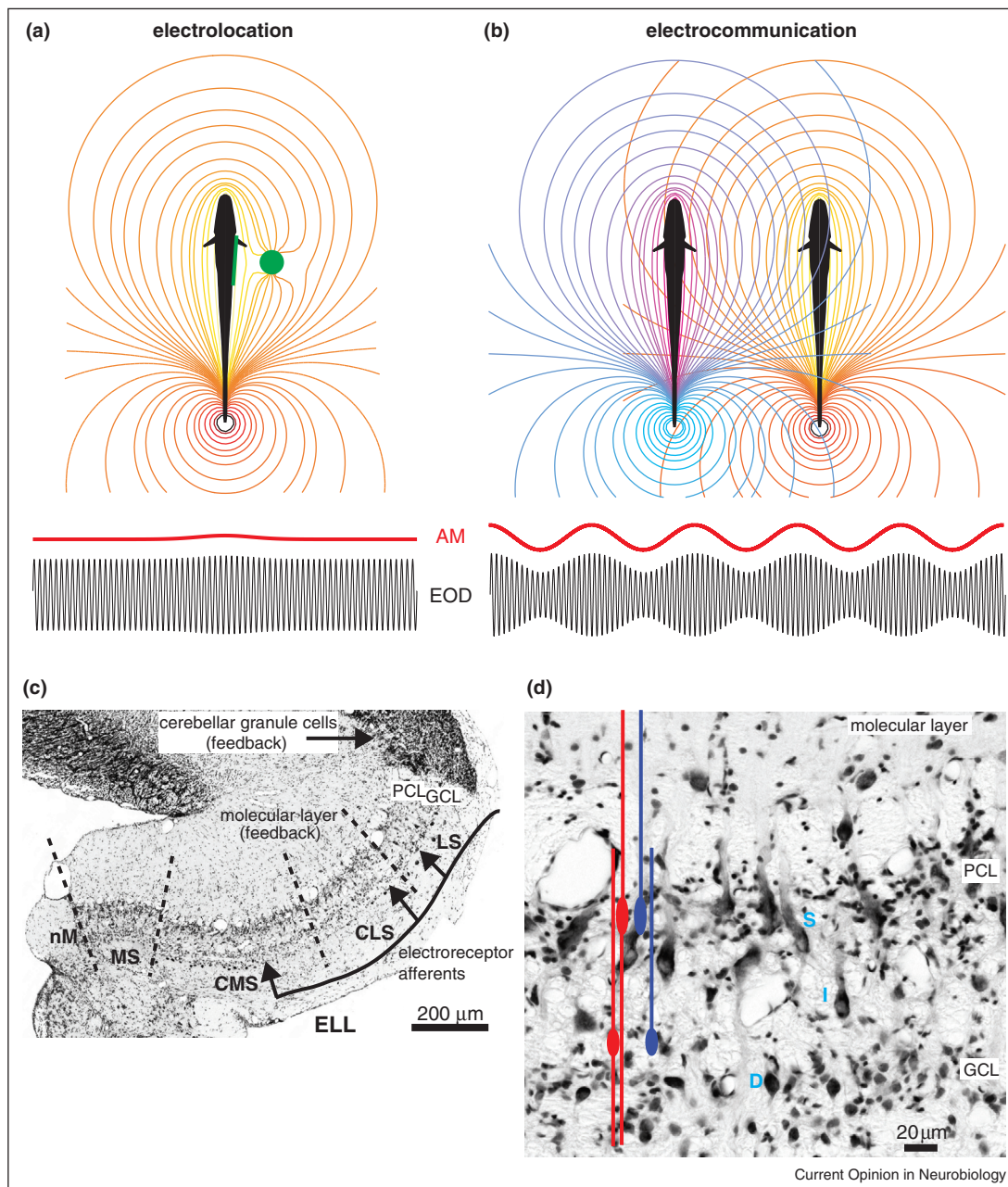
The active electrosense and its topographic maps of the electroreceptive body surface in the electrosensory lateral line lobe (ELL). **(a)** Weakly electric fish generate an oscillating dipole field around their body, the electric organ discharge (EOD), which creates an oscillating potential difference 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

(Figure 1c). There are relatively few lateral line (130, one side) and ampullary receptors (360) in comparison to tuberous receptors (6500–8500) [10]. This large increase in receptor number is reflected in the differentiation of their corresponding maps. The n. medialis is a crudely organized cell mass whose principal cells receive feedback via their apical dendrites. The ampullary map retains this organization, but displays a fine-grained topographic mapping [11] while the tuberous maps are far more differentiated.

Most tuberous electroreceptor afferents (P-units) fire in a phase-locked skipping manner to the EOD. P-unit firing rate conveys information about amplitude modulations (AMs) of the EOD associated with electrolocation and electrocommunication (Figure 1a,b). Low-frequency AMs related mostly to electrolocation are linearly encoded as deviations from the P-unit's baseline discharge, while high-frequency communication-associated AMs are encoded by synchronized discharge phase locked to the AM [12•,13•].

Multiple maps and columnar organization in the ELL

Each P-unit trifurcates and projects topographically to the three tuberous ELL maps: the centromedial (CMS), centrolateral (CLS) and lateral (LS) segments. The structure of these maps is identical (Figure 1c) — from ventral to dorsal there is a deep neuropil layer, where P-units terminate, layers of GABAergic interneurons and pyramidal cell somata, and a molecular layer containing the apical dendrites of pyramidal cells and descending feedback input. There are multiple classes of pyramidal neurons. The most basic distinction is between E-cells and I-cells: E cells have basal dendrites that receive P-unit input and respond to EOD amplitude increases. I-cells receive P-unit input relayed disynaptically via inhibitory interneurons and increase their spike rate in response to EOD amplitude decreases. Both E-cells and I-cells are subdivided into deep, intermediate and superficial cell types based on molecular, morphological and physiological criteria (Figure 1d) [14]. The E-cells and I-cells come in pairs and the superficial, intermediate and deep varieties lie within vertical columns within an ELL map (Figure 1d). The pyramidal cells of all six classes within a column share the same receptive field (RF) but process identical spatial input in different ways. Columns are basic units of the ELL and the computations they perform vary systematically across the three sensory maps. Deep cells receive minimal feedback input, have no antagonistic surround [15] and are relatively linear encoders of AMs [16]; these cells are the source (via intermediate brain regions) of massive feedback projections to the apical dendrites of the other pyramidal cells [17]. Superficial and intermediate cells encode AMs in a highly nonlinear manner [16], display a pronounced center-surround organization of their RF [15], and their responses to P-unit inputs are strongly modulated by feedback to their apical dendrites [17,18•]. All pyramidal cell types project to the torus semicircularis (TS) [17].

The CMS map is the largest (∼470 columns/2800 pyramidal cells) and the LS map the smallest (∼150 columns/ 900 pyramidal cells) with the CLS intermediate (∼235 columns/1400 pyramidal cells) in size. Correspondingly, the RF sizes are smallest (6–14 mm^2/25–50 P-units) in CMS, very large in LS (160–360 mm^2/640–1400 P-units) and intermediate in CLS (26–60 mm^2/100–240 P-units). There are therefore effectively $6 \times 3 = 18$ electrosensory maps: the cells within one ELL segment have similar RF sizes and P-unit convergence numbers, but process this input in very different ways [14]. One striking puzzle emerges from an electrophysiological comparison of the maps: the mean firing rate of pyramidal cells is similar across the three ELL segments while the convergence numbers would suggest that the direct excitatory drive to the LS E-cells should be about $640/25 = \sim25$ times greater than for CMS E-cells. Clearly some form of biophysical normalization equalizes the firing rate [19].

Molecular and network mechanisms of frequency tuning

The ELL maps and columns provide parallel information streams tied to different behavioral contexts. The temporal processing properties of E-cells of the three maps are tightly linked to their RF sizes, whereas most I-cells are low-pass filters across the maps (Figure 2) [20,21]. E-cells in CMS are low-pass filters, those in LS are high-pass. Remarkably, CLS pyramidal cells switch their frequency tuning depending on context. In a communication situation, the electric fields of the interacting fish summate and the resulting beat signal affects the entire body surface (Figure 1b), saturating the cells' RF center. CLS E-cells then act as high-pass filters and process high-frequency signals associated with opposite-sex encounters. In a foraging context (Figure 1a), when only part of the RF center is driven by a small prey's electric image (a low-frequency signal [22]), the same cells become low-pass filters [12•]. This switch is mediated by two effects. RF center

(Figure 1 Legend Continued) (blue) — are illustrated. The E-cells have basal dendrites (downward running lines) that receive direct input from the electroreceptor afferents; the I-cells lack such basal dendrites and receive disynaptic sensory input via small inhibitory interneurons (GABAergic) within the granule cell layer (GCL). Within each class there is a further subdivision into larger superficial cells with large apical dendrites (upward running lines) that ramify in the molecular layer and smaller deep cells with only short apical dendrites; a third class, intermediate between superficial and deep types, are not shown for clarity of illustration. All three classes of E-cells and I-cells are organized into a columnar arrangement as illustrated for one column. All cells within a column share the same receptive field but process that identical sensory input in very different ways. The location of individual superficial (S), intermediate (I) and deep (D) pyramidal cells is shown.

Figure 2
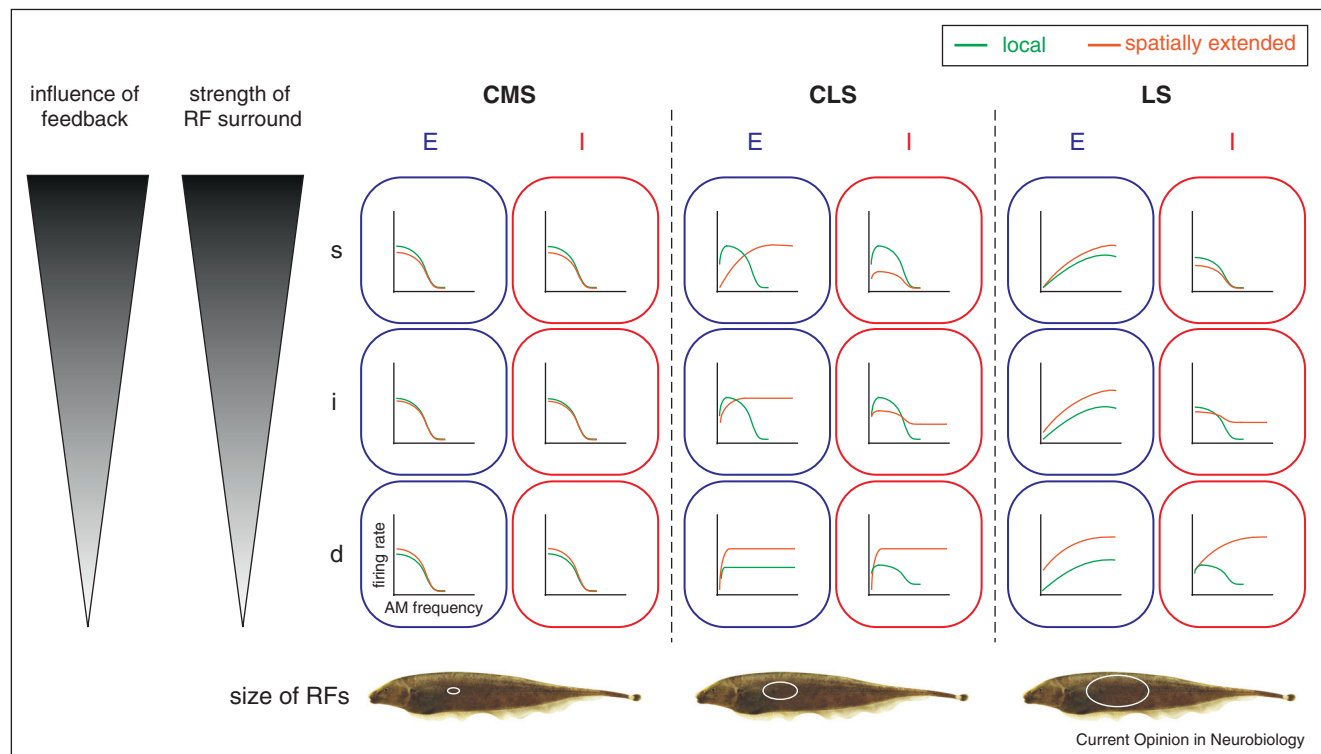
Frequency tuning varies widely between the 18 topographic representations of the electroreceptive body surface in the ELL. For each of the three maps of the ELL, typical tuning curves for the six pyramidal cell classes of a column are shown. Each panel shows the firing rate (y-axis) of a neuron as a function of the frequency of amplitude modulation (AM) of the fish's electric field (x-axis). The receptive field (RF) sizes increase systematically from the centromedial segment (CMS) over the centrolateral segment (CLS) to the lateral segment (LS), as indicated by the size of the white ovoids on the surface of the fish at the bottom of the figure. Blue frames indicate E-cells, red frames indicate I-cells. Superficial pyramidal cells (s, top row) receive strong feedback onto their apical dendrites (indicated by width of left triangle), which is activated by spatially extended stimuli and attenuates responses to low-frequency signals. Their RFs have strong center-surround antagonism (right triangle), which attenuates responses to global stimuli. Deep pyramidal cells (d, bottom row) receive very little feedback input, their RFs have only weak antagonistic surround, and they show tuning curves similar to primary afferent neurons. Intermediate pyramidal cells (i, middle row) are intermediate in all these respects. Responses to high-frequency stimulation become stronger from CMS over CLS to LS.

saturation drives most P-units in the RF and boosts E-cell responses to all frequencies. Feedback input to the apical dendrites of the pyramidal cells cancels the responses to low-frequency, predictable stimuli, but is activated only by spatially extended stimuli [12[•],13[•],23[••]].

LS E-cells receive approximately 25 times greater RF center input than CMS E-cells, implying greater depolarization and synaptic conductance fluctuation. Nevertheless, E cells of all maps have similar firing rate means and variability [20]. How firing rate normalization can be achieved and how it shapes the cells' frequency tuning was analyzed via experiment and modeling [24]. LS E-cell excitation is constrained by multiple mechanisms including a cell-intrinsic high firing threshold [21] and stronger after-hyperpolarizing potentials (AHPs) compared to CMS E-cells. The strong AHPs are due to SK2 channels [25] and keep the membrane potential from reaching firing threshold. Massive excitatory input

and strong AHPs put LS E-cells in a high-conductance, fluctuation-driven regime, rendering them sensitive to the synchronized P-unit input driven by high-frequency stimuli [12[•],24,26]. CMS E-cells receive fewer P-unit inputs, have lower spike thresholds and weaker AHPs [21,25], keeping them in an integration regime driven by the nonsynchronized activity evoked by low-frequency communication-associated and prey-associated signals. Thus, a combination of network (RF size) and intrinsic properties leads to firing rate normalization and also tunes neurons with large RFs to high stimulus frequencies.

Extraction of behaviorally relevant stimulus features in ELL maps

ELL pyramidal cells have a well-characterized burst mechanism [27] that has been implicated in the detection of behaviorally relevant stimulus features [28–30]. Bursts can indicate different stimulus events depending on the ELL map [31]. Superficial LS E-cells burst selectively for

small chirps, a communication signal for inter-male aggression. Superficial E-cells of CMS and CLS do not respond to communication signals, but produce bursts for locally presented prey mimics. I-cells of all maps respond to big chirps, a communication signal that may be relevant in reproductive contexts, but also respond to local environmental features, for example, rocks [18•,32,33].

The physiological responses of ELL pyramidal cells are also under the control of neuromodulators. Acetylcholine has been shown to increase excitability and burst firing and shift frequency tuning to lower frequencies [34]. It acts via type-3 muscarinic receptors, which are homogeneously expressed across all three ELL segments [35]. In contrast to the cholinergic system, serotonergic fibers show highly map-specific innervation with the highest density of fibers found in LS [36]. Serotonin application to LS pyramidal cells *in vitro* increased excitability and burst firing as well as information transmission by isolated spikes, by downregulating currents mediated by SK and M-type K^+ channels. Increased serotonin levels, as they are expected in subordinate animals [37], are therefore predicted to enhance detection of aggressive chirps by bursts of LS E-cells [36].

## Functional implications of multiple parallel maps

The functional picture of ELL map organization that emerges is that of great heterogeneity of pyramidal cell types within columns and across maps. Each map provides a full topographic representation related to specific functional tasks. The RF size differences across maps determine their preferred spatial scale and are linked, via numerous molecular/biophysical specializations, to differences in their preferred temporal/frequency ranges (Figure 2). The small RFs/low-frequency tuning of the CMS E-cells is associated primarily with high spatial resolution for prey/landmarks (low frequency, but see [38]). The large RF/high-frequency tuning of LS E-cells is associated with sensitivity to spatially extensive communication signals. I-cells (all maps) will respond to environmental features and communication signals. Within each column of every map, further specialization results in linear and nonlinear processing at different spatial scales.

The CLS map appears to be an all-purpose map able to respond to the entire behaviorally relevant frequency range. It may correspond to the original electrosensory map with CMS and LS specialization emerging after evolutionary map-duplication events [20].

Higher level electrosensory maps

All three ELL maps project to the midbrain TS with their topography preserved (Figures 3 and 4). The TS is composed of twelve layers and contains ∼50 neuron types whose dendrites distribute in a complicated manner across layers. ELL input terminates mainly in layers 3,
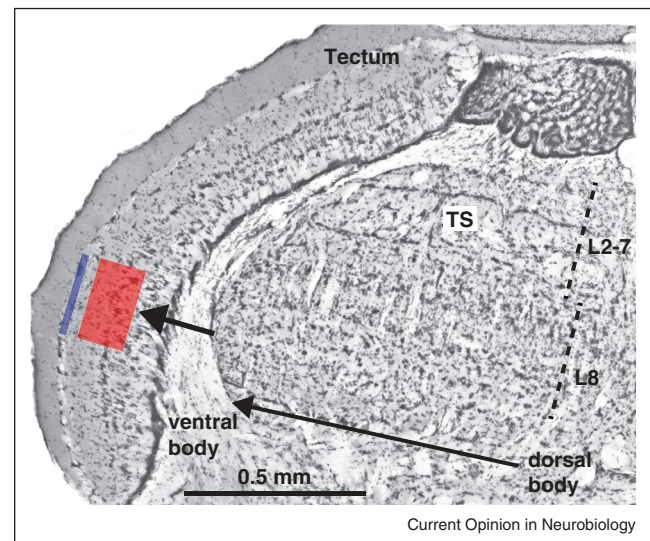
A transverse cross section through the dorsal midbrain of the *Apteronotus leptorhynchus* brain. The lateral surface of the dorsal midbrain is covered by the laminated optic tectum; the tectum provides input to and receives input from the dorsal telencephalon (pallium). Below the tectum the hypertrophied and highly differentiated torus semicircularis (TS) can be observed. A comparison with Figure 1 shows that the TS contains a far greater number of neurons than the ELL, and that they are organized into many more layers (12 in all). The upper layers (L2–l7) receive extensive ELL pyramidal cell input; the majority of neurons in these layers may respond to relatively simple transformations of their electrosensory input. The deeper layers (e.g., the complex L8) receive minimal ELL input and their neurons respond in a highly transformed and much more selective manner to electrosensory input. Layer 8 (L8) provides input to and receives strong input from the pallium. Several layers of the TS project massively to the deeper layers of tectum (red bar) preserving the topographic relationships; in fact, the electrosensory input to the tectum is dominant over the much smaller retinal input (blue bar). The TS to tectum map is believed to underlie these fish's ability to use their electrosensory system for motor control (navigation and prey capture) in total darkness.

5 and 7 [39], but there is no detailed understanding of the differential TS targets of the ELL maps or of the different pyramidal cell types within the columns of each map. Earlier studies did suggest that cells responding to communication stimuli might be located in the deeper TS layers [40–43]. Recently, striking examples of feature extraction have been demonstrated, for example, cells that respond only to directional object movement [44••,45•,46,47], small or large chirps or higher-order 'envelope' signals [44••,45•]. It is possible that new principles of map organization will be revealed as function is connected to TS layers and cell types. One possibility is that the TS layers may extract and process specific electrosensory features related to electrolocation versus communication.

The TS projects topographically to the multi-layered tectum and in register with its visual input map [48].

Figure 4
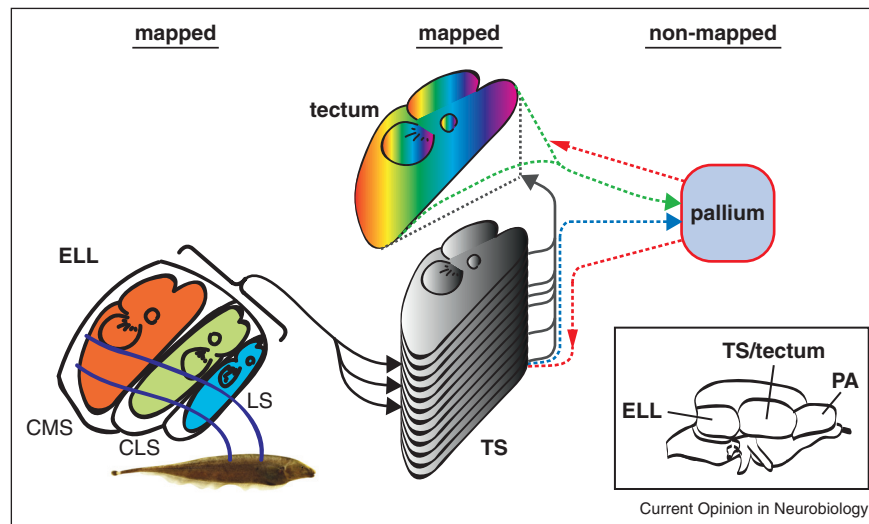
Summary graph of the flow of topographically mapped electrosensory information in the brain of wave-type weakly electric fish. The axons of the pyramidal cells of all three ELL maps target layers 3, 5, and 7 of the torus semicircularis (TS) whose output neurons of multiple layers project to tectum, there preserving the topographic relationships of the lower-order maps. Electroreceptive and visual receptive fields of tectal neurons are in spatial register [48]. Certain output neurons of the deeper layers of TS provide indirect input to pallium, which is not topographically organized [56••]. Nevertheless, the same layers of TS receive nontopographic (nonmapped) descending input from pallium. Similarly, tectum provides indirect input to, and receives descending input from, pallium. The inset on the lower right shows an overview of the brain with the locations of ELL, TS/tectum and pallium indicated.

The morphology of the gymnotiform tectum is nearly identical to that of other fish [49], although it processes mostly electrosensory signals. We speculate that the TS acts to 'adapt' the electrosensory signals so that the tectum can re-map them to the conserved motor outputs for navigation and prey capture. Gymnotiform fish are adept at high-speed maneuvering during social interactions in the dark. They likely utilize higher-order stimuli ('envelopes' of AMs) to guide these movements [50,51,52,53•] and such social electrosensory signals may be topographically represented in the tectum [54]. Thus, the tectal maps of gymnotiform fish may serve as a model for how sensory maps guide both prey capture/navigation and social interaction-related movements.

The TS and tectum project, via the diencephalic preglomerular nucleus, to the dorsal telencephalon (pallium) [55•]. However, all topographic map information is lost in the pallium [56••]. The pallium is important for learning [57], but can only regulate electrosensory processing and motor output via its descending projections to TS and tectum [55•]. This sets up a conundrum: the map organization preserved from ELL to TS and tectum is lost in pallium, and yet pallium-associated memory stores, lacking an evident map structure, must act via descending projections back to the TS/tectal maps. The teleost pallium contains regions similar to mammalian hippocampus and cortex [58], and this scenario is reminiscent of the relations between cortex and hippocampus. For example, the visual cortices provide mapped information to place cells of the hippocampus, but place cells are not organized in any known topographic map form [59]. Hippocampal spatial information available in nonmapped form is then presumably used to guide movement via cortical sensory/motor maps. The nature and interactions of information processing present in mapped versus nonmapped neural structures is a deep and general problem, and the electrosensory system may provide a useful model for its study.

Conclusions

Studies in weakly electric fish illustrate direct links between the network architecture of topographic sensory maps and the molecular and biophysical specializations of their constituent neurons; when these data sets are combined, they connect to behavioral function. The network/biophysical interactions shape the spatiotemporal filtering properties of sensory neurons. In particular, the combination of output rate normalization with differences in afferent convergence is shown to determine frequency tuning. Multiple parallel maps at the first-order processing stage converge on multiple superimposed maps in the multi-layered midbrain electrosensory regions, suggesting that different behaviorally relevant stimulus features might be extracted by specific layers. At the pallial level of processing, topographic mapping appears to be missing even though pallium can regulate processing by the midbrain maps. We expect future studies of

weakly electric fish to provide exciting insights into how topographic sensory maps guide locomotion and into the interaction between mapped and nonmapped representations of sensory information in the brain.

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