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Why are there so many sensory brain maps?

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Multiple brain maps are found in essentially every vertebrate sensory system. These maps usually represent topographic replicas of the respective sensory epithelium, such as the retina of the eye or the cochlea in the inner ear. The topographic mapping can be continuous, as in most of the auditory brain centers, or it can be fractured, as in the cerebellum. In addition, maps usually assign a larger space to the area of greatest behavioral relevance to the animal. For example, the first-order nucleus in the mammalian auditory pathway, the cochlear nucleus, contains at least six different cell systems that give rise to parallel projections to higher-order auditory nuclei [1]. These parallel systems show dramatic differences in their morphology and numerous physiological properties. Similarly, the first-order nucleus in the electrosensory system, the electrosensory lateral line lobe (ELL) contains four complete somatotopic maps of the electroreceptors distributed over the entire body surface. These parallel ELL maps are virtually identical morphologically and, similar to the parallel systems in the mammalian cochlear nucleus, project in parallel to higher-order brain structures.

What is the functional and behavioral significance of these multiple sensory brain maps? Multiple sensory maps are often specialized in processing distinct sensory parameters. Hence, they seem to be part of separate processing streams of sensory information [2–6]. However, at some points in the sensory-motor command chain, information processing appears to span across maps to yield the coherent percepts needed to recognize particular higher-order stimulus features and elicit adaptive behavior [5–10]. In the visual system of cats and primates, for example, three separate processing streams extend from the retina up to the cortex, each carrying different behaviorally low level stimulus variables, such as different spatial and temporal frequency contents of stimuli [5, 7]. In another prominent example, the two auditory subsystems in owls process sound intensity and phase information independently [8, 9]. In each of these cases, however, the initial segregation of information processing is abandoned and information streams converge at higher-order levels in the brain yielding the computation of specific and behaviorally relevant stimulus features. The some 30 visual areas in macaques, for example, are interconnected by more than 300 cortico-cortical pathways [7], and the up to 50 nuclei of the mammalian auditory brainstem are linked by countless converging, diverging, and commissural connections [4].

Results from recent inactivation experiments in the electrosensory system [11, 12] combined with various studies on the premotor circuitry [13–17], however, suggest that this is not generally the rule. These studies indicate that the 'distributed hierarchical' organization found in most sensory systems in higher vertebrates is not a general organizational principle, but is, instead, most likely linked to the combinatorial nature of complex sensory features extracted by these systems.

The existence of very obvious multiple sensory maps with identical receptor inputs and mirror image boundaries in the ELL has always been a mystery [10], in particular, since all maps display the same cytoarchitecture and only show apparent differences in their overall size and the relative abundance of one cell type. For electrolocation and communication purposes, the electric fish that have been studied monitor the electric field that is produced by discharges of an electric organ with electroreceptors distributed over the body surface [10]. Two distinct types of electroreceptors exist: low-frequency ampullary and high-frequency tuberous receptors. All electroreceptor afferents terminate in a somatotopic manner in the ELL of the hindbrain, where the rostral ELL represents the head region of the fish (fig. 1). The ELL consists of four mediolaterally adjacent segments: the medial segment (MS) receives input from ampullary afferent axons, whereas tuberous primary afferents trifurcate and each collateral innervates the three remaining segments, the centromedial (CMS), centrolateral (CLS), and lateral segment (LS). No intermap connections have been found. Despite the lack of qualitative differences between the three tuberous maps, previous investigations yielded some quantitative differences in their physiological and immunohistochemical properties. Their behavioral significance, however, remained unclear. Information from the ELL is transmitted to higher-order levels of the electrosensory system, particularly to the torus semicircularis dorsalis in the midbrain, which is homologous to the inferior colliculus in the auditory system.

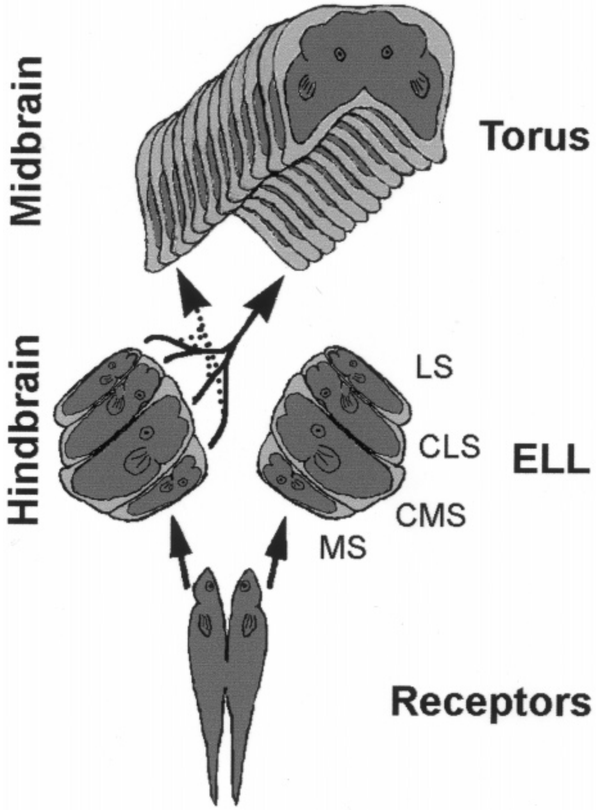

Figure 1. Multiple representations of the array of electroreceptors situated in the fish skin are found at various levels of the electrosensory pathway. This sketch depicts the multiple maps in the first-order nucleus of the electrosensory system, the electrosensory lateral line lobe (ELL) in the hindbrain, and the subsequent midbrain level, the torus [modified after refs 10, 24]. Four representations of the electroreceptive periphery are found in the ELL (MS, medial segment; CMS, centromedial segment; CLS, centrolateral segment; LS, lateral segment), and one complete map is found in each of the twelve distinct layers of the torus.

Results from recent lesion experiments in the electrosensory system of *Eigenmannia* and *Apteronotus*, however, shed some light on the different behavioral roles of the various ELL maps [11, 12]. Pharmacological inactivations of different maps resulted in markedly different behavioral deficits. The centromedial map is both necessary and sufficient for a particular behavior related to orientation, the so-called jamming avoidance response (JAR), whereas it does not affect the communicative response to external electric signals. Conversely, the lateral map does not affect the JAR but is necessary and sufficient to evoke communication behavior. The behavioral role of the centrolateral map is still unclear. It does not seem to be involved, however, in encoding signals yielding a JAR or evoking chirping. The findings from these inactivation studies are consistent with numerous earlier behavioral, physiological, and histochemical studies.

Why is the tuberous electrosensory system in these fish organized in such a strictly distributed manner? Or, in other words, why are there so many maps in the ELL and how did they evolve? Various kinds of phylogenetic changes have been suggested that could lead to the increasing number of sensory maps found in several lines of brain evolution. Gradual differentiation and separation of single brain areas into additional areas and/or changes in connection patterns are among the most commonly assumed mechanisms [e.g., 18–21]. The multiple maps in the ELL of the electrosensory system and their remarkably different behavioral significance, however, represent a stunning example of how sudden replications of already existing brain structures, for example by means of gene duplication, might have yielded a multiplication of brain maps: electrosensory systems might share a common evolutionary lineage with the mechanosensory (lateral line) system. It has been suggested repeatedly that electrosensory brain structures could have evolved by duplication from mechanosensory areas. Hence, it is tempting to speculate that duplication of existing brain maps could efficiently accommodate the increased information flow associated with a growth in the behavioral repertoire, with each map being dedicated to processing information related to one particular behavior. This idea was originally proposed for the mirror image organization of sensory maps in mammalian cortex [19]. A further evolutionary increase in the complexity of sensory scenes and motor actions, as in visually guided primate behavior, might eventually have required a greater flexibility in information processing. This might have yielded the shared use of circuit elements originally anchored in separate information streams by bridging between maps and, thus, resulted in the present distributed hierarchical organization of most vertebrate sensory systems. It is conceivable that the relatively simple nature of electric signals controlling a limited behavioral repertoire in electric fish caused the tuberous electrosensory system to retain this 'primitive' character of a distinct modularity.

Various studies have demonstrated that the premotor pathways controlling communication behavior and the JAR are composed of separate pathways as well [10, 12–17]. Hence, it is puzzling how the intermediate brain structures, such as the torus semicircularis in the midbrain, onto which these parallel sensory pathways appear to converge, are able to sort out the incoming information and activate the distinctly different premotor pathways. A similar convergence occurs in the auditory system at the level of the inferior colliculus, the mammalian analogue to the torus semicircularis. One reason for this could be that descending feedback and neuromodulatory projections, which are found in both the electrosensory and auditory systems, require separate maps at the level of the first-order nucleus, i.e., the ELL and cochlear nucleus, respectively, to function properly [1].

Additional 'crosstalk' between ascending parallel electrosensory pathways also occurs when considering both electrosensory (sub-)modalities, tuberous and ampullary. Earlier neurophysiological [15, 22, 23] and recent inactivation studies [12] suggest that in the context of the two behaviors mentioned above, the JAR and communicative behavior, tuberous and ampullary information converge. While the convergence of tuberous and ampullary information is still puzzling for behavior related to the animal's orientation, it appears to increase the overall signal-to-noise ratio during communication: ampullary information could secure the neuronal detection system for communication signals against high-frequency background noise caused by lightning, which is very common in the fishes' tropical habitat and travels over hundreds of kilometers. Tuberous information, on the other hand, could correct for low-frequency fluctuations caused by the relative movement of the fish [15, 22].

Hence, the electrosensory system combines the two opposite organizational traits of sensory systems, distributed and hierarchical, in a very distinctive fashion, revealing both the advantages and the limitations of multiple brain maps in the processing of sensory information. Multiple maps represent an efficient way to accommodate the processing of information streams associated with different behaviors. Bridging across maps, on the other hand, can provide a simple tool to reduce ambiguities contained in a single processing stream that might occur during certain behavioral tasks.

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