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## Editorial overview: Neural maps

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David Fitzpatrick PhD is scientific director and chief executive officer of the Max Planck Florida Institute for Neuroscience, the only institute of the Max Planck Society located outside of Europe. Before assuming this position, he was the James B Duke Professor of Neurobiology at the Duke University School of Medicine and founding director of the Duke Institute for Brain Sciences. Dr Fitzpatrick did his undergraduate work at Penn State University and received his PhD from Duke University. Research in the Fitzpatrick lab employs state of the art *in vivo* imaging techniques to probe the functional architecture and development of neural circuits in visual cortex.

Nachum Ulanovsky received his PhD in neural computation from the Hebrew University of Jerusalem, where he studied the auditory cortex of cats, with subsequent post-doctoral work at the University of Maryland on spatial representation in the hippocampus of bats. Since 2007, he has been a senior scientist at the Department of Neurobiology of the Weizmann Institute of Science, Israel. His research focuses on the neural basis of spatial cognition, navigation, and spatial memory in the mammalian hippocampal formation, using bats as animal models: in particular, how place cells, grid cells and head-direction cells encode 2D and 3D space.

No one would argue the value of maps for navigating in an unfamiliar city. Maps in the brain, however, continue to elicit a wide range of opinions in the neuroscience community, from the view that they are fundamental for neural coding, to considering them little more than epiphenomena of development. While the significance of maps remains enigmatic, the arrangement of neurons into sheets that exhibit a well-defined functional topology is ubiquitous: from invertebrates to primates, from sensory processing and motor control to cognition, orderly representations have emerged as a prominent feature of circuit organization. This volume of *Current Opinion in Neurobiology* reviews the state of our knowledge of neural maps: how they are organized, how they develop, how they evolve, and how they contribute to behavior, across a wide range of species. Consideration is also given to other neural architectures that perform their functions with little sign of organized topology. Whether arranged as columnar maps or ‘salt and pepper’, the spatial arrangement of neurons with different response properties remains a defining property of circuit organization, and a mystery that only deepens as we learn more about circuit structure, function and development.

As reviewed by *Giessel and Datta*, the olfactory system in mammals embodies the extremes of neural spatial organization. The glomeruli of the olfactory bulb present a beautiful example of an orderly map of the receptor surface; but this order turns to disorder in central targets such as the piriform cortex and the olfactory tubercle, where widely distributed connections may enable the construction of behaviorally relevant representations through learning. *Knaden and Hansson* review the evidence for the mapping of valence in the fly olfactory system. They conclude that there is a very clear segregation of the circuits in the fly that convey information about pleasant and unpleasant odors, starting just one synapse from the receptors—an organization that seems ideally suited for ensuring innately determined stereotyped responses that are critical for survival and reproduction.

*Dhande and Huberman* review recent studies that have explored the remarkable degree of segregation in central maps that are generated by the terminal fields of retinal ganglion cells in mouse and zebrafish. Ganglion cells with preferences for different directions of motion terminate in narrow strata within the superior colliculus, forming functionally distinct retinotopic maps for different directions of motion. A similar laminar stratification of direction-selective responses has recently been identified in the lobular plate of drosophila, providing further support for the broad generality of this circuit design for the initial stages of visual information processing.

The primary visual cortex of carnivores and primates has provided the most striking evidence for fine scale functional mapping of stimulus properties, beginning with the pioneering work of Hubel and Wiesel that defined columnar maps of orientation preference and ocular dominance. *Nauhaus*

and *Nielson* review studies using 2-photon imaging of calcium signals that support the existence of additional fine scale maps of spatial frequency, binocular disparity, and direction. They consider the possibility that cortical maps are built on the segregation of parallel afferent pathways, a framework that would account for the orderly interrelationships between maps. The absence of segregated afferent pathways might explain the ‘salt and pepper’ spatial arrangement of orientation and ocular dominance in rodent visual cortex. But, as emphasized by *Kaschube*, ‘salt and pepper’ is unlikely to be simply a shuffled version of the circuits that are found in species that exhibit maps. Instead, the organization found in rodents is likely to reflect different demands of sensory processing, and different mechanisms for building cortical response properties.

While the spatial arrangement of response properties within rodent primary visual cortex appears fundamentally different from that of primates and carnivores, a large body of work in the mouse exploiting new functional imaging techniques suggests a fundamental similarity in the organization of extrastriate areas. As reviewed by *Glickfeld et al.*, there are multiple extrastriate areas in the mouse, each with its own retinotopic map and bias in visual response properties. Although there is not a one-to-one correspondence with the cortical areas in other species, recent evidence points to parallel streams of areas that are specialized for action versus recognition, a distinction that bears at least a functional homology to the parallel streams in primates.

Parallel maps of the sensory surface are not unique to the visual system. *Krahe and Maler* provide an overview of neural maps in the electrosensory system of weakly electric fish, where there are 18 different topographic representations of the fish electroreceptive body surface in just one brain structure, the electrosensory lateral line lobe — and additional maps in other brain regions. Each map is comprised of different neuronal classes, with distinct filter properties, an organization that is suggested to be well configured to allow small prey to be distinguished from conspecifics.

Functional maps have also been central to the study of audition, although there are fundamental differences in the auditory maps of insects versus vertebrates. As reviewed by *Hildebrandt*, both share peripheral tonotopic maps, but insects lose this map structure in subsequent auditory stations, while mammals exhibit maps all the way to the primary auditory cortex and beyond. It is suggested that maps in vertebrates facilitate diverse and plastic behavior, while the non-mapped auditory filters of insects facilitate rapid stereotyped responses. While tonotopic maps are a prominent feature of auditory cortex, *Mizrahi et al.* emphasize that the responses of single neurons as well as map architecture differ substantially

for natural sounds versus artificial tone stimuli. *Schreiner and Polley* review the plasticity of auditory cortex maps, discussing the variety of mechanisms, including bottom-up and top-down effects, as well as local homeostatic plasticity, that contribute to dynamic map reorganization.

A number of the reviews focus on the organization of computational maps—maps that are not inherited from the periphery but are computed de novo in the brain. Computational maps of spatial location in the auditory system are fundamental to auditory spatial perception in bats and birds. *Kössl et al.* review the functional architecture of maps for sonar-target range in echolocating bats, emphasizing that these maps are innate, being pre-wired in the brain even before the bat pups start emitting echolocation calls. An additional example of a computational map is the space map found in the inferior colliculus and optic tectum of barn owls. As reviewed by *Peña and Gutfreund*, recent evidence suggests that the inferior colliculus contains a spatial map — but the optic tectum comprises a multimodal saliency map rather than a map of space per se.

Additional examples of computational maps are found far away from the sensory periphery, in the hippocampus and entorhinal cortex. While spatial responses in the inferior colliculus and optic tectum of barn owls are tied to the coordinate system of the head (egocentric coordinates), the hippocampus and entorhinal cortex of rodents, bats and primates contain place cells and grid cells — neurons that signal the animal’s position in absolute space (in ‘allocentric coordinates’). *Rowland and Moser* review the recent discovery of modules of grid cells in the rat entorhinal cortex: discrete units containing grid cells of particular scale (wavelength) and orientation. The discretized map in entorhinal cortex is quite unique, in that grid scale increases in discrete jumps along the dorso-ventral axis of the medial entorhinal cortex, forming approximately 10 functional modules — with grid wavelength increasing in steps of  $\sim\sqrt{2}$  between successive modules. The authors propose that this cortical modularity can subserve combinatorial memory capacity. *Burgalossi and Brecht* review the functional as well as anatomical modularity of the medial entorhinal cortex, emphasizing the rich modular structure of subnetworks of different neuronal types. Finally, *Wills and Cacucci* provide an overview of recent work exploring the role of experience in the development of the neural map of space in the hippocampus and entorhinal cortex. Different classes of spatially tuned neurons emerge at different ages, with head-direction cells being evident before the animals have begun to explore their environment. In contrast, the responses of place cells and grid cells emerge after the onset of exploratory behavior, and the properties of place cells are then gradually refined by experience.

As exemplified by the maps and modules in the entorhinal cortex and hippocampus, there is mounting evidence for the existence of orderly maps in many higher brain regions—and their functional significance for behavior and cognition remains an area of active exploration. *Sereno and Huang* review the evidence from fMRI studies in humans for parcellation of parietal cortex into a number of small areas with multimodal topographic representations. These areas combine responses to visual and somatosensory information that could be used to coordinate eye and limb movements in peripersonal space, ideal for object manipulation, hand-to-mouth movements and body defense. Recent studies on the significance of cortical maps for the control of the uniquely human capacity for speech are reviewed by *Conant et al.* While fMRI studies have been able to document the somatotopic organization of the vocal tract within the ventral sensorimotor cortex, new studies employing electrocorticography have visualized the spatiotemporal patterns of neural activity that are associated with the production of consonants and vowels, revealing phonemic feature maps that underlie speech production.

Even if the functional significance of neural maps remains under debate, there is no question about the pivotal role that maps have played in elucidating fundamental principles of neural circuit development and plasticity. The topographic projection from the retina to the superior colliculus has served as a valuable model for identifying the molecular mechanisms that guide map formation. *Triplet* reviews the gradients of cell surface molecules that have been identified as critical for map formation, as well as recent evidence for axon–axon interactions that suggest a combination of mechanisms that guide early map development. While activity-independent mechanisms provide the initial scaffolding for map development, the refinement of map structure rests on activity-dependent mechanisms of plasticity that are driven by the spatiotemporal patterns of activity generated by developing neural circuits. *Ackman and Crair* review the sources of endogenous activity that are responsible for patterning map structure, emphasizing the important role of retinal waves in guiding map refinement in the superior colliculus and the visual cortex.

One of the challenges in understanding map formation and map plasticity has been the difficulty in following the

changes in morphology and functional properties in individual neurons over time. *Margolis et al.* review recent studies employing novel *in vivo* imaging and electrophysiological studies that permit longitudinal analysis of individual neurons and reveal the heterogeneous changes in neuronal properties that accompany sensory deprivation and that must be considered in understanding mechanisms of map plasticity. *Hidalgo and Schummers* emphasize that efforts to understand map development and plasticity need to consider the unique role that astrocytes are positioned to play. Work in the visual cortex, in particular, illustrates the tight coupling of astrocyte activity with synaptic function at a spatial scale that could be instrumental in cortical map function and plasticity. *Harrison and Murphy* review recent studies on motor maps, and emphasize the utility of novel optogenetic stimulation techniques for conducting longitudinal studies of motor map function, stability and plasticity.

Finally, *Krubitzer and Stolzenberg* consider plasticity of cortical maps from an evolutionary perspective, suggesting that phenotypic changes in the brains and behavior of modern humans were uniquely driven by epigenetic mechanisms that allowed for context-dependent changes to the cortical phenotype.

So, what are maps good for? One theme that emerges from this volume is that there is no single answer to this question. Maps have evolved a multitude of times over the course of evolution, likely instantiating a range of benefits that include economy of wiring, sharpening of neural tuning via lateral inhibition, rapid reflexive behaviors, as well as facilitating plasticity and enabling efficient computations for a broad range of sensory, motor and cognitive functions. An equally important theme, however, is that the lack of orderly structure may carry just as much functional significance for neuronal computations as maps, representing an efficient solution that meets a different set of biological constraints.

As our understanding of the relation between neural circuits and behavior becomes more refined, so will our appreciation of the roles of order and disorder in the mapping of the neural response properties that underlie behavior.