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EDITORIAL

Understanding structure–function relationships in the mammalian visual system: part one

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Vision is an essential sensory modality that allows animals to obtain information about their environment and to plan for immediate or future actions. The visual system of primates is particularly well-developed, and perhaps for this reason it has become the most widely studied mammalian sensory system. Much of the basic anatomy (including topographic organization), perceptual performance, and functional response properties of the visual system are relatively well understood. The advances in visual neuroscience have led to the establishment of journals focusing on the basic science of the visual system, such as *Visual Neuroscience*, *Vision Research*, *Journal of Vision*, and *Annual Review of Vision Science*.

However, the integration of knowledge about visual systems across different research sub-disciplines remains a challenge. Specifically, there is still a long way to go before we can state, in unambiguous terms, that we understand the relationship between the function of the visual system and its underlying neuroanatomy. Detailed information about structure–function relationships remains a major missing component in the vast majority of neuroscience-inspired computational models of visual processing. Addressing this question may require an investigation of the visual system at different scales, combining multiple methods, and performing comparative studies to understand the evolutionary history of brain structure and its relationship to visual functions.

These considerations motivated us to organize a special issue of *Brain Structure and Function*, which is a journal focusing on the structure–function relationships in mammalian brains (Zaborszky and Zilles 2007; Zaborszky 2021). The broad aim of this collection is to highlight current approaches to bridge neuroanatomy with the functional and computational aspects of visual processing at different levels. We have received an enthusiastic response from the scientific community in response to this brief, leading to the publication of two *Brain Structure and Function* issues (i.e., “Structure and Function of the Visual System” part 1 and part 2). The following sections summarize the contents of part 1.

Three papers in this special issue report on anatomical investigations of the subcortical visual system, including the lateral geniculate nucleus (LGN), superior colliculus, and pulvinar. While the main types of retinal ganglion cells that project to different layers of the LGN are relatively well studied, there is still much to be understood about the specific anatomy of retinal cells that input to other subcortical nuclei. By using an MRI-guided tracer injection approach in the marmoset monkey (a rapidly emerging animal model of the primate visual system; Solomon and Rosa 2014; Mitchell and Leopold 2015), the first study, Grünert et al. (2021) identifies the types of retinal ganglion cells that form projections to the inferior pulvinar and superior colliculus. Both of these structures are thought to play key roles in residual

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visual function following damage to the primary visual area (V1); this topic is investigated in the second study, Atapour et al. (2021), also using marmosets. Atapour et al. (2021) show that such lesions trigger changes in the neurochemical characteristics of LGN neurons, revealing a potential for plasticity, which may have implications for blindsight. The third study, by Adusei et al. (2021), "closes the loop" by investigating the feedback connections from the ferret extrastriate cortex to the LGN. This study reveals a variety of cell- and area-specific projections, suggesting parallel corticogeniculate feedback pathways, which also have implications for residual vision following V1 damage.

The topic of anatomical pathways and their specificity is continued by Rockland (2021), who offers a critical review of past and present progress in our understanding of one of the most intriguing examples of modular organization in the visual system: the cytochrome oxidase "blobs" of primate V1. This paper, which highlights several unknowns about the segregation and integration of parallel pathways in the early visual cortex, provides a good introduction to the next six papers in this special issue, which involve investigations of the relationship between cortical maps and other anatomical, molecular and functional features of the first stages of processing in the visual cortex.

The formation of retinotopic maps is a fundamental aspect of early processing stations of the visual system, and area V1 is a quintessential example of a retinotopic map. In this special issue, Gomez et al. (2021) combined neuroimaging, gene analysis and cytoarchitectonics to report that gene expression patterns vary from the central to the peripheral visual field representation of human V1; this finding has wide implications for models aimed at understanding the molecular mechanisms underlying retinotopic map formation. Three other papers explore the functional properties of V1 and how they change according to different conditions. Alvarez et al. (2021) report that human V1 shows larger population receptive fields (pRF; Dumoulin and Wandell 2008) for disparity-defined stimuli, compared with other types of stimuli, and that this observation can be explained based on the binocular energy model (Ohzawa et al. 1990). Further, Silva et al. (2021) report that pRF estimates are affected by aging, revealing correlations between visual acuity, retinal thickness, and cortical visual area size in human participants. In addition, Brown et al. (2021) build on the topic of adult brain plasticity using a simulated lesion approach, supplementing earlier investigations of the source of stimulus-evoked blood oxygen level-dependent (BOLD) responses in V1 of human macular degeneration patients (Baker et al. 2005; Masuda et al. 2020).

The paper by Li et al. (2021) investigated the topic of structure–function relationships in the extrastriate cortex, by exploring the relationship between retinotopic maps and myelin density in the macaque brain. Using ultra-high resolution functional and structural MRI, this study proposes a new way to parse this region into functionally meaningful areas, which includes significant differences between the dorsal and ventral "early" extrastriate cortex (Angelucci and Rosa 2015). Finally, Correia et al. (2021) address the function of retinotopically organized connections between different cortical and subcortical areas, by demonstrating the effects of inactivation of sites in the pulvinar and various extrastriate areas on the responses of neurons in area V2 to visual stimuli.

A key function of the visual system is spatial information processing with the objective of guiding action. A predominant view is that such spatial information is processed in the dorsal visual cortex ("dorsal stream"; Ungerleider and Mishkin 1982; Goodale and Milner 1992). Eight papers in this volume address spatial information processing towards visuomotor action. Not only do they describe detailed investigations on the dorsal visual areas, but also expand our view of what constitutes the "dorsal stream".

In dorsal stream areas, the organization of cortical maps based on retinal coordinates is complemented by other types of spatial selectivity, and maps based on different principles occur in different areas. Cottereau et al. (2021) review electrophysiological, neuroimaging and psychophysical evidence that support the existence of a privileged response to visual objects located right in front of the body, both in V1 and in extrastriate areas. This provides a clear example of how brain maps based on retinal coordinates interact with other types of spatial representation during primate behavior, and how this affects visuomotor performance.

Neural processing of the optic flow, which is a powerful motion-based spatial cue for locomotory behavior, is addressed by two papers. In the first of these, Pitzalis et al. (2021) evaluate the optic flow selectivity of areas in the macaque parieto-occipital sulcus, including V6, by contrasting the responses obtained with two commonly used types of stimuli (coherently moving dot fields, versus expanding and contracting ring patterns). Smith (2021) takes the topic of optic flow analysis to another stage of hierarchical processing, in a review of the response properties, connectivity and function of the cingulate sulcus visual area (CSv), integrating data obtained in both humans and macaques.

The structure and function of the superior parietal lobule, which is a brain region crucial for the integration of visual and somatosensory information for visually guided actions, is the topic of the next two papers. Gamberini et al. (2021) review the neuronal response properties and anatomical connections of the various cytoarchitectural areas in this region of the macaque monkey brain, providing a global view of how different cortical processing modules contribute to reaching and grasping behavior. Maltempo et al. (2021) investigated BOLD responses in area hPEc, which is a likely homolog of macaque PEc, and found that this area is strongly activated by limb movement directed towards visual stimuli presented in the lower visual field (where visually guided limb movements are most most likely to occur).

Using a combination of single neuron recordings and neural network analyses, Churan et al. (2021) explore how neurons in another subdivision of the dorsal stream, the lateral intraparietal area, encode visual information to enable saccadic eye movements that allow us to intercept moving objects[1].

The section on dorsal stream is capped by two review papers. D'Souza et al. (2021) review the progress in our knowledge of the fronto-parietal network in the marmoset monkey, a species that has been recently used in studies of visuomotor behavior. This paper highlights the potential advantages of using marmosets to understand the anatomical and functional bases of behavior, which are complementary to those found in the more commonly used macaque monkey. Finally, Orban et al. (2021) address the question of how we use visual information in different ways to guide our own actions and to interpret the actions of others. Based largely on their studies of macaque monkeys, the authors propose a global model of the function of posterior parietal areas, which provides a rich foundation for the generation and testing of hypotheses.

Three papers in this volume address the topic of categorical processing, which has often been considered to be processed mainly by areas in the ventral occipitotemporal cortex (VOTC; "ventral stream"; Ungerleider and Mishkin 1982; Goodale and Milner 1992). Komatsu et al. (2021) provide the first report about the anatomical connections of a specific region of the inferotemporal cortex in macaque monkeys, where neurons selectively respond to the glossiness of visual objects. Hagen et al. (2021) explore a different aspect of the organization of the ventral stream by investigating the spatial dissociation of face- and word-selective responses in the human VOTC, based on intracranial electroencephalographic recordings. Caffarra et al. (2021) review the literature on structural and functional studies of human word-selective visual cortex and discuss its implications in understanding the organization of human VOTC and reading circuitry.

The final paper in this volume addresses the link between neural activity and visual perception. Using electroencephalography in human participants, Aydin et al. (2021) report how neural activity is associated with a perceptual phenomenon known as metacontrast masking, in which the perception of target stimuli is interrupted by mask stimuli that are presented near the target stimuli. Based on the fact that metacontrast masking significantly depends on the contrast polarity of mask stimuli and stimulus onset asynchrony, they demonstrated a human neural response showing properties similar to the perceptual effect of metacontrast masking.

In summary, the present volume encompasses contributions focused on the entire visual system, from retina to higher-order association cortical areas, including studies on several different species and many combinations of methods. However, it should be noted that this volume is just half of the story. The second volume of the special issue on "Structure and Function of the Visual System" is almost ready, and we believe that the original papers and reviews of the second part will be just as relevant to the relationship between the structure and function of the visual system.

[1] The paper by Churan et al. was published early (Brain Struct Funct 226(8):2707–2723), but should be considered as an integral part of the present special issue.

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