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Current research on the organization and function of the visual system in primates

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All primates, including humans, are highly visual creatures.¹⁻³ We rely heavily on visual cues for basic adaptive behaviors such as finding food, mates, and shelter; as well as more complex behaviors such as parental care and the formation of social hierarchies. Throughout the course of primate evolution, our dependence on visual cues has increased with each adaptive advantage acquired from visually guided behavior; and so has the demand for greater and more efficient processing of visual information in primate brains. Consequently, the number, size, and complexity of brain structures involved in visual processing has expanded dramatically in the primate order, far more than those of any other species in the mammalian lineage.^{2,4} As we have learned to interact with the world using visual cues, our brains have evolved to absorb, manipulate, and react to visual information in increasingly effective ways. Individual brain structures dedicated to vision in primates also frequently exhibit anatomical and functional specializations that are not present in other mammals. These adaptations are not present in most nonprimate mammals, partly because many species rely on other sensory modalities for their individual behaviors. Thus, understanding how we, as humans, perceive the visual world around us begins with learning how vision is processed in the primate brain. Furthermore, learning how vision in primates differs both structurally and functionally from vision in nonprimate mammals, and determining how those changes enable adaptive traits in the primate lineage, will allow us to understand the truly unique phenomenon of human visual behavior.

To that end, we have decided to include a special issue of *Eye and Brain* on the organization and function of the visual system in nonhuman primates. Such research is becoming rare and increasingly difficult to conduct, but remains crucial in our effort to understand vision in humans. A review of several published neuroscience studies shows that in major neuroscience journals, almost 75% of studies conducted on mammalian brains focus on mice, rats, and humans, while only 4.3% focuses on non-human primate species.⁵ Yet the vast majority of human behaviors, particularly visually guided ones, are not implemented in the same way by rats and mice. However, we cannot say that valuable information is not

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being obtained from rodent studies. We have learned a great deal about the individual characteristics of visually responsive neurons, as well as many of the cellular processes that underlie the coding of visual stimuli from rodents. Indeed, the advantage of genetic and other manipulations that are now common in rodents, especially mice, coupled with low maintenance costs per animal, rapid breeding and developmental cycles, and a large database of previous knowledge on rodent brains, makes studies in rodent species very attractive. However, rodent and primate brains differ significantly in a number of ways, particularly with respect to the visual system and its associated brain structures. As a brief tour, some of these differences are outlined to follow.

All mammals appear to share two main visual pathways from the eye to visual cortex. The individual structures and functions of these two pathways however, vary considerably between primates and other mammals.⁶⁻¹² The first pathway, known as the geniculostriate pathway, begins with retinal ganglion cells (RGCs) in the eye that project to the lateral geniculate nucleus (LGN) of the thalamus, followed by LGN cells that project to the primary visual cortex, or V1. The second, known as the extrastriate pathway, begins with a separate (in rodents) or overlapping (in primates) group of RGCs that project to the superior colliculus (SC) in the midbrain. Cells in the SC then project to the lateral posterior nucleus (in rodents), or the pulvinar complex (in primates) of the thalamus, and these nuclei project to extrastriate or nonprimary visual cortical areas. Each step along these pathways differs between primates and nonprimate mammals. First, 80% of all retinal ganglion cells project to the lateral geniculate nucleus in primates, while in rodents and other mammals, the dominant target is the superior colliculus. Next, the SC primarily receives contralateral RGC projections, and represents the entire visual field of the contralateral eye in most mammals, but in primates, the SC receives inputs from both eyes and only represents the contralateral visual hemifield. RGC inputs from each eye also terminate in different patterns within the primate SC; some primates exhibit segregated layers of retinal input from each eye while other primates possess regularly interdigitated inputs from each eye in the same collicular layer. The other major input to the superior colliculus is from areas of neocortex. As the numbers and types of cortical areas that project to the superior colliculus vary greatly in primates and rodents, the functions of the superior colliculus must reflect these differences in visual representations, inputs from the retina, and especially, inputs from areas of neocortex. In this special issue Cerkevich et al describe the relative contributions of different cortical areas to the superior colliculus, including visual and posterior parietal areas that are not found in nonprimate mammals, many of which guide visuomotor behavior. Similarly, the primate LGN is uniquely organized, compared to the LGN of most nonprimate mammals, with multiple layers that segregate functional classes of retinal and cortical inputs. Shostak et al describe putative differences in glutamatergic signaling through each of these geniculate pathways in primates and provide evidence for the segregation of multiple processing channels through the LGN. Another visually responsive region of the thalamus, known as the lateral posterior nucleus or pulvinar complex is massive in primates compared to other mammals, and contains several distinct nuclei with specialized functions in each primate species.

In the neocortex V1 is common to all mammals, but V1 in primates occupies a larger proportion of the neocortex than V1 of nonprimates,¹³⁻¹⁶ and its neurons are modularly

organized in a manner not shared with other mammalian species.¹⁷ Here, Rockoff et al analyze the well-known blob and inter blob modules of V1 in prosimian galagos using multiple anatomical markers that reflect different features of V1 neurons, thus gaining further insight on the functional contributions of these neural groups to intrinsic neural processing in V1. Maier et al show that synchronized neural activity in primate V1 varies as a function of distance between individual V1 locations, but can also differ significantly between V1 layers at the same location. In the same vein, Liu et al show that many neurons in V1 maintained extraordinarily long horizontal connections, and these long ranging inputs may facilitate the integration of neural responses across V1, thus contributing to a holistic representation of the visual field. These findings highlight the modular and systematic organization of V1 across primate species. The second visual area, V2, is another cortical visual area common to nearly all mammals,¹⁸ yet V2 in primates is organized differently compared to V2 in other species. In primates, V2 contains discrete modules known as the “V2” bands or “stripes” that appear to integrate different aspects of form and color perception. Here, Parajuli et al used multi electrode recordings of local field potentials in V2 of Macaque monkeys, to provide further evidence for the different functional roles of the four types of modular stripes of V2 in response to varying visual stimuli. Ramsden et al also describe patterns of neural activity in V2 that distinguish between real and illusory contours, thus identifying further compartments within V2 that are crucial to our perception of object locations and surfaces. In addition to V2, primates have an array of extrastriate temporal and parietal visual areas – the middle temporal area, medial superior temporal area, the fundus of the superior temporal area, the middle temporal crescent area, and the dorsomedial visual area, to name a few – that have not been identified in other mammals. Moreover, all primates have an expanded region of posterior parietal cortex that is subdivided into regions and areas devoted to visuomotor behaviors, most notably the lateral intraparietal area, which is involved in directing gaze towards objects of interest.¹⁹ Finally, the visuomotor areas of frontal cortex, the frontal eye field and the supplementary eye field, are subdivisions of cortex that are well defined in most primates²⁰ but missing or poorly developed in other mammals.

All these, and other differences indicate that scientific conclusions about how the visual system codes for visual stimuli, mediates behavior, and is impaired by various disease states or injuries are likely to be most applicable, if the results are derived from studies of primates. That being said, it is also important to recognize that all primates are not alike.^{1,2} Prosimian primate brains are smaller than anthropoid primate brains, and generally considered more primitive in organization. Tarsiers that form a small, but interesting and ancient branch of the primate radiation, are specialized as visual predators, with a primary visual cortex that is proportionately larger and more differentiated than V1 in other primates. Visual structures in New World monkeys are highly varied between species with and without color vision, while visual structures in nocturnal owl monkeys are specialized for vision in dim light instead. As for humans, the human brain is immense compared to those of other primates, with 80% of its mass devoted to cortex. Much of this mass is devoted to processing visual information, as in other primate species. Cortical processing of visual stimuli depends on the number and specialization of cortical visual areas in each species, and Old World monkeys have a proposed 35 or so visual areas while humans likely have

more. The differences in the visual system across primate taxa provide a research advantage, as differences in visual system organization can be related to visual abilities, but such differences can also lead to confusion when comparing the structure and function of specialized visual areas between species. In this special issue Balaram et al discuss the importance of consistent comparisons when describing features of visual areas across primate groups. Altogether, the research included in this special issue will hopefully encourage others to tap into the potential of a comparative approach in studies of visual function in primates.

Research on the visual system of primates has benefited in recent years from methodological advances in anatomy, physiology, cellular biology, and brain imaging, which allow us to explore the mechanisms behind visual processing, from individual neuronal synapses to whole brain activity. This special issue presents a number of recent advances in our understanding of visual processing in primates, and highlights the need for further studies on nonhuman primates. Such studies, although rare, offer a more precise description of visual perception in the human brain and ultimately, will lead to a better understanding of visual processing and improved therapeutics for visual disorders in humans.

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