displacement during spring migration. Curr. Biol. *18*, 188–190.
14. Lohmann, K.J., Lohmann, C.M.F., and Putman, N.F. (2007). Magnetic maps in animals: nature's GPS. J. Exp. Biol. *210*, 3697–3705.
15. Jacobs, L.F., and Schenk, F. (2003). Unpacking the cognitive map: the parallel map theory of hippocampal function. Psychol. Rev. *110*, 285–315.
16. Walker, M.M., Diebel, C.E., Haugh, C.V., Pankhurst, P.M., Montgomery, J.C., and Green, C.R. (1997). Structure and function of the vertebrate magnetic sense. Nature *390*, 371–376.
17. Putman, N.F., Lohmann, K.J., Putman, E.M., Klimley, A.P., Quinn, T.P., and Noakes, D.L.G. (2013). Evidence for geomagnetic imprinting as a homing mechanism in Pacific salmon. Curr. Biol. *23*, 312–316.

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544-1003, USA.
E-mail: gould@princeton.edu

http://dx.doi.org/10.1016/j.cub.2014.01.030

Visual Circuits: Mouse Retina No Longer a Level Playing Field

Unlike humans, monkeys, or carnivores, mice are thought to lack a retinal subregion devoted to high-resolution vision; systematic analysis has now shown that mice encode visual space non-uniformly, increasing their spatial sampling of the binocular visual field.

Onkar S. Dhande and Andrew D. Huberman

Our brains evolved to accurately represent the world around us. This process begins with the sense organs: the skin, eyes, ears, mouth and nose. Thus, just as knowledge about the type and density of pixels in a digital camera will tell you a lot about the quality of images that the camera will take — monochrome *versus* color, low *versus* high resolution, and so on — knowing the type and layout of receptors harbored within the sense organs is crucial for understand sensory processing. In a recent issue of *Current Biology*, Bleckert *et al.* [1] report an unexpected distribution of a specific subtype of visual receptors in the mouse eye, raising the question: what does a mouse see?

A common feature among the various sensory modalities is topographic mapping whereby neighboring receptors are represented by neighboring sets of neurons in the brain [2]. Despite this point-to-point organization, the geometry of these maps is by no means uniform. For example, our fingertips contain a denser collection of touch receptors and more cortical area is devoted to them, relative to the cortical representation of body regions such as the back, which is less sensitive. Indeed, this biased representation is evident in our ability to discern smaller separations of contact on our fingertips as compared to on our torso [3].

Non-uniform mapping is a well-established feature of primate and carnivore visual circuits; the photoreceptors and the neurons that signal visual information to the brain, the retinal ganglion cells (RGC), are far more numerous in the central as compared to the peripheral retina [4]. This dependence of RGC density on distance from the central retina, or 'eccentricity', is propagated to higher visual processing centers in the brain and has profound consequences on the spatial acuity when viewing central *versus* peripheral space.

As the mouse has become an increasingly popular model for studies of visual processing over the last decade [5], it has become crucial to determine if and how their visual systems differ from that of more traditionally studied model species such as cats and monkeys. One key difference is that the mouse lacks a steep eccentricity gradient of photoreceptors or RGCs [6,7] and hence its visual system is thought to encode all points in visual space relatively uniformly. Bleckert *et al.* [1] report the surprising finding that not all subtypes of mouse RGCs are uniformly arrayed across the retina. They show that a well-known type of RGC called the alpha cell [4,8] exhibits dramatic variation in size and density according to position along the nasal-to-temporal retinal axis. From the overall layout of these gradients in the two eyes, the data suggest that such variation may afford the mouse an enhanced representation of the central, binocular field of view.

Previous work explored cell densities across the mouse retina and found that RGCs exhibit a modest two-fold reduction in density from center to periphery [6,7]. However, such studies considered RGCs as a singular population and did not distinguish among the two-dozen or so RGC subtypes that exist in this species [9]. In their study, Bleckert *et al.* [1] combined molecular markers and electrophysiological characterization of alpha-RGCs to reliably identify these cells. By meticulously surveying the distribution and dendritic size of one subtype of alpha-RGCs, On-sustained alpha or 'Aon-s' RGCs, as a function of eccentricity and retinal quadrant, they discovered that Aon-s RGCs are much more numerous and densely packed within the temporal retina. They also found that temporal Aon-s RGCs accomplish this because their dendritic arbors are much smaller than those of nasal Aon-s RGCs.

In primates, the increase in RGC density towards the fovea is accompanied by a decrease in the convergence of cells that provide input to them, such as bipolar cells. The net result is increased spatial sampling of the visual scene in the fovea [4,8]. Bleckert *et al.* [1] asked whether this was also the case in the mouse. A systematic measurement of the bipolar neurons that provide excitatory inputs to Aon-s RGCs revealed that their distribution and axonal size was unchanged across the retina. Thus, in contrast to the primate fovea, these data suggest that in the mouse, the eccentricity gradients of different retinal neurons (such as RGCs, bipolar cells, photoreceptors) are not yoked to each other.

Generally, the dendritic arbor size of a RGC closely matches its receptive field size [10]. Surprisingly, Bleckert *et al.* [1] also found that, whereas the dendritic and receptive

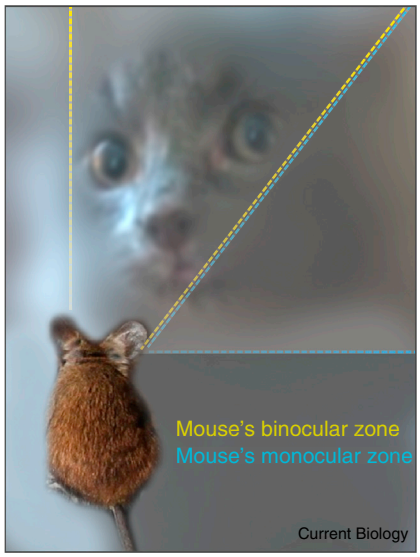

Figure 1. The mouse's view of central (binocular; yellow) and peripheral (monocular; blue) visual space.

New findings from Bleckert *et al.* [1] reveal dramatic variation in the size and spatial sampling of alpha retinal ganglion cells, which may underlie variation in the resolution for different parts of the visual scene. For data on complete binocular maps in mice see [11].

field sizes of nasal Aon-s RGCs were closely matched, the receptive fields of temporal Aon-s RGCs were significantly larger than their dendritic span. Furthermore, Aon-s RGCs in the temporal retina had a greatly increased 'coverage factor', owing to increased overlap of their dendritic arbors. Together, this means that Aon-s RGCs in the temporal retina sample visual space much more densely than do Aon-s RGCs located in other regions of the retina. Given the way the visual field is mapped onto the mouse retina (Figure 1), this should afford the mouse an enhanced representation of the central visual field. Moreover, because the central ~50° of visual field corresponds to the region viewed by both eyes [11] that is used to perceive depth (the 'binocular zone'), it is tempting to speculate that spatial resolution within the binocular zone is high compared to other locations in visual space (Figure 1).

Like many RGC subtypes, alpha-RGCs include several distinct subtypes that encode either increments or decrements in light and sustained versus transient stimuli [4,8]. Do all three types of alpha-RGCs vary in size and density across the retina? Interestingly, Bleckert *et al.* [1] found that just like Aon-s RGCs, Off-sustained alpha-RGCs also display a steep nasal-to-temporal gradient; however, the third alpha-RGC type, the Off-transient alphas, are uniformly distributed throughout the retina. Together with other recent studies [12,13], these data suggest that each of the 20 or so parallel eye-to-brain pathways in the mouse carry distinct information not only about specific *features* in the visual scene such as brightness and direction of motion, but they can also be biased to over-represent specific *regions* of visual space.

Previous work exploring the representation of visual space in different brain regions of mice did not report any dramatic over-representations of particular visual coordinates [14–17]. However, the data in Bleckert *et al.* [1], and recent advances in understanding of the spatial and functional organization of early visual pathways in mice [18], call for a re-examination of this issue. In this context, it is important to resolve whether or not the specific features of the visual scene encoded by alpha-RGCs, such as motion [8], are non-uniformly mapped in subcortical and cortical areas.

In addition, one wonders about the ethological significance of having different gradients for the various functionally distinct RGC types. The number of laboratory visual tasks that mice have been shown capable of performing has increased substantially in recent years [19,20]. Going forward it would be interesting to modify these tasks to include visual stimuli that tap into the function of different RGC subtypes in order to discover how this important model species uses its visual system to navigate the world. In the meantime, the results of Bleckert *et al.* [1] indicate that certain features of the mouse visual system may bear more similarities to that of cats and primates than previously recognized.

References

1. Bleckert, A., Schwartz, G.W., Turner, M.H., Rieke, F., and Wong, R.O.L. (2014). Visual space is represented by nonmatching topographies of distinct mouse retinal ganglion cell types. Curr. Biol. *24*, 310–315.
2. Luo, L., and Flanagan, J.G. (2007). Development of continuous and discrete neural maps. Neuron *56*, 284–300.
3. Kandel, E.R., Schwartz, J.H., and Jessell, T.M., eds. (2000). Principles of Neural Science, fourth ed. (New York: McGraw Hill Health Professions Division).
4. Wässle, H., and Boycott, B.B. (1991). Functional architecture of the mammalian retina. Physiol. Rev. *71*, 447–480.
5. Baker, M. (2013). Through the eyes of a mouse. Nature *502*, 156–158.
6. Dräger, U.C., and Olsen, J.F. (1981). Ganglion cell distribution in the retina of the mouse. Invest. Ophthalmol. Vis. Sci. *20*, 285–293.
7. Jeon, C.J., Strettoi, E., and Masland, R.H. (1998). The major cell populations of the mouse retina. J. Neurosci. *18*, 8936–8946.
8. Stone, J. (1983). Parallel Processing in the Visual System (New York: Plenum).
9. Völgyi, B., Chheda, S., and Bloomfield, S.A. (2009). Tracer coupling patterns of the ganglion cell subtypes in the mouse retina. J. Comp. Neurol. *512*, 664–687.
10. Yang, G., and Masland, R.H. (1992). Direct visualization of the dendritic and receptive fields of directionally selective retinal ganglion cells. Science *258*, 1949–1952.
11. Sterratt, D.C., Lyngholm, D., Willshaw, D.J., and Thompson, I.D. (2013). Standard anatomical and visual space for the mouse retina: computational reconstruction and transformation of flattened retinae with the Retistruct package. PLoS Comput. Biol. *9*, e1002921.
12. Zhang, Y., Kim, I.J., Sanes, J.R., and Meister, M. (2012). The most numerous ganglion cell type of the mouse retina is a selective feature detector. Proc. Natl. Acad. Sci. USA *109*, E2391–E2398.
13. Hughes, S., Watson, T.S., Foster, R.G., Peirson, S.N., and Hankins, M.W. (2013). Nonuniform distribution and spectral tuning of photosensitive retinal ganglion cells of the mouse retina. Curr. Biol. *23*, 1696–1701.
14. Dräger, U.C., and Hubel, D.H. (1976). Topography of visual and somatosensory projections to mouse superior colliculus. J. Neurophysiol. *39*, 91–101.
15. Wagor, E., Mangini, N.J., and Pearlman, A.L. (1980). Retinotopic organization of striate and extrastriate visual cortex in the mouse. J. Comp. Neurol. *193*, 187–202.
16. Schuett, S., Bonhoeffer, T., and Hübener, M. (2002). Mapping retinotopic structure in mouse visual cortex with optical imaging. J. Neurosci. *22*, 6549–6559.
17. Mrsic-Flogel, T.D., Hofer, S.B., Creutzfeldt, C., Cloëz-Tayarani, I., Changeux, J.P., Bonhoeffer, T., and Hübener, M. (2005). Altered map of visual space in the superior colliculus of mice lacking early retinal waves. J. Neurosci. *25*, 6921–6928.
18. Dhande, O.S., and Huberman, A.D. (2014). Retinal ganglion cell maps in the brain: implications for visual processing. Curr. Opin. Neurobiol. *24*, 133–142.
19. Huberman, A.D., and Niell, C.M. (2011). What can mice tell us about how vision works? Trends Neurosci. *34*, 464–473.
20. Carandini, M., and Churchland, A.K. (2013). Probing perceptual decisions in rodents. Nat. Neurosci. *16*, 824–831.

Department of Neurosciences, Neurobiology Section in the Division of Biological Sciences and the Department of Ophthalmology, University of California, San Diego, CA 92093, USA.
E-mail: odhande@ucsd.edu (O.S.D.), ahuberman@ucsd.edu (A.D.H.)

http://dx.doi.org/10.1016/j.cub.2013.12.045