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Review article

Visuomotor control in mice and primates

E.J. Tehovnik [a,b,*], E. Froudarakis [c], F. Scala [a,b], S.M. Smirnakis [d], S.S. Patel [a,b], A.S. Tolias [a,b,e]

[a] *Department of Neuroscience, Baylor College of Medicine, Houston, TX, USA*
[b] *Center for Neuroscience and Artificial Intelligence, Baylor College of Medicine, Houston, TX, USA*
[c] *Institute of Molecular Biology and Biotechnology, Foundation for Research and Technology Hellas, Heraklion, Greece*
[d] *Department of Neurology, Brigham and Women's Hospital and Jamaica Plain Veterans Administration Hospital, Harvard Medical School, Boston, MA, USA*
[e] *Department of Electrical Engineering and Computer Engineering, Rice University, Houston, TX, USA*

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ABSTRACT

We conduct a comparative evaluation of the visual systems from the retina to the muscles of the mouse and the macaque monkey noting the differences and similarities between these two species. The topics covered include (1) visual-field overlap, (2) visual spatial resolution, (3) V1 cortical point-image [i.e., V1 tissue dedicated to analyzing a unit receptive field], (4) object versus motion encoding, (5) oculomotor range, (6) eye, head, and body movement coordination, and (7) neocortical and cerebellar function. We also discuss blindsight in rodents and primates which provides insights on how the neocortex mediates conscious vision in these species. This review is timely because the field of visuomotor neurophysiology is expanding beyond the macaque monkey to include the mouse; there is therefore a need for a comparative analysis between these two species on how the brain generates visuomotor responses.

1. Introduction

There are many parallels between the visual systems of the mouse and the macaque monkey, the latter of which has been studied to the finest detail over the last half century (Schiller and Tehovnik, 2015). With the advent of optogenetics and two-photon imaging, two methods that are heavily focused on the mouse, there has been renewed interest in studying the visual system of the mouse (Froudarakis et al., 2019; Koch and Reid, 2012). Presently, research efforts have concentrated on deducing the genetic, anatomic, and electrophysiologic characteristics of the mouse brain and on the computational analysis towards an algorithmic understanding of visual processing. Much less effort has gone toward performing a direct comparison of the visual systems of the mouse and the macaque monkey while keeping in mind the vast differences in their behavioral capacities. Here we discuss the following: visual-field overlap which has implications for stereovision, visual spatial resolution which limits how well visual scenes can be resolved, and the V1 cortical point-image which assesses the amount of tissue devoted to analyzing the visual attributes of an image based on the cortical magnification factor. Moreover, the substrates for both object vision and motion perception are considered for both cortical and subcortical brain regions, including the cerebellum. Additionally, the motor characteristics of visual processing are compared which includes the oculomotor range and how the eyes, head, and body of an animal are made to move with respect to a visual image. Finally, we revisit how the brain mediates conscious vision in rodents (i.e., the mouse, hamster, and gerbil) and primates (i.e., the macaque monkey and human) vis-à-vis blindsight.

2. Field of view, spatial resolution, and retino-V1 connectivity

Striking differences exist between the mouse and the macaque monkey with respect to their visual field of view and visual spatial resolution via the primary visual cortex (V1). These differences impact the way the visual systems of these two animals are innervated at the level of V1 by way of the lateral geniculate nucleus (LGN) which receives projection from the retina. The mouse unlike the macaque monkey has laterally displaced eyes such that the eyes project outward at approximately 50 degrees with respect to the longitudinal axis of the head (Heesy, 2004; Samonds et al., 2019) thereby restricting the aligned binocular overlap to about 40 degrees of visual angle for straight-ahead viewing (Fig. 1, Rodent). Furthermore, the eyes of the mouse are

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Abbreviations: ALS, amyotrophic lateral sclerosis; AMC, anteromedial cortex; LGN, lateral geniculate nucleus; LIP, lateral intraparietal area; MT, middle temporal cortex; MST, middle superior temporal cortex; STS, superior temporal sulcus; V1, primary visual cortex.

* Corresponding author at: Department of Neuroscience, Baylor College of Medicine, Houston, TX, USA.
E-mail address: tehovnikej@gmail.com (E.J. Tehovnik).

oriented slightly upwards which provides an animal with an expansive view of the world such that objects approaching from the front, the side, overhead, or behind can be viewed (Van Alphen et al., 2010). In the case of the macaque monkey, the eyes are oriented forward and roughly parallel with respect to the longitudinal axis of the head when the eyes are centered in the orbit (Fig. 1, Primate). This permits for a higher degree of binocular overlap (about 130 degrees) which can be utilized for stereovision. The shortcoming here is that macaque monkeys cannot see objects approaching from above and behind.

This difference in viewing experience translates to a varied wiring between the retina and area V1, the first station in the neocortex to receive a substantial input from the visual thalamus, the lateral geniculate nucleus (Fig. 1). Unlike the macaque monkey, the visual projections in the mouse are largely crossed with only around 10 % of the projections passing ipsilaterally to the lateral geniculate nucleus (Guido, 2018). The macaque monkey has a far more developed lateral geniculate nucleus that is composed of six layers, three dedicated to projections from one eye and the remaining dedicated to projections from the other eye (Hubel and Wiesel, 1977). A consequence of this segregation is that area V1 is organized into ocular dominance columns such that at the level of lamina IV (the input layer) the cells receive input from one eye only. As one advances an electrode parallel to the V1 surface the ocular dominance shifts every 0.5 mm or so from being left eye dominant to right eye dominant and so on. It is the segregation of ocular dominance columns that sets up the cortical wiring for stereovision (Poggio and Fischer, 1977). In the case of the mouse, which has no ocular dominance columns (Dräger, 1975), it is believed that depth perception is mediated mainly by monocular cues such as motion parallax (Ellard et al., 1986; Legg and Lambert, 1990), which maps the differential movements of objects across the retina to different depth planes. Cells in mouse V1 respond to a wide range of velocities (from 5 to 200 degrees/sec) that can support parallax evaluation (Dräger, 1975; Ellard et al., 1986; Legg and Lambert, 1990).

In addition, mouse V1 contains neurons that respond to inputs from the two eyes encoding visual field regions of binocular overlap (Dräger, 1975; Garrett et al., 2014; Scholl et al., 2013). It has been estimated that the disparity tuning of mouse V1 binocular cells is about 2 to 10 degrees of visual angle (Samonds et al., 2019; Scholl et al., 2013) which is far less sensitive for stereopsis than the tuning of V1 binocular cells in the macaque monkey (i.e., 0.2 to 0.5 degrees, Poggio and Fischer, 1977). Macaque monkeys have no difficulty detecting stereo-depth cues presented at a disparity of 0.1 degrees of visual angle (Schiller and Tehovnik, 2015), whereas mice can discriminate disparities from 2 to 5 degrees of visual angle (Samonds et al., 2019). Finally, monocular depth cues, such as interposition, perspective, and shading, could be used by both the mouse and the macaque monkey, although these cues have yet to be studied systematically in these species.

Another difference between the mouse and the macaque monkey is in how the visual field is represented in area V1. In the case of the mouse, the entire visual field is represented on the surface of the neocortex with the center of gaze (i.e., the zero coordinates of the azimuth and elevation visual axes) represented centrally and with the nasal field represented antero-laterally and the temporal field represented postero-medially in the neocortex (Fig. 2, derived from Garrett et al., 2014). In the case of the macaque monkey, half the visual field out to 7 degrees is represented on the surface of the neocortex (also called the operculum) with the remainder folded in a sulcus (Fig. 2, Schiller and Tehovnik, 2015). Furthermore, the foveal representation (which is highly magnified) in the macaque monkey is situated laterally in the neocortex and the temporal representation of the visual field is located medially. The mouse does not have a fovea, but the region of the retina subserving the primary optical axis into the nasal representation is minimally magnified (Fig. 7A, D of Garrett et al., 2014).

The visual spatial resolution of rodents including mice is a couple orders of magnitude below that of the primate (Fig. 3). Rodents have a visual spatial resolution of 0.5–2.0 cycles per degree with mice exhibiting acuity at the lower end of this range at 0.5 cycles per degree (Ingle, 1981; Prusky et al., 2000). The visual spatial resolution of macaque monkeys as well as humans extends to about 60 cycles per degree (Schiller and Tehovnik, 2015; Souza et al., 2011). In macaque monkeys
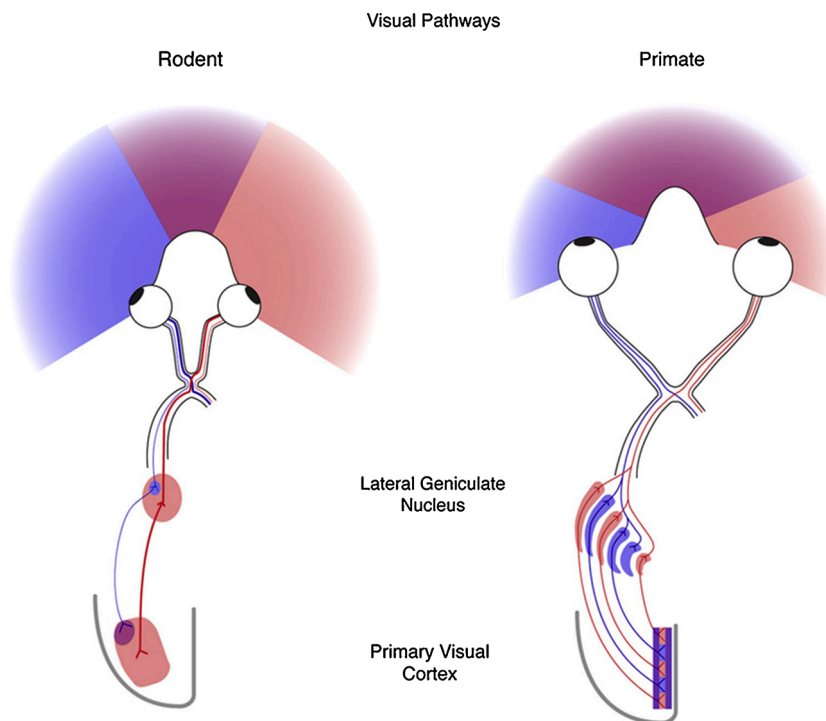

Fig. 1. On the left is shown the field of view of the rodent (e.g. the mouse) and on the right is shown the field of view of the primate (e.g., the macaque monkey/human). Shown is the innervation scheme between the retina and V1, which is the first major station of the neocortex that receives visual information in these animals (from Priebe and McGee, 2014: the figure was made by the Priebe laboratory and replicated with permission).
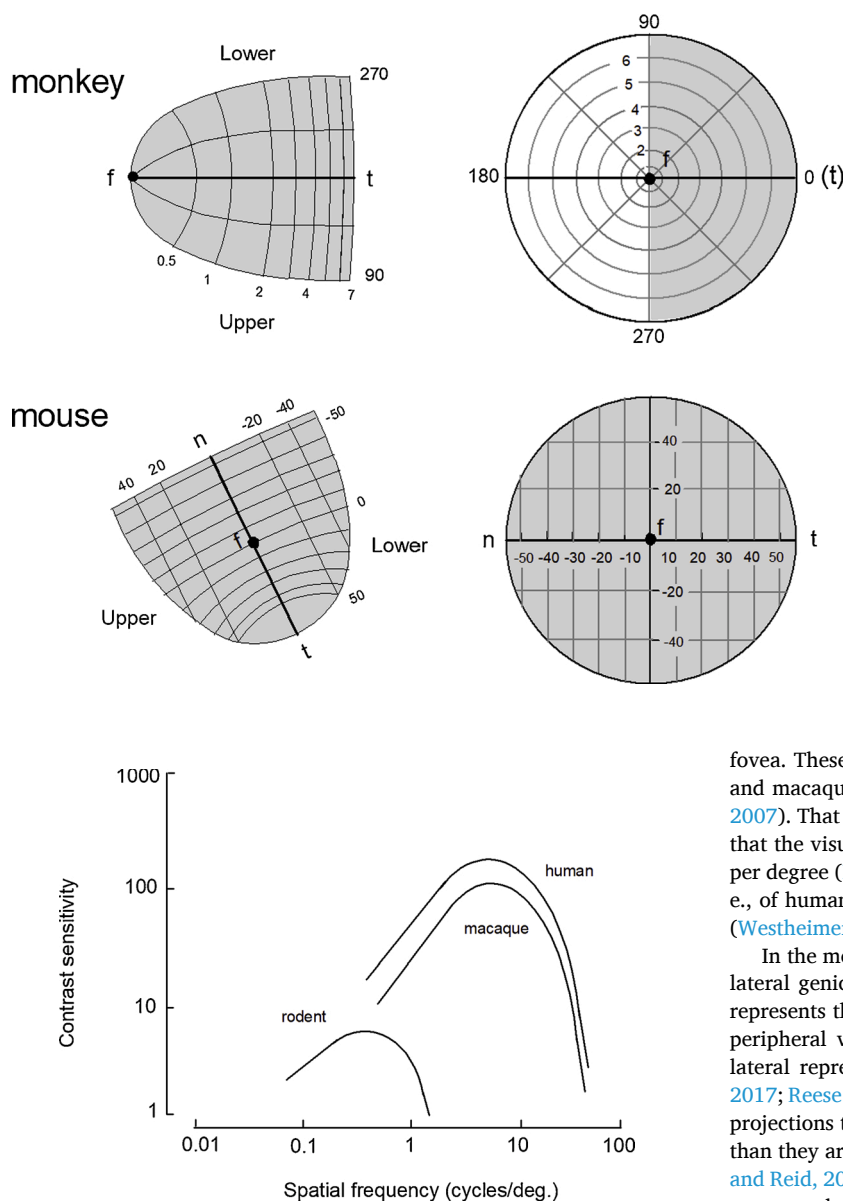
V1 Operculum Topography: Monkey vs. Mouse

Fig. 3. Contrast sensitivity functions plotted as a function of spatial frequency in cycles per degree for primates (e.g., the macaque monkey and human) and rodents (e.g., rats, mice, gerbils, etc.; derived from Souza et al., 2011).

the acuity is maximal at the fovea which is restricted to a 1-degree region of the central visual field and which contains a high concentration of cone receptors (Schiller and Tehovnik, 2015); for the mouse, the acuity is more uniform throughout the visual field at 0.5 cycles per degree (Prusky et al., 2000). Also, the mouse (unlike the macaque monkey) is sensitive to ultraviolet light originating from the sky above which is an adaptation for the detection of over-head flying predators (Szatko et al., 2019; Tan et al., 2015).

This difference in visual spatial resolution between the mouse and the macaque monkey is further highlighted by the following. If we consider 30 μm of V1 tissue in both the mouse and the macaque monkey, which is the amount of tissue believed to encode a single feature (Ji et al., 2015; Ohki and Reid, 2007; Peters, 1994), this amount of tissue in the mouse represents about 1 degree of visual angle (i.e., 3600 s), while in the macaque monkey it represents about 1 s of visual angle at the

fovea. These estimates are based on the magnification factor of mouse and macaque monkey V1 (Garrett et al., 2014; Tehovnik and Slocum, 2007). That these values are reasonable is supported by the observation that the visual spatial resolution of the mouse does not surpass 1 cycle per degree (Prusky et al., 2000) and that the hyperacuity of primates (i. e., of humans) amounts to several seconds of visual angle at the fovea (Westheimer and McKee, 1977).

In the mouse, like all mammals including the macaque monkey, the lateral geniculate nucleus has a standard retinal topography: anterior represents the central to the nasal visual field, posterior represents the peripheral visual field, medial represents the lower visual field, and lateral represents the upper visual field (Kerschensteiner and Guido, 2017; Reese and Jeffery, 1983; Schiller and Tehovnik, 2015). The retinal projections to the lateral geniculate are far less numerous in the mouse than they are in the macaque monkey (cf., 45,000 vs. 1.6 million, Koch and Reid, 2012; Perry and Cowey, 1985). Like macaque retinal ganglion neurons, the retinal ganglion neurons of the mouse that innervate the lateral geniculate nucleus have center-surround properties with either an ON-center field or an OFF-center field that responds to a spot of light (Kerschensteiner and Guido, 2017; Stone and Pinto, 1993; Schiller and Tehovnik, 2015; Tang et al., 2016). In addition, the retinal ganglion cells of the mouse can detect the direction of motion, information that is conveyed to V1 (Borst and Euler, 2011; Kerschensteiner and Guido, 2017; Sanes and Masland, 2015; Tang et al., 2016) and neurons in the lateral geniculate nucleus are orientation tuned (Kondo and Ohki, 2016; Roth et al., 2016). In the macaque monkey, all orientation and direction tuning starts at the level of V1 (Schiller and Tehovnik, 2015). Unlike the macaque monkey that has three cone types each for resolving blue, green, or red for trichromatic visual processing (Schiller and Tehovnik, 2015), the mouse does not have trichromatic vision. Yet it has 'cone' retinal receptors that are tuned to either green (i.e., 500 nm) or ultraviolet light (i.e., 350 nm, Szatko et al., 2019); the green-sensitive receptors are concentrated in the dorsal retina, whereas the ultraviolet-sensitive receptors are concentrated in the ventral retina. This functional bifurcation allows for the viewing of a green terrain and an ultraviolet emitting sky (Szatko et al., 2019).

In both the mouse and the macaque monkey, the strongest projections from the lateral geniculate nucleus (dorsalis) terminate in area V1 (Frost and Caviness, 1980; Schiller and Tehovnik, 2015; Simmons et al., 1982). In the case of the mouse there are weaker projections to extrastriate areas (e.g., the lateromedial area, the lateral intermediate area, the posterior area, and the postrhinal area) including the retrosplenial cortex (Ji et al., 2015). The macaque monkey, however, has few such projections terminating in extrastriate cortex albeit there are konicellular projections that directly innervate the middle temporal cortex, area MT (Warner et al., 2010). The terminations of the lateral geniculate nucleus in V1 of both the mouse and the macaque monkey are ordered topographically such that they terminate in regions represented by patches as defined by acetylcholine staining (i.e., muscarinic acetylcholine receptor staining or acetylcholine esterase staining) in the mouse and by acetylcholine or cytochrome oxidase staining in the macaque monkey (Horton, 1984; Ji et al., 2015). These patches are repeated systematically through the retinotopic map of V1. The patches have been used to determine the amount of V1 tissue dedicated to representing features falling within the receptive field of neurons at a V1 map location. The features include orientation, spatial frequency, direction of motion, binocular disparity, and color. The extent of this tissue is called a V1 cortical point-image. For both the mouse and the macaque monkey it has been estimated that seven patches (each arranged in a hexagonal configuration to optimize spacing) are sufficient to represent the V1 cortical point-image (Ji et al., 2015). For the mouse this represents roughly 240 μm by 240 μm of tissue running parallel to the V1 surface, whereas for the macaque monkey this represents 1000 μm by 1000 μm of tissue (Blasdel, 1992; Fahey et al., 2019; Ji et al., 2015; Marshel et al., 2011; Nauhaus et al., 2016; Ohki and Reid, 2007). What this means is that this tissue in the mouse and the macaque monkey is sufficient to encode orientation, spatial frequency, the direction of motion, binocular disparity, and color for a given region of visual space as defined by the receptive field of the neurons at a V1 map location (Ji et al., 2015; Schiller and Tehovnik, 2015). In terms of visual-field coverage, the V1 cortical point-image of the mouse represents a region of 13 degrees by 13 degrees throughout most of the visual field, which is the approximate size of the receptive field (Ji et al., 2015); the receptive field size is largely uniform throughout the map of V1 of the mouse, since the cortical magnification is minimal. The V1 cortical

point-image of the macaque monkey represents a region as small as 0.2 by 0.2 degree^2 of visual field at the fovea (Tehovnik and Slocum, 2007), which is related to the cortical magnification factor and which attests to the superior visual spatial resolution of the macaque monkey at the center of gaze.

Accordingly, V1 of the mouse is much less sensitive for the processing of visual information per unit receptive field than is V1 of the macaque monkey, and as such these two species employ different behavioral strategies when using their visual systems. As well, the anatomical differences of the visual systems of these two species reflect different behavioral adaptations: mice are ground dwellers and as such are prey to many species, whereas macaque monkeys can live in the trees and they are well-known for their predation of many species.

3. Object versus motion vision in extrastriate cortex

Area V1 of the mouse innervates nine distinct extrastriate areas that have been defined using the nomenclature of the Allen Mouse Brain Connectivity Atlas (Fig. 4A, Froudarakis et al., 2019; Wang and Burkhalter, 2007; Wang et al., 2011, 2012). Extrastriate areas proximate to V1 tend to receive stronger innervations than areas distal to V1, which is in keeping with the projection scheme found in macaque monkeys (Felleman and Van Essen, 1991). Recently, Froudarakis et al. (2020) trained mice to discriminate between objects in their home cage with the purpose of identifying regions in the visual cortex that are responsive to objects. Once the mice were trained, the entire extrastriate cortex and area V1 were studied using two-photon calcium imaging so that the responses of individual neurons could be recorded, as the trained mice were presented with objects whose size, orientation, shading, and background clutter varied from the training set. It was found that three areas in particular were selective for objects: the anterolateral area, the lateromedial area, and the lateral intermediate area (Fig. 4B). It is noteworthy that these areas are all located lateral to the areas that have been identified for motion processing including the rostrolateral area and the anteromedial area (Garrett et al., 2014; Marshel et al., 2011; Rasmussen et al., 2020). Also, the anterolateral area contains neurons that encode motion (Marshel et al., 2011); the anterolateral area may be a transition point between the object encoding areas and motion encoding areas. Significantly, the extrastriate cortex of the mouse is
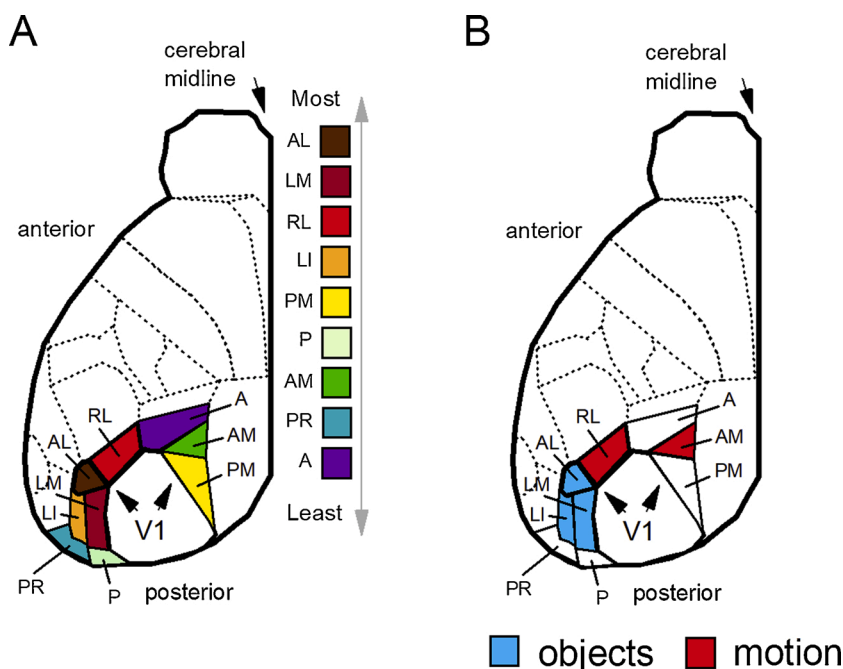

Fig. 4. (A) Extrastriate areas of the mouse are listed from top to bottom according to the density of innervation from V1 from maximal to minimal as derived from Froudarakis et al. (2019): the anterolateral area (AL), the lateromedial area (LM), the rostrolateral area (RL), the lateral intermediate area (LI), the posteromedial area (PM), the posterior area (P), the anteromedial area (AM), the postrhinal area (PR), and the anterior area (A). **(B)** Neurons that are modulated by objects have been identified in the anterolateral (AL), lateromedial (LM), and lateral intermediate (LI) areas (defined in blue); neurons modulated by complex motion stimuli (e.g. flow fields) have be identified in the rostrolateral (RL) and anteromedial (AM) areas (defined in red). Regions of the extrastriate cortex that encode objects are located lateral to the regions that encode motion. Complete details of the mouse visual cortex can be found in Froudarakis et al. (2019, 2020), Garrett et al. (2014), Marshel et al. (2011), Rasmussen et al. (2020), and Wang et al. (2012).

organized roughly similar to that of the macaque monkey whereby objects are represented in lateral regions of the neocortex and motion is represented in medial regions (Fig. 5; Felleman and Van Essen, 1991; Schiller and Tehovnik, 2015).

Whether the mouse has a definitive area V2 is unclear. After V1, areas posteromedial and lateromedial have the largest coverage of the visual field after V1 at 56 % and 44 %, respectively, as compared to the coverage of V1 set to 100 % (Fig. 6). Also, these two areas are the largest immediately after V1 (cf., Felleman and Van Essen, 1991; Froudarakis et al., 2019). There is no clear agreement on what structure is homologous with primate V2, but some have suggested that area lateromedial satisfies this distinction (Wang and Burkhalter, 2007). In the macaque monkey, area V2 is distinct from V1 for having neurons that respond to illusory contours (Von der Heydt and Peterhans, 1989).

Finally, in the mouse it has been shown that areas anterior, rostro-lateral, and anterolateral send and receive axonal projections by way of
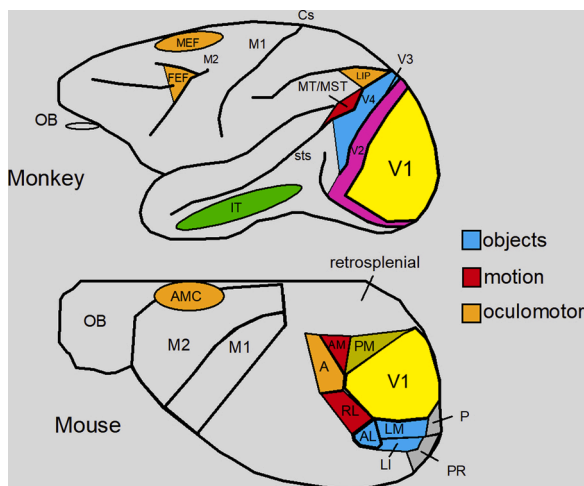

Fig. 5. The visual areas of the neocortex of the macaque monkey and the mouse are summarized. Both species have homologous areas for processing visual information starting at V1 which process stationary and moving oriented lines. Object encoding has been described for V4 in the macaque monkey and for areas AL (anterolateral), LM (lateromedial) and LI (lateral intermediate) in the mouse. V4 of the macaque monkey ultimately innervates the IT (inferior temporal) cortex which contains cells that respond to faces and other complex objects. The object encoding areas of both the mouse and the macaque monkey contain a central-field representation. Motion encoding has been described for MT/MST (middle temporal cortex/middle superior temporal cortex) in the macaque monkey and for areas AM (anteromedial) and RL (rostrolateral) in the mouse. MT and MST ultimately innervate LIP (the lateral interparietal area) which is an oculomotor area that mediates eye movements and active fixation in macaque monkeys (Andersen and Mountcastle, 1983; Mountcastle et al., 1975). Area A (anterior) of the mouse may be a homologue of LIP for eye movements can be evoked from this region (Itokazu et al., 2018) and this area has been implicated in spatial vision in rats (Kolb and Walkey, 1987). In the macaque monkey, the visual signals of the posterior cortex eventually arrive in the frontal lobes at one of the two major oculomotor areas: the FEF (the frontal eye fields) and the MEF (the medial eye fields). The FEF is a central controller of eye movements (saccadic, smooth pursuit, and vergence) and the MEF is involved in eye, head, and body part coordination. Activation of the AMC (anteromedial cortex) in the mouse evokes eye movements (Itokazu et al., 2018) as well as head movements in rodents such as rats (Tehovnik and Yeomans, 1987). Whether the AMC contains FEF and MEF homologues is not known. V2, V3, sts (superior temporal sulcus), and Cs (central sulcus) are indicated for the macaque monkey and areas PM (posteromedial), P (posterior), and PR (postrhinal) are indicated for the mouse. The remaining labels include M1, M2, the retrosplenial cortex, and the olfactory bulb (OB). The inset to the right color codes some of the areas according to function: objects (blue), motion (red), and oculomotor (orange). For further details see: Froudarakis et al. (2019), Garrett et al. (2014), Marshel et al. (2011), Rasmussen et al. (2020), and Schiller and Tehovnik (2015).
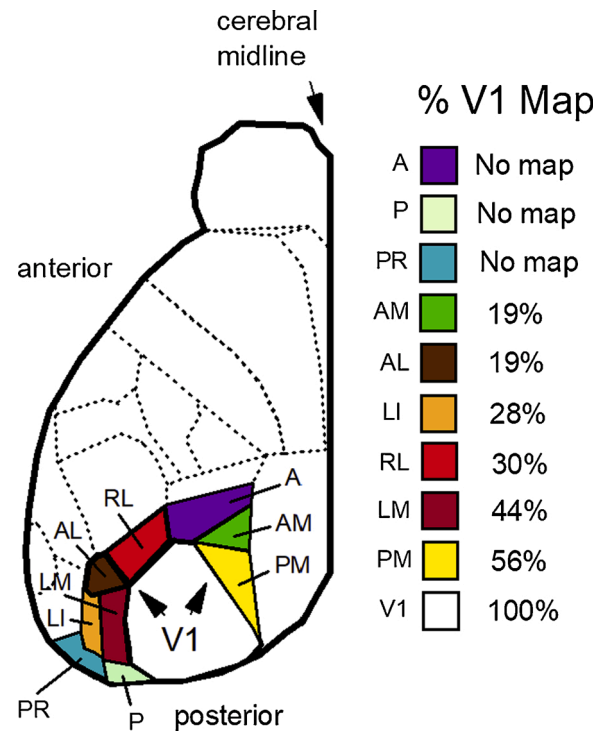

Fig. 6. Extrastriate areas of the mouse are listed from top to bottom according to the percent of the visual field represented as a fraction of that represented by the V1 map using the data of Fig. 5B, C of Garrett et al. (2014). All maps contained a central visual field encoding the primary optical axis. Regions are list from no topographic coverage (no map) to maximal coverage: the anterior area (A), the posterior area (P), postrhinal area (PR), the anteromedial area (AM), the anterolateral area (AL), the lateral intermediate area (LI), the rostrolateral area (RL), the lateromedial area (LM), the posteromedial area (PM), and area V1 (V1).

the anteromedial cortex of the frontal neocortex (Fig. 5, areas A, RL, AL, and AMC). When areas anterior, rostrolateral, or anterolateral are stimulated electrically with pulses of 200 μA (at 0.3-ms pulse duration) saccadic eye movements are induced (Itokazu et al., 2018). Such current activates axons directly within 1 mm from the electrode tip (Tehovnik, 1996) which means the induced saccades cannot be attributed to passive current spreading from areas anterior, rostrolateral, or anterolateral to the anteromedial cortex, which is located 4 mm anterior to these areas (Kirkcaldie et al., 2012) and which contains neurons mediating eye movements as demonstrated by neural stimulation (Fig. 5, AMC; Itokazu et al., 2018; Zhang et al., 2014). Of course, this does not rule out anti-dromic activation which can only be tested by disabling the anteromedial cortex and stimulating areas anterior, rostrolateral, or anterolateral of the mouse. Most relevant here for the mouse, however, is that area anterior (i.e., a lateral intraparietal area homologue; Kolb and Walkey, 1987), area rostrolateral (i.e., a motion encoding area), and area anterolateral (i.e., an object encoding area) have direct access to frontal regions that control eye movements, which concurs with what is found in the macaque monkey for functionally comparable areas, namely, the lateral intraparietal area, areas MT/MST (middle temporal cortex/middle superior temporal cortex), and area V4 (Felleman and Van Essen, 1991; Rao et al., 2016; Schiller and Tehovnik, 2015).

In conclusion, our homology scheme for the mouse coincides with that proposed by others (e.g., Laramée and Boire, 2015; Murakami et al., 2017). To strengthen this scheme, additional behavioral experiments will be required as have been done on macaque monkeys (e.g., described in chapters 6–13 of Schiller and Tehovnik, 2015).
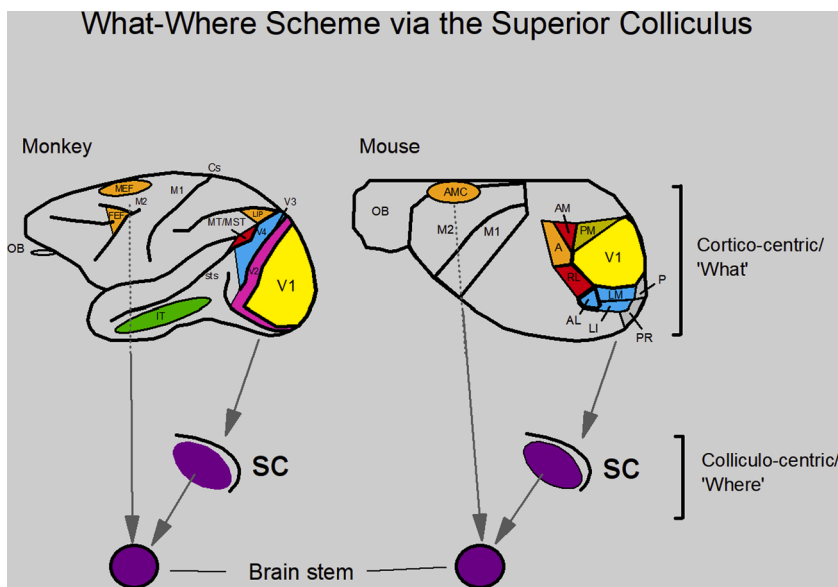
What-Where Scheme via the Superior Colliculus

Fig. 7. The what-where scheme as originally proposed by Ingle and colleagues in 1967 with respect to the superior colliculus. In this scheme the neocortex is designated as a feature detector (cortico-centric 'what') which then sends information to the superior colliculus (SC) for orienting the eyes and head toward peripherally located objects using a retinotopic map in both the mouse and the macaque monkey. In order to move the eyes and head, the brain stem (which is innervated by the superior colliculus and the eye fields in the frontal cortex—FEF and MEF/AMC) contains neurons whose firing rate increases to bring about a precise orientation of the eyes and head to position a visual target in the center of gaze by contracting the muscles (Ingle, 1973; Ingle et al., 1967; Schiller and Tehovnik, 2015). For other details see the caption of Fig. 5.

4. Eye movements in the mouse and the macaque monkey

Eye movements are central to object vision both for object identification as well as a means by which to minimize retinal adaptation (Schiller and Tehovnik, 2015; Yarbus, 1967). Unlike a mouse and other rodents whose eyes remain relatively immobile as well as centered in orbit and conjugate during head-fixed conditions (Payne and Raymond, 2017; Van Alphen et al., 2010; Wallace et al., 2013), the eyes of a macaque monkey are in constant motion being displaced within ±30 degrees of the primary optical axis roughly three times per second and achieving velocities as high as 800 degrees per second (Schiller and Tehovnik, 2015). Such displacement continues for the duration of a monkey's life and most eye movements generated in macaque monkeys are yoked such that the eyes move together (even when disjunctive through vergence) so that objects situated in depth can be identified effectively by projecting the image precisely onto the fovea while adjusting the lens for accommodation. The mouse, however, during head-fixed conditions does exhibit low-amplitude (< 5 degrees) and low velocity (< 10 degrees/sec) spontaneously-generated eye movements (Payne and Raymond, 2017) which refreshes the image on the retina. And with training, a mouse can be made to evoke 5–15 degree conjugate saccadic eye movements toward visual targets while the head is fixed (Itokazu et al., 2018). It is unclear whether rodents including mice have a well-developed system of vergence and accommodation by which to adaptively focus visual images (Hughes, 1977). In this regard, rodents (including mice) are known for exhibiting non-yoked, independent eye movements during which there can be no vergence (Meister and Cox, 2013; Wallace et al., 2013; Samonds et al., 2019).

When the head is free to move in both the mouse and the macaque monkey (as well as in all other vertebrates), the visual image is stabilized on the retina by way of the vestibulo-ocular reflex (Payne and Raymond, 2017; Schiller and Tehovnik, 2015). After an abrupt head displacement, the eyes remain fixated on a visual target (as the head moves) but thereafter the eyes are re-centered in the orbit with an eye displacement so that visual analysis can commence from an optimal eye-head orientation for the acquisition of new targets. In the mouse, this optimal orientation is centered at roughly 50 degrees with respect to the longitudinal axis of the head, and in the macaque monkey, it is centered at roughly zero degrees with respect to the longitudinal axis (Heesy, 2004; Samonds et al., 2019; Schiller and Tehovnik, 2015). This interplay between the head and eyes to maintain a stable visual image on the retina also extends the oculomotor range (with respect to the body axis) well

beyond the head-fixed condition (oculomotor range will be discussed later in detail). The mouse is more dependent on head movements than is the macaque monkey to extend this range but both animals rely on head movements for their survival in their natural habitats (Froudarakis et al., 2019; Schiller and Tehovnik, 2015).

5. What-where scheme and the superior colliculus

The developers of the 'What and Where Hypothesis', David Ingle and his associates, asserted that the mammalian neocortex identifies objects whereas the superior colliculus orients an animal to locate them irrespective of what the object is (Ingle et al., 1967). Future generations intent on moving 'what' and 'where' into the neocortex posited that the ventral stream of primates passing through area V4 mediates 'what' and the dorsal stream passing through area MT mediates 'where' (Mishkin et al., 1983). This cortico-centric hypothesis has had two shortcomings. First, it produced an evolutionary partition between primates and other mammals whose visual systems depend more (but only superficially so) on the superior colliculus for locating objects. Second, there are several unexplained observations: Damage of areas MT (a putative 'where' module) and V4 (a putative 'what' module) in macaque monkeys spares visual functions such as stereopsis and color vision (Schiller and Tehovnik, 2015). Motion (a MT 'where' function) can be used to provide information about object shape as in structure-from-motion, and eye movements (a putative 'where' attribute) are used to identify objects such that damage to the inferior temporal cortex can disable movements that scan the outline of objects (Ingle, 1973; Schiller and Tehovnik, 2015; Yarbus, 1967). As well, 'what' and 'where' are coupled in many visual areas that have retinotopic maps (Schiller and Tehovnik, 2015). Therefore, the scheme adopted in this report is to have the superior colliculus assume the function of locating objects in visual space, which concurs with the views of many (e.g., Goldberg and Wurtz, 1972; Mlinar and Goodale, 1984; Robinson, 1972; Schiller and Stryker, 1972; Schneider, 1969; Sparks, 1986; Tehovnik, 1989; Tehovnik and Yeomans, 1986). Indeed, as early as 1946 the mammalian superior colliculus was implicated in the 'visual grasp reflex' by Hess and colleagues based on the electrical stimulation of the colliculus in alert, behaving cats (Hess et al., 1946).

In both the rodent and the monkey including the macaque monkey, the posterior neocortex gains access to the oculomotor generator in the brain stem via the superior colliculus, whereas the frontal cortex gains access to this region by way of direct projections, albeit the frontal

cortex also innervates the superior colliculus directly (Fig. 7; note that the fronto-collicular projections are not illustrated; Barret et al., 2020; Benavidez et al., 2020; Comoli et al., 2012; Fries, 1984; Froudarakis et al., 2019; Ingle, 1973; Kunzle and Akert, 1977; Kuypers and Lawrence, 1967; Leichnetz, 1981; Lund, 1966; Sherman et al., 1979; Shook et al., 1990; Spatz et al., 1970; Stanton et al., 1988; Tehovnik et al., 1989). The superior colliculus of mammals is a seven-layered structure such that superficial layers (layers I to III) receive direct visual input whereas the intermediate and deep layers (layers IV to VII) receive strong input from the neocortex and they send motor projections into the brain stem (Ingle, 1973; Schiller and Tehovnik, 2015). If the superior colliculus is lesioned in the macaque monkey, all ocular responses evoked electrically from the posterior neocortex (i.e., from V1 to the lateral intraparietal area) are abolished while sparing such responses elicited from the frontal and medial eye fields (Keating and Gooley, 1988; Keating et al., 1983; Schiller, 1977; Tehovnik et al., 1994). Furthermore, employing suprathreshold currents in the macaque monkey, the shortest-to-longest latency for evoking saccadic eye movements occurs in the frontal eye fields [15 ms], the medial eye fields [23 ms], the lateral intraparietal area [25 ms], and finally in area V1 [50 ms; Robinson and Fuchs, 1969; Shibutani et al., 1984; Tehovnik and Lee, 1993; Tehovnik et al., 1994, 2003]. The latency value for the superior colliculus is 20 ms (Robinson, 1972). This systematic increase in latency moving from anterior to posterior regions of the neocortex of the macaque monkey is indicative of a diminished directness and robustness of connectivity between the neocortex and the brain stem for evoking ocular responses.

Finally, and most importantly, if both the frontal eye fields and superior colliculus are removed bilaterally in macaque monkeys, the animals lose all ability to generate visually guide eye movements even though skeletomotor orienting responses remain intact, i.e., the animals can still turn their heads toward and reach to visual targets (Schiller et al., 1980). Also, the vestibulo-ocular reflex and optokinetic nystagmus remain intact even though the gains are reduced following the paired ablations (Schiller et al., 1980). These findings reinforce the notion that neocortical oculomotor-control is made up of a posterior system going through the colliculus on the way to the brain stem and an anterior system having direct access to the brain stem (Schiller and Tehovnik, 2001), as illustrated in Fig. 7. The foregoing has yet to be established in the mouse, but similar results would be expected based on the known anatomy of the rodent (including the mouse), which is similar to that of the macaque monkey, as referenced above.

As one moves closer to the oculomotor controller of the brain stem of rodents and macaque monkeys (as depicted in Fig. 7), there is a gradual transition from sensory encoding to motor encoding such that in the neocortex a full range of sensory computations are performed (e.g., orientation, spatial frequency, direction of motion, binocular disparity, and color) but by the time the signal reaches the superior colliculus, the sensory-encoding capacity of the cells is reduced to specifying the retinotopic location of a target even if the cells contain visual receptive fields (Dräger and Hubel, 1975; Ingle, 1973; Schiller and Tehovnik, 2015). In the hamster, it is known that if the occipital cortex is removed the motion encoding capability of cells in the superficial and intermediate layers of the superior colliculus is lost (Rhoades and Chalupa, 1978) and gerbils with lesions of the visual cortex can no longer anticipate the trajectory of moving targets (Ingle, 1981; Ingle et al., 1979). Such lesions in gerbils abolish motion parallax used to compute the distance of edges (Ellard et al., 1986). Finally, by the time the signal reaches the brain stem, which houses the oculomotor controller, the location signal that is encoded according to a retinotopic map is converted into a code that is devoid of visuo-sensory attributes such that the greater the discharge of the neurons the greater the magnitude of the response as initiated by the contraction of the ocular and skeletal muscles, a process realized by a firing-rate code to contract the muscles (Schiller and Tehovnik, 2015).

6. Blind-sight, superior colliculus and tegmentum

Blindsight is believed to be mediated by subcortical mechanisms. This phenomenon was first discovered in human subjects who had their visual cortex, specifically area V1, damaged bilaterally (Pöppel et al., 1973); however, evidence for this idea first came from work done on macaque monkeys showing that all pattern, color, and motion vision is abolished following damage to the visual cortex (Humphrey and Weiskrantz, 1963; Weiskrantz, 1963). As well, stereopsis is eliminated (Schiller and Tehovnik, 2015). In primates, if a high contrast spot of light (e.g., > 95 % contrast) is presented to V1-damaged subjects they can discern its location even though there is no awareness of having done so in humans (Cowey and Stoering, 1995; Ingle, 1981; Moore et al., 1995; Pöppel et al., 1973; Segraves et al., 1987). It is believed that the superior colliculus mediates this residual vision although projections from the lateral geniculate nucleus to the extrastriate cortex may be sufficient for the mediation (Schmid et al., 2010).

In rodents (e.g., hamsters and gerbils) when the visual cortex including the putative object and motion encoding areas (see Figs. 5 and 7) is lesioned, the animals can still orient to visual targets (Mlinar and Goodale, 1984; Schneider, 1969), but they lose the capacity to perform feature vision such as discriminating between horizontal versus vertical black and white stripes or between speckled patterns versus diagonal stripes (Schneider, 1969). Moreover, orientation discrimination is abolished in such animals (i.e., in mice, Schnabel et al., 2018) and the tracking of component motion as assessed using plaid stimuli is compromised (i.e., in mice, Palagina et al., 2017). As already mentioned, animals (i.e., gerbils) with lesions of the visual cortex fail to anticipate the trajectory of moving stimuli and to perform motion parallax (Ellard et al., 1986; Ingle, 1981; Ingle et al., 1979). Animals (i.e., hamsters and gerbils) that receive only collicular lesions can still discriminate between patterned stimuli and demonstrate motion parallax (Schneider, 1969; Ellard et al., 1986), but they fail to orient to punctate targets (at 98 % contrast) beyond 40 degrees of eccentricity (Mlinar and Goodale, 1984) and they fail to respond to looming visual stimuli (> 20 degrees in size) throughout their 'panoramic' visual field [Schneider, 1969; also see Shang et al., 2018 for pulvinar participation in response to looming stimuli], a function that moreover depends on an intact retrosplenial cortex (Ellard and Chapman, 1991). Note that the superior colliculus of rodents (i.e., mice) contains neurons that respond to expanding flow fields presented from overhead (Dräger and Hubel, 1975; also see Li et al., 2020). When both the visual cortex and the superior colliculus are lesioned, gerbils are no longer able to orient to visual stimuli anywhere in the visual field including to high contrast targets of 98 % (Mlinar and Goodale, 1984). Hence, rodents with lesions of the visual cortex and colliculus are rendered totally blind, failing to exhibit blindsight.

A structure not discussed much in the literature is the pretectum, which is composed of several nuclei situated immediately anterior to the superior colliculus and which is best known for mediating the pupillary reflex in both the rodent and primate (Clarke and Gamlin, 1995; Clarke and Ikeda, 1985). A pupillary enlargement, as part of the reflex, is triggered when animals enter a dark tunnel. Ingle (1981) found that gerbils with lesions of the superior colliculus (much like normal animals) had no difficulty acquiring a low-contrast aperture (a brown tunnel) located on a striped background such that to get a sunflower seed an animal had to enter a chamber by going through the aperture. The lesioned gerbils performed as well as the normal animals for aperture locations anywhere within 90 degrees with respect to the left and right side of the head in the horizontal visual field. This result concurs with the results based on frogs and toads whose pretectal nuclei have been found to mediate aperture detection (Ingle, 1973, 1980). If the gerbils (i.e., those with collicular lesions or those with no lesions) were given lesions of V1, they failed to orient to the low-contrast aperture, but if the aperture was of high contrast (a black aperture on a white background) the animals could respond to the aperture, which could be considered an additional type of blindsight (Ingle, 1980). Indeed, a

human subject with bilateral V1 damage and with no visual awareness was able to walk around and avoid large, salient obstacles as placed within a hallway (De Gelder et al., 2008).

So, how does one secure total blindness, namely, the abolition of blindsight (to punctate targets, for instance) along with pattern vision? There are two ways to accomplish this. If one lesions the superior colliculus and the dorsal tegmentum, which carry neocortical fibres from extrastriate cortex as well as from the retrosplenial, temporal, and parietal cortices (Ingle, 1973), an animal becomes totally blind to the presentation of visual stimuli (Casagrande et al., 1972). Another way to achieve total blindness is to lesion area V1 and the extrastriate cortex including the retrosplenial, temporal, and parietal cortices (Ingle, 1973; Schmid et al., 2010). Accordingly, information about object vision is communicated to the brain stem via the superior colliculus and dorsal tegmentum after being processed and finalized in the posterior neocortex.

7. The oculomotor range and the superior colliculus

If the superior colliculus is an eye movement controller (Stryker and Schiller, 1975), which contains a 'sensory' retinotopic map that extends well beyond the oculomotor range—i.e., beyond 40 degrees peripherally in all mammals—how are the eyes put on target for objects situated beyond this range? Macaque monkeys, which confine their eye movements to within 30 degrees of central gaze under head-fixed conditions (Schiller and Tehovnik, 2015), exhibit a head movement when the head is free to move to extend the oculomotor range (Stryker and Schiller, 1975). What this does is orient the head in the direction of a peripherally-located visual object such that as the head moves a series of saccadic eye movements are generated each punctuated by fixations (controlled by the vestibulo-ocular reflex) such that at the end of the gaze shift the eyes are centered in orbit (Land, 1999) so that the object can be manipulated efficiently with the forelimbs, for example. Under head-fixed conditions, rodents exhibit few eye movements (i.e., in mice, Froudarakis et al., 2019; Meyer et al., 2018), but once the head is free to move these animals exhibit a combination of eye and head movements to keep the eyes centered in orbit (Meyer et al., 2018; Michaiel et al., 2020; Van Alphen et al., 2001, 2010). It is noteworthy that some have suggested that the superior colliculus controls both eye and head movements to produce gaze shifts to extend the oculomotor range (e.g., Freedman et al., 1996), but there are some concerns about these experiments since there was no explicit control over head position (Chen and Tehovnik, 2007).

The superior colliculus in rodents is configured such that anterior regions encode central 'nasal' gaze (for grasping prey) and posterior, lateral, and medial regions encode, respectively, peripheral gaze, lower-field lateral gaze, and overhead gaze (all for avoiding predators) (i.e., in mice, Dräger and Hubel, 1975). This topographic layout is similar in macaque monkeys (Schiller and Tehovnik, 2015) but there is no overhead representation since the eyes project forward (Fig. 1). McHaffie and Stein (1982) electrically stimulated the colliculus of head-fixed rats and hamsters and found that the size of an evoked saccadic eye movement depended on the site of activation (which concurs with what is found in the macaque monkey); if stimulation was continued a series of saccades were induced, each of the same amplitude. Eighteen degrees was the largest saccadic eye movement evoked from the caudal superior colliculus directed temporally. What this means is that the maximal amplitude of the evoked eye movement falls short of the temporal visual field representation of the colliculus, which in rodents surpasses 50 degrees (i.e., in mice, rats, and hamsters, Dräger and Hubel, 1975; Siminoff et al., 1966; Tiao and Blakemore, 1976). Note that even behaviorally evoked eye movements by head-free rodents fall short of this representation (i.e., all within 35 degrees for mice and rats, Van Alphen et al., 2010; Wallace et al., 2013). The only way the oculomotor range can be extended is through head movements accompanied by multiple discrete eye movements (Michaiel et al., 2020; Van Alphen

et al., 2001, 2010) as occurs in the macaque monkey (Stryker and Schiller, 1975). Just how the superior colliculus coordinates this process with head movements is unclear.

Most experiments that study the vestibular system of primates confine their investigations to eye-in-orbit deviations of no more than 50 degrees of visual angle (e.g., Lisberger et al., 1984). If the eyes are deviated beyond this limit when the head is allowed to move with respect to the body, a reflex triggered by the neck proprioceptors evokes a blink of the eyes (i.e., in humans, Berkovic et al., 1985; Schaefer et al., 1979; Tinuper et al., 1989) during which time the eyes can be returned to the center of orbit ready to continue their visual analysis upon opening. This process extends the oculomotor range of primates so that there is a correspondence between the visual-field representation of the retinotopic maps [e.g., up to and beyond 70 degrees of visual field as encoded by the primate superior colliculus and area V1, Adams and Horton, 2003; Schiller and Tehovnik, 2015; Sparks, 2002] and the oculomotor output. A similar mechanism may exist in rodents to complement their highly developed vestibular reflexes (Van Alphen et al., 2001, 2010). Major portions of the neocortex (e.g., the frontal and medial eye fields, the motor and premotor cortex, and the parietal cortex including the intraparietal area) and brain stem are devoted to blinking at least in the primate (i.e., in humans and macaque monkeys, Benbadis et al., 1996; Bodis-Wollner et al., 1999; Esteban, 1999; Shibutani et al., 1984).

8. The frontal and medial eye fields

The frontal and medial eye fields of macaque monkeys (as illustrated in Fig. 7) coordinate the eye movements and the gaze by centering the eyes in orbit to expedite an efficient transformation between retinal and skeleto-motor space for optimal object manipulation or avoidance. The frontal eye fields contain a topographic map that encodes the direction and amplitude of saccadic eye movements (Bruce and Goldberg, 1985; Bruce et al., 1985). Moreover, neurons have been identified in the frontal eye fields that encode smooth pursuit and vergence eye movements (Gamlin and Yoon, 2000; Gottlieb et al., 1993, 1994). The frontal eye fields have properties that are very similar to those of the superior colliculus (Hikosaka and Wurtz, 1985; Schiller and Tehovnik, 2003, 2015): electrical stimulation evokes fixed-vector saccadic eye movements and multiple saccades of the same size and direction are elicited when using long durations of stimulation (i.e., to evoke staircase saccades); when muscimol, a GABA agonist, is injected into either region, saccadic eye movements made into the receptive field of the affected neurons are disrupted; when bicuculine, a GABA antagonist, is injected into either region, irrepressible saccades are induced whose size and direction are determined by the location of the injection site. These results indicate that the frontal eye fields, much like the superior colliculus, encode eye movements with respect to the fovea. Since ablation of both the frontal eye fields and superior colliculus abolish all visually guided saccadic eye movements while preserving skeleto-motor responses (i.e. in the macaque monkey, Schiller et al., 1980), this reinforces the idea that these regions are dedicated to eye-movement control.

The medial eye fields of the macaque monkey have a totally different organization from that of the frontal eye fields. When electrical stimulation is delivered to this region the size and direction of the eye movements varies are a function of starting eye position such that the eye movements are made to terminate in one location of craniotopic space (i.e., eye in orbit with respect to the head; Schiller and Tehovnik, 2015; Tehovnik and Lee, 1993; Tehovnik et al., 1998). Furthermore, the termination location varies topographically such that stimulation of anterior sites terminates the eye movements in extreme parts of contralateral craniotopic space, stimulation of posterior sites terminates the eye movements in central craniotopic space, stimulation of medial sites terminates the eye movements in lower craniotopic space, and stimulation of lateral sites terminates the eye movements in upper

craniotopic space. If the head of an animal is tilted with respect to the gravitational axis, the termination positions remain fixed in relation to the head. Also, if the stimulation is maintained while the eyes are in a termination position, all visually-evoked saccades are delayed for the duration of stimulation. Neurons have been identified in the medial eye fields that respond maximally when the eyes fixate targets positioned in a termination position as defined by electrical stimulation (Lee and Tehovnik, 1995). When the medial eye fields are disabled there are few deficits in eye movement control in head-fixed macaque monkeys (as reviewed in Tehovnik et al., 2000), albeit animals are impaired at generating saccades to multiple remembered target positions (Sommer and Tehovnik, 1999). Accordingly, this region maintains a record of the location of the eyes in orbit. It is believed that the medial eye fields are involved in centering the eyes in orbit once a saccadic eye movement has been initiated thereby participating in the vestibulo-ocular reflex in the head-free condition (Chen and Tehovnik, 2007; Fukushima et al., 2011).

So, how do the foregoing results coincide with studies done on rodents and especially on the mouse? It is known that stimulation of the anteromedial cortex (AMC) of the mouse (illustrated in Figs. 5 and 7) can evoke saccadic eye movements using both electrical stimulation and optogenetics (Itokazu et al., 2018; Zhang et al., 2014). As well, this region sends projections to area V1 that modulate the gain of orientation-tuned neurons when transitioning between locomotion and immobility (Niell and Stryker, 2010; Zhang et al., 2014) and this region projects to parietal and extrastriate cortex as mentioned previously (Itokazu et al., 2018). Neurons in the anteromedial cortex are modulated by visually guided saccadic eye movements and inactivation of this area abolishes saccadic eye movements directed contralateral to the side of inactivation (Itokazu et al., 2018). Additionally, this region innervates V1 topographically conveying information about head and body orientation (Bouvier et al., 2020; Leinweber et al., 2017). Electrical stimulation of the anteromedial cortex in freely moving rats evokes contraversive head and body movements such that the orientation of the head with respect to the axis of the body (as measured from overhead) is about 70 degrees and the animal continues to circle for stimulation train durations up to 40 s (Tehovnik and Yeomans, 1987; Yeomans and Tehovnik, 1988). Moreover, the stimulation evokes vertical head movements as well as vibrissa movements. Since 1909 it has been known that electrical stimulation of the medial eye fields in unrestrained primates (i.e., first in humans and later verified in macaque monkeys) elicits head movements such that the head begins to move before the eyes which differs from the frontal eye fields for which the eyes begin to move before the head when and if a head movement is even evoked (Chen, 2006; Chen and Walton, 2005; Levinsohn, 1909). Furthermore, lesions of the internal capsule at the caudate nucleus abolish all head movements evoked from the frontal lobes (Jansen et al., 1955; also see Yeomans and Buckenham, 1992). Whether the anteromedial cortex of the mouse contains representations of the frontal and medial eye fields is currently not known, but parts of the anteromedial cortex of rodents that encode head movements send a robust projection to the superior colliculus, the tegmentum, and the pontine nuclei that innervate the cerebellum (i.e., in the rat, Tehovnik et al., 1989), all regions that have been implicated in oculomotor control.

9. The brain stem including the cerebellum

As indicated in Fig. 7, once the visual signal propagates into the brain stem it is converted into a firing-rate code which is utilized by the muscles to bring about a muscle contraction [Adrian, 1922; Enoka and Duchateau, 2017; Gasser, 1930; Schiller and Tehovnik, 2015; neural recruitment is also involved in this process and some have speculate that the pattern of spike discharge affects the contraction of skeletal muscles, Zhurov and Brezina, 2006]. In the macaque monkey, the oculomotor nuclei and many of the neurons in the brain stem composing the eye movement generator operate such that increasing the pulse frequency and/or train duration of electrical stimulation increases the magnitude

of an ocular displacement (Cohen and Komatsuzuki, 1972; Schiller and Stryker, 1972). Furthermore, the greater the displacement the higher the firing frequency of the neurons (Fuchs et al., 1985; Schiller, 1970). Finally, head displacement and the rate of lateral locomotion (i.e., circling behavior), as induced from the brain stem via stimulation, increases systematically as a function of pulse frequency and train duration, as illustrated in rats (Tehovnik and Yeomans, 1986, 1987; Yeomans and Tehovnik, 1988). Whether the pattern of neural firing affects ocular responses evoked from the brain stem has yet to be deduced.

In primates (e.g., macaque monkeys), the cerebellum also utilizes a firing-rate code when transmitting signals to the cerebellar nuclei, which are the output neurons that innervate the eye movement generator as well as circuits that regulate head and body movements (Kheradmand and Zee, 2011; Manto et al., 2012). By increasing the frequency of pulses or train duration, the size of saccadic eye movements evoked electrically from the cerebellar vermis (lobules VI and VII) increases (Noda and Fujikado, 1987b). Moreover, the discharge duration of cerebellar neurons defines the size of a saccadic eye movement such that the longer the duration, the greater the displacement (Fuchs et al., 1993; Ohtsuka and Noda, 1991). Furthermore, current pulses as low as $2-3\,\mu A$ delivered in 20 ms trains are sufficient for evoking saccades from the cerebellum (Noda and Fujikado, 1987a). By comparison, current pulses higher than $10\,\mu A$ and at much longer train durations (i.e., from 50 to 200 ms) are needed to generate ocular responses from the neocortex (Schiller and Tehovnik, 2015; Tehovnik and Slocum, 2004; Tehovnik and Sommer, 1997). A major reason for this difference is that Purkinje cells respond well to high-frequency stimulation (i.e., optimally at 600 Hz, Noda and Fujikado, 1987b), which attests to the extreme excitability of their axon initial segments (Foust et al., 2010). Finally, if electrical stimulation is introduced to the cerebellum during an ongoing saccadic eye movement, the movement is interrupted instantly and a new saccade is generated as encoded by the site of stimulation (Noda and Fujikado, 1987a; Noda et al., 1991). A similar result occurs for stimulation of the oculomotor generator (Cohen and Komatsuzuki, 1972). Accordingly, the cerebellum has priority access to the oculomotor generator in the brain stem for saccade execution. This is not true of the neocortex. Electrically-evoked ocular responses elicited from the neocortex can readily be interrupted by an animal's ongoing behavior (Chen and Tehovnik, 2007; Tehovnik and Slocum, 2004). Thus, the cerebellum's oculomotor control is predicated on having direct access to the movement controllers by way of a firing-rate code. This permits for the execution of effortless body movements as triggered by a specific sensory context once a task has been learned (Swain et al., 2011; Thach et al., 1992).

The neocortex is connected to the cerebellum via the pontine nuclei. These nuclei project to the cerebellar cortex via the middle cerebellar peduncle whose massive size (as compared to the other peduncles) indicates the importance of this pathway for transferring sensory information between the neocortex and cerebellum (Baumann et al., 2015; Kratochwil et al., 2017; Ramnani, 2006). Incidentally, the object encoding areas of macaque monkey temporal and extrastriate cortex do not project directly to the pontine nuclei for access to the cerebellum (Baumann et al., 2015). The superior colliculus, which is innervated by the posterior neocortex (Fig. 7), is an alternative path for the transfer of visual information from the inferior temporal cortex and area V4 to the pontine nuclei en route to the cerebellum (Kratochwil et al., 2017; Manni and Petrosini, 2004; Matsuzaki and Kyuhou, 1997). The oculomotor regions of the frontal cortex in both the rodent and macaque monkey, however, send direct projections to the pontine nuclei (Shook et al., 1990; Stanton et al., 1988; Tehovnik et al., 1989).

The cerebellum has been associated with computing the eye, head, and limb position with respect to the body (Fuchs and Kornhuber, 1969; Fukushima et al., 2011; Lisberger and Fuchs, 1978; Thach et al., 1992). If macaque monkeys are required to generate saccadic eye movements to a remembered target position in darkness, once their eyes are displaced by electrically stimulating the brain with a brief train of pulses it is

typical for the eyes to arrive on target following the displacements via a corrective saccade (Schiller and Sandell, 1983; Sparks and Mays, 1983; Tehovnik and Sommer, 1996). This occurs when stimulating sites at or dorsal to the superior colliculus including the frontal and medial eye fields. If, on the other hand, the eyes are perturbed by stimulating cerebellar sites, the eyes never arrive on target as though to suggest that the visual image has been shifted by the stimulation (Noda et al., 1991). A similar result occurs when stimulating sites within the oculomotor generator including the oculomotor nuclei (Schiller and Sandell, 1983; Sparks et al., 1987). If the proprioceptors of the eyes are stimulated, human subjects report that a visual image is made to jump (Roll and Roll, 1987; Roll et al., 1991; Valey et al., 1994, 1995, 1997). Indeed, the cerebellum resolves the discrepancy between the proprioceptive signal and the visual signal by shifting the visual percept in favor of proprioception given that proprioceptive signals arrive in the cerebellum at latencies as short as 3 ms, whereas it takes a visual signal over 30 ms to reach the cerebellum (Fuchs and Kornhuber, 1969).

That the cerebellum is involved in computing the position of the body is, furthermore, supported by the finding that prism adaptation is abolished in macaque monkeys and humans following cerebellar damage (Braizer and Glickstein, 1973; Braizer et al., 1999; Deuschl et al., 1996; Martin et al., 1996; Morton and Bastian, 2004; Thach et al., 1992; Weiner et al., 1983). When human subjects are asked to throw a dart once the eyes have been deviated by 15 degrees using a prism, under normal circumstances they adapt to this situation after twenty or so trials (Thach et al. 1992). Following cerebellar damage, there is no adaptation. The foregoing has implications for object vision. It has been known for some time that if human subjects wear a prism that bends a physical straight line, that after wearing the prism for an extended period of time the subjects will perceive the line as straight (Hebb, 1969). This adaptation comes about by having the visual system put the curved line, as induced by the prism, in register with the non-visual senses of the body. It is believed that the cerebellum has the last say in this process by integrating all the senses to produce a coherent motor response through learning (Swain et al., 2011; Thach et al., 1992).

The cerebellum of humans is polysynaptically connect to the neocortex, including to regions that process object vision. The cerebellum consists of three lobes: an anterior lobe composed of lobules I to V, a mediolateral lobe composed of lobules VI to VII, and a posterior lobe composed of lobules VIII to IX (Fig. 8, based mainly on Boillat et al., 2020). The somatotopy for all the lobes starts with an eye represented in the mediolateral lobe and terminates with a foot representation in each of the other two lobes (a property of the macaque monkey as well, Adrian, 1943; Manni and Petrosini, 2004; Noda and Fujikado, 1987a;

Thach et al., 1992); the somatotopy for the mediolateral lobe is least well developed. There is also a head representation in lobule VI and a vestibular representation in lobule X for vestibulo-ocular control (Lisberger and Fuchs, 1978). Using resting-state functional-connectivity MRI in humans, it has been found that the sensorimotor regions of the neocortex (i.e., M1 and S1) are preferentially linked to the anterior lobe, that the object encoding areas including the extrastriate, temporal, and orbital cortices are linked to the mediolateral lobe, and that the motion encoding areas including MT, MST, STS (superior temporal sulcus), and posterior parietal and supplementary motor cortices are linking to the posterior lobe (Buckner, 2013; Buckner et al., 2011; Diedrichsen et al., 2019; Marek et al., 2018). Using both fMRI and brain-damaged patients, the mediolateral lobe has been implicated in language processing and mathematics (Guell et al., 2018; Mariën et al., 2017; Schmahmann and Sherman, 1998) both of which rely heavily on object vision.

Thus far, the precise topographic order of the mouse cerebellum has yet to be deduced. Given that the mouse has a well-developed object encoding system in neocortex (Figs. 4 and 5) and that its cerebellum includes a mediolateral sector composed of lobules VI to VII (White and Sillitoe, 2012) it would be surprising if it did not have real estate dedicated to object vision. On this point, using two-photon calcium imaging, neurons (i.e., granular cells) have been identified in lobule VI of the mouse that respond to visual stimuli and that can be conditioned to evoke an eye-blink response to those stimuli (Figs. 1–3 of Giovannucci et al., 2017). Muscimol inactivation of lobule VI abolished the conditioned response without affecting the unconditioned response. The conditioning of cerebellar neurons has been described as the creation of an efference-copy representation (Giovannucci et al., 2017).

The cerebellum of rodents and primates contains about 80 % of all neurons in the brain with the remainder residing mainly in the neocortex (Herculano-Houzel, 2009, 2010, 2012). As well, in these animals the number of neurons in the cerebellum varies positively and systematically with the number of neurons in the neocortex (Fig. 4B of Herculano-Houzel, 2010). The large number of neurons in the cerebellum that is mainly composed of granular cells is believed to permit the storage of learned motor routines (Giovannucci et al., 2017; Huang, 2008). The internal circuitry of the cerebellar cortex is made up of Purkinje neurons whose discharge inhibits the firing of the neurons of the cerebellar nuclei, the exclusive output channel of the cerebellum. Thus, increases in Purkinje discharge decreases the firing of the deep cerebellar nuclei neurons whereas decreases in the discharge increase their firing (Lisberger and Fuchs, 1978; Noda et al., 1988; Swain et al., 2011; Thach et al., 1992). Purkinje neurons receive two inputs, one from the mossy fibres and a second from the climbing fibres. The mossy fibres carry
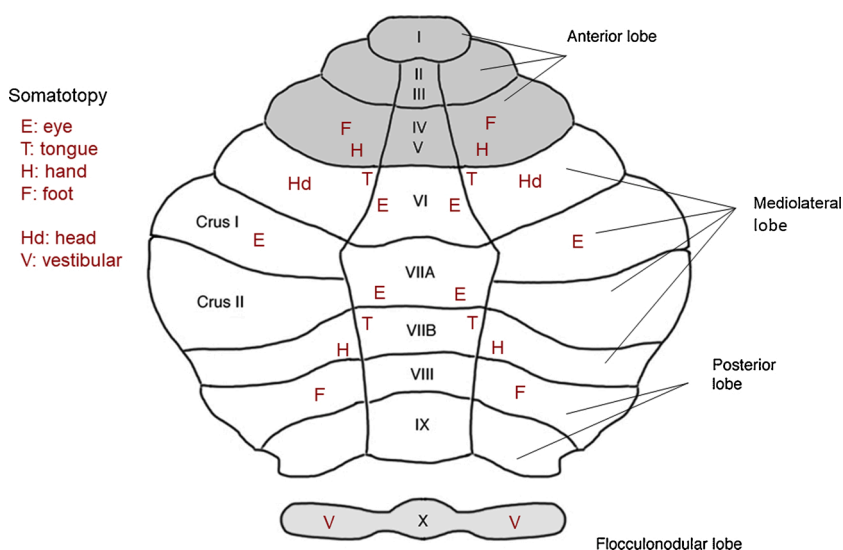

Fig. 8. Schematic of a top view of human cerebellum divided into three lobes: anterior, mediolateral, and posterior. According to the fMRI experiments of Boillat et al. (2020) who used a 7-tesla scanner, a somatotopy—for eye, tongue, hand, and foot—is found for anterior and posterior lobes, but an eye representation without a clear somatotopy is found for the mediolateral lobe. A head representation is found in lobule VI (Manni and Petrosini, 2004) and vestibular control of the head is found in lobule X (Lisberger and Fuchs, 1978). The text inset in the upper left defines the movement of the body part or sense that triggered a maximal response within the cerebellar cortex.

sensory input from the neocortex, brain stem, and spinal cord; the climbing fibres, which originate from the inferior olive, are able to change the gain of firing of Purkinje neurons when new routines are being learned by eliciting complex spikes in the Purkinje neurons. The process, which is documented by a large amount of experimental data (e. g., Boyden et al., 2004; Gilbert and Thach, 1977; Kitazawa et al., 1998; Medina and Lisberger, 2008; Miles and Lisberger, 1981; Soetedjo and Fuchs, 2006; Soetedjo et al., 2008; Swain et al., 2011; Thach et al., 1992; Yang and Lisberger, 2014), works as follows: when complex spikes are emitted at a low rate ($<$2 Hz) the firing frequency of Purkinje spikes (i.e., the simple spikes) is elevated whereas when the complex spikes are emitted at a high rate ($>$ 2 Hz) the firing frequency of these spikes is reduced. This bi-directional change to the gain of Purkinje neurons has recently been confirmed by others (Loyola et al., 2019; Shadmehr, 2020) and has implications for the storage of learned routines (Huang, 2008; Swain et al., 2011; Thach et al., 1992; Yang and Lisberger, 2014). Indeed, optogenetic perturbation of Purkinje circuits in mice disrupts left versus right, vibrissae tactile-memory (Fig. 1g, h of Gao et al., 2018), suggesting that the recollection of touch and body position, i.e. proprioception, is mediated by the cerebellum.

Using modern methods on the cerebellum of the mouse [e.g., optogenetics, two-photon calcium imaging, and patch-clamp recording, Froudarakis et al., 2020; Gao et al., 2018; Giovannucci et al., 2017; Scala et al., 2020] the following questions can now be answered: (1) Does the pattern of spike discharge at the level of the cerebellum have an effect on the learned behaviors mediated by the cerebellum given that a spike-rate code is believed to be operative here. (2) How are communications established between the object encoding areas vis-à-vis the neocortex and cerebellum as mice learn to discriminate between objects (e.g., using the methods of Froudarakis et al., 2020; Gao et al., 2018, and Giovannucci et al., 2017). (3) Can the bidirectional gain-control mechanism of the Purkinje cells be manipulated to alter systematically the relationship between vision and movement as has been done using the electrical perturbation of cerebellar circuits and the donning of prisms.

10. Outstanding items

10.1. Conventional versus modern methodologies

Many studies conducted on the mouse visual system have utilized optogenetics and two-photon calcium imaging (Froudarakis et al., 2019). In the experiments conducted on macaque monkeys it has been typical to use older methodologies: single-cell recording, electrical brain stimulation, and lesion methods from ablations to chemical inactivation or excitation (Schiller and Tehovnik, 2015). One concern when comparing the mouse to the macaque monkey is that the differences that may arise are based on nothing more than methodological differences. It is known that optogenetics has generally failed to evoke saccadic eye movements from the neocortex of macaque monkeys yet electrical stimulation readily evokes such movements (Schiller and Tehovnik, 2015), but if the behavioral conditions for eliciting saccades are optimized (Tehovnik et al., 2003), saccades can be induced from the neocortex using optogenetics (Jazayeri et al., 2012). A major difference between the two techniques is that optogenetic stimulation activates a fraction of the neurons within a tissue volume, whereas electrical stimulation likely drives most neurons and the axonal fibres of passage within the volume. Moreover, the latency to evoke spike discharges using optogenetics can be as long as 8−9 ms (Isa et al., 2020), which would delay the evocation of optogenetically-elicited behavior. When evoking eye movements electrically from the abducens nucleus the latency can be as short as 3–4 ms (Miyashita and Hikosaka, 1996). Finally, it is known that calcium imaging can be used optimally for those neurons that have moderate firing frequencies thereby failing to capture extremely low and high firing rates (Nauhaus et al., 2012; Tehovnik and Slocum, 2013). This is less of a problem for single cell recording (Schiller and Tehovnik, 2015).

10.2. The function of the binocular overlap in the mouse

In macaque monkeys, it has been common to attribute the binocular overlap of the visual field of the two eyes for the purpose of conducting stereopsis. The overlap in the mouse is much less. Nevertheless, these animals can perform coarse stereovision both at the level of V1 and extrastriate cortex including area lateromedial, which has been implicated in object encoding (Fig. 4; La Chioma et al., 2020; Samonds et al., 2019; Scholl et al., 2013). Also, it has been suggested that an additional purpose of the overlap in rodents is to enhance an animal's ability to detect moving stimuli in the field of overlap and to orient the head. Ingle (1981) showed that gerbils can anticipate the trajectory of a moving stimulus (a disc bated with a sunflower seed) such that a 30–40 degree per second movement (temporally or nasally) compelled the animal to orient its head and body 5–10 degrees in advance of the movement to intercept the stimulus. However, beyond 40 degrees (i.e., outside the region of binocular overlap), the animals treated the disc as stationary. This result will no doubt need to be replicated in the mouse who has a similar visual system to that of the gerbil.

10.3. Object encoding in the mouse

In Froudarakis et al. (2020), three areas in mouse extrastriate cortex were activated by objects based on previous training: the anterolateral area, the lateromedial area, and the lateral intermediate area. Two areas were noticeably non-active: the posterior area and the postrhinal area, which could be homologues of the inferotemporal cortex (Wang et al., 2012), an object encoding area in macaque monkeys. It is noteworthy that bilateral lesions at and anterior to area postrhinal disrupt object recognition memory in rodents (i.e., in rats, Ho et al., 2011). There are four possible reasons for the non-activity of the posterior and postrhinal areas. First, these areas are best observed by viewing the cortex from the side and back rather than from overhead; all experiments conducted by Froudarakis et al. were done by imaging from overhead. Second, passive viewing was used to identify objects even though the animals learned the object sets in their home cage. It is well known that neurons in the visual cortex are best activated if animals (i.e., macaque monkeys) are required to use visual information to perform a behavioral task for reward especially if studying regions beyond V1 (e.g., Haenny and Schiller, 1988). Third, in the experiments of Froudarakis et al. the mice were trained for only three weeks on the various objects such that the overall identification of objects did not surpass 70 % correctness (with chance at 50 %). Some believe that in order for objects to be archived in the temporal lobes an extensive period of training is required (Hikosaka et al., 2014). Indeed, large medial temporal lobe lesions in elderly adult humans can induce retrograde amnesia of 'declarative' objects that spans 40–50 years (Squire et al., 2001). Finally, the posterior and postrhinal areas of the mouse may have nothing to do with object vision. Which of the foregoing best accounts for the lack of activity to objects in the posterior and postrhinal areas needs clarification.

10.4. Expanding the oculomotor range in the mouse

Head movements extends the oculomotor range in mice and primates including macaque monkeys. In these animals, input from vestibular sensors, which coordinate eye and head movements, are highly distributed. These inputs reach vast sections of the neocortex including the supplementary motor area (which includes the medial eye fields), the neck and forelimb representation of M1 and S1, the orbital cortex (area 13), the temporal lobe (area 14), and areas LIP (lateral intraparietal), MST, and STS, and the retrosplenial cortical area (Chen et al., 2011; Fukushima et al., 2011; Guldin and Grüsser, 1998; Rancz et al., 2015). Also, the vestibular system transmits to the thalamus, the striatum, and the superior and inferior colliculi. In order to deduce how the mouse extends its oculomotor range, eye and head movements will need to be recorded simultaneously in freely-moving mice orienting toward

and away from visual stimuli (e.g., Meyer et al., 2018) as neurons are examined at various sites within the eye and head movement control system.

10.5. Efference-copy representation and the cerebellum

The consensus is that the cerebellum is responsible for producing the efference-copy representation for all movements that arises once animals, such as mice and macaque monkeys, become highly trained on a task (Ebner and Pasalar, 2008; Giovannucci et al., 2017; Huang et al., 2013; Ito, 2008; Miall et al., 1993; Robinson, 1981; Wolpert et al., 1998). This has been studied best for the vestibulo-ocular reflex such that the movement of the head triggers an eye movement that counter-rotates with respect to the head at a latency as short as 12 ms following the head movement (Miles and Lisberger, 1981), a process which stabilizes the visual image on the retina. This short latency cannot be attributed to vision given that it takes over 30 ms for a visual signal to arrive in the brain stem (Fuchs and Kornhuber, 1969; Miles and Lisberger, 1981) Cerebellar circuits are involved in tuning the short latency (Miles et al., 1980; Miles and Lisberger, 1981). Furthermore, adapting the vestibulo-ocular reflex to prisms is abolished following cerebellar lesions (Lisberger et al., 1984). When studying the grey matter volume of the cerebellum in athletes (all under the age of thirty) it was found that ballet performers had an enhancement of the posterior lobe including the vestibular circuitry (Dordevic et al., 2018), sprinters had an augmentation of the anterior lobe which subserve lower limb locomotion (Wenzel et al., 2014), and basketball players had a potentiated mediolateral lobe which subserves eye-hand, object coordination (Park et al., 2009). The latter, the mediolateral lobe, mediates object vision as well as language (Buckner et al., 2011; Diedrichsen et al., 2019; Guell et al., 2018; Mariën et al., 2017; Park et al., 2009; Schmahmann and Sherman, 1998; Sendhilnathan et al., 2020; see Fig. 8 for details of lobe location). In the case of language, it can take as much as a decade to acquire through reading (which depends on object vision), writing, and speaking but once acquired the anticipatory interchange between two individuals in conversation occurs at a fraction of a second (Levinson and Torreira, 2015), which could not be realized without an efference-copy representation of speech anticipation. Incidentally, patient HM who had bilateral removal of his hippocampus—but an intact cerebellum—could still engage in conversation even though minutes later he would not remember having had the conversation (Annese et al., 2014; Corkin, 2002). Just how the cerebellum interacts with extra-cerebellar mechanisms to support an efference-copy representation is not yet understood.

10.6. Information transfer vis-à-vis objects

Information transfer expressed in bits (as derived from the number of possibilities) per unit time has been used to quantify the behaviors produced by rodents, monkeys, and humans (Tehovnik and Chen, 2015; Tehovnik and Teixeira-e-Silva, 2014; Tehovnik et al., 2013). In humans, learning compresses information flows (Miller, 1956) by adding more sensory items into memory and by having each item evoke a precise motor output at the shortest latency (e.g., via the cerebellum: Huang, 2008; Sultan and Heck, 2003; Tehovnik and Chen, 2015). Once versed in a language, one can transfer over 40 bits per second as delivered through speaking (Reed and Durlach, 1998). By comparison, the ant pheromone system transfers 1.4 bits per second based on its 20 pheromone-alphabet (Hölldobler and Wilson, 1990; McIndoo, 1914). The late physicist, Stephen Hawking who suffered from ALS (amyotrophic lateral sclerosis) was able to transfer 0.4 bits of information per second without the assistance of his computer (De Lange, 2011), a computer that acted like a cerebellum to increase his rate of communication. Every animal must store in its memory a collection of objects (expressed as the number of possibilities) so that upon encountering those objects a behavioral response is evoked at the shortest latency. In the case of the mouse, the

collection of objects necessary for survival is found in the animal's natural habitat (Gibson, 1972). The upper limit to the storage of objects for a mouse is not known, but the carrying capacity of the mouse brain is 0.08 % of the human brain based on the total number of neurons, with the cerebellum possessing most of this capacity [i.e., $\{(71 \times 10^{6}) / (86 \times 10^{9})\} \times 100$, Herculano-Houzel, 2009]. An outstanding question is how the neocortex in combination with the cerebellum establishes the high information transfer rates needed to survive in an ever changing environment. In the case of the human cerebellum, it has been estimated to have an information storage capacity of 10^{14} bits based on the large number of granular cells and their connectivity (Huang, 2008). Only now are investigators beginning to study the relationship between the neocortex and cerebellum in behaving animals (e.g., in the mouse, Gao et al., 2018), which has the potential to address the issue of object-based information flow so that the storage and transfer of information can be estimated for different species.

11. Conclusions

1. The visual spatial resolution of a mouse is many orders of magnitude less than the visual spatial resolution of a macaque monkey; a mouse does not have a fovea but instead has a visual system designed for panoramic and overhead viewing.
2. The extrastriate cortex of the mouse and macaque monkey are similarly organized such that lateral regions encode objects and medial regions encode motion. In both species these regions mediates complex perception that depends on learning.
3. Areas in the frontal cortex along with the superior colliculus coordinate the eye movements and gaze shifts of the mouse and macaque monkey by centering the eyes in orbit to expedite an efficient transformation between retinal and skeleto-motor space for optimal object manipulation or avoidance.
4. The cerebellum much like the visual cortex contains a separate representation for objects and motion processing as demonstrated in humans. It is believed that this structure in mice and macaque monkeys stores efference-copy routines for the immediate execution of well-learned behaviors.
5. The brain stem of the mouse and macaque monkey utilizes a firing-rate code independent of sensory information to contract the eye and head muscles to orient the body toward or away from visual objects, a coding scheme that is also utilized by the cerebellum.

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