Structural and functional evidence supports re-defining mouse higher order visual areas into a single area V2

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Abstract:
The mouse has become one of the main organisms for studies of the visual system. As a result, there is increased effort to understand universal principles of visual processing by comparing the mouse visual system to that of other species. In primates and other well-studied species including cats and tree shrews, the visual cortex is parcellated into an area V1 and several higher order areas defined by structural and functional differences, and a near complete map of the visual field. In mice, the visual cortex beyond V1 is parcellated into several higher order areas, with less notable structural and functional differences, partial coverage of the visual field, and areal boundaries defined by reversals in progression of the visual field. Notably, recent work in tree shrews and primates has shown that reversals in progression of the visual field can be a hallmark of complex retinotopic mapping within a single visual area. This, and other lines of evidence discussed here, provides a compelling case that the apparent existence of multiple higher order visual areas in the mouse is related to the false assumption of simple retinotopy. Specifically, we use simulations to show that complex retinotopy within a single visual area can recapitulate the appearance of multiple areal borders beyond mouse V1. In addition, we show that many reported differences in functional properties between higher order visual areas can be better explained by retinotopic differences rather than areal identity. Our proposal to reclassify some of the higher order visual areas in the mouse into a single area V2 is not mere semantics because areal definitions influence experimental design and data analysis. Furthermore, such a reclassification would produce a common set of rules for defining areal boundaries among mammals and would bring the mouse visual system into agreement with evolutionary evidence for a single area V2 in related lineages.

Beyond V1, the mouse visual cortex has recently been parcellated into many higher order visual areas (Figure 1A). These modern area delineations are largely based on anatomical (Wang & Burkhalter, 2007a) and functional (Garrett et al., 2014a; Kalatsky & Stryker, 2003; Zhuang et al., 2017) signatures of a reversal in the progression of the visual field (Figure 1A). Such reversals, also known as mirror maps, indicate a new map of the visual field, and therefore a new visual area, under the assumption of simple retinotopic mapping. However, recent work (Sedigh-Sarvestani et al., 2021; Yu, Rowley et al., 2020) has shown that visual field reversals are a hallmark of complex retinotopic mapping within V2 and other higher order visual areas of primates and tree shrews (Figure 1B). This prompted us to ask whether some of the higher order areas of the mouse, delineated by reversals, may in fact be a sub-parts of a single area V2 (Figure 1C). This would explain the partial visual field coverage of higher order areas in the mouse (Figure 1A, Zhuang et al., 2017), which only when combined provide near-full coverage of the visual field.

The parcellation of higher order visual cortex in the mouse has a contentious history (Glickfeld & Olsen, 2017) with different studies parcellating the cortex beyond V1 into between 2 (Rose, Maximillian, 1929) and 16 areas (Zhuang et al., 2017). Many of these studies determine areal boundaries largely based on the projection pattern of V1 terminals in higher order visual cortex. Under the assumption of simple one-to-one mapping, each point in V1 should send projections to only one point in a higher order visual area. Therefore, the presence of multiple segregated projection terminals suggests the presences of multiple higher order areas (Wang and Burkhalter, 2007), but this relationship does not hold if the retinotopic map beyond V1 is complex (Sedigh-Sarvestani et al., 2021; Yu et al., 2020). However, the complexity of retinotopic mapping in the mouse visual cortex has not been investigated, which leads us to consider the areal definitions with skepticism. We are not the first to raise caution regarding this definition. Kaas et al. (1989) argued for a simple higher order cortex with repeated modules within a single area V2. Rosa and Krubitzer (Rosa & Krubitzer, 1999) used comparative anatomical analyses to argue that the presence of multiple visual areas beyond V1 “is not supported by studies of the organization of extrastriate cortex in other mammals, nor by the variability in this organization among extant rodents.” Their words of caution did not impact the next two decades of research into the organization of mouse visual cortex, in part due to the strength of anatomical tracer injections showing multiple visual field reversals beyond V1 (Wang and Burkhalter, 2007), as well as the assumption that retinotopic maps are simple and do not exhibit reversals within a single visual area.

In the past decade, we have gained a better understanding of the diversity of retinotopic transformations in visual areas. Specifically, we have gained structural and functional evidence that visual field reversals can occur in single visual areas when the retinotopic transform within that area is complex. These reversals, and the underlying complex retinotopy, can be explained by wiring minimization principles related to visual field coverage constrained by the anatomy of cortex beyond V1, and have now been reported in tree shrews (Sedigh-Sarvestani et al., 2021), marmosets (Yu et al., 2020), ferrets (Manger et al., 2002a) and squirrels (Gould III, 1984). Therefore, it stands to reason that the mouse visual system could also exhibit complex retinotopic mapping beyond V1, resulting in the false appearance of multiple visual areas, where only a single unified area V2 exists.

However, if there is only a single area beyond V1 in the mouse, how can we explain the observed functional differences reported between the higher order visual areas? These include differences, varying smoothly across all higher order areas, in spectral sensitivity (Denman et al., 2018; Rhim et al., 2017), temporal and spatial frequency preferences (Han et al., 2022; Marshel et al., 2011), receptive field size, latency, binocular disparity and several other features. The simplest explanation is that these functional differences are reflective of the different visual field bias of each area (Sedigh-Sarvestani & Fitzpatrick, 2022). For instance, we would expect differences in spatiotemporal frequency and receptive field size between area RL and P, simply due to their bias towards lower central and upper peripheral parts of the visual field, which can be cone or rod-driven depending on experimental conditions.

Here we use computational models and a survey of published studies to test the hypothesis that many higher order visual areas beyond V1 can be unified into a single area V2. Specifically, we wondered a) whether published data supports the existence of a complex retinotopic transform beyond V1 and b) what accounts for the observed functional property differences among higher order visual areas as currently defined. We show that established wiring minimization rules that explain the simple retinotopic maps in mouse V1 can be used to explain a complex map beyond V1, belonging to a single secondary area. We also show that the reported functional property differences among higher order areas can be better explained by their visual field bias. More broadly, we find that many differences attributed to distinct areas can be better explained by a single area V2 if one considers two simple facts: visual field reversals are possible under complex retinotopic maps and 2) functional differences exist along the gradient of eccentricity within the same visual area.

The proposed re-unification of mouse higher order visual areas into a single V2 would result in similar rules used to define higher order visual areas across a large array of mammals and marsupials. In addition, the existence of a single area V2 in mice would make the visual cortex of this species consistent with other rodents, and mammals, who exhibit a single area V2 beyond V1 (Rosa & Krubitzer, 1999). As it stands, the current definition of visual areas in the mouse makes the organization of visual cortex in this species distinct from nearly all other studied mammals (Figure 1C), questioning the generalizability and translational potential of findings in the mouse.

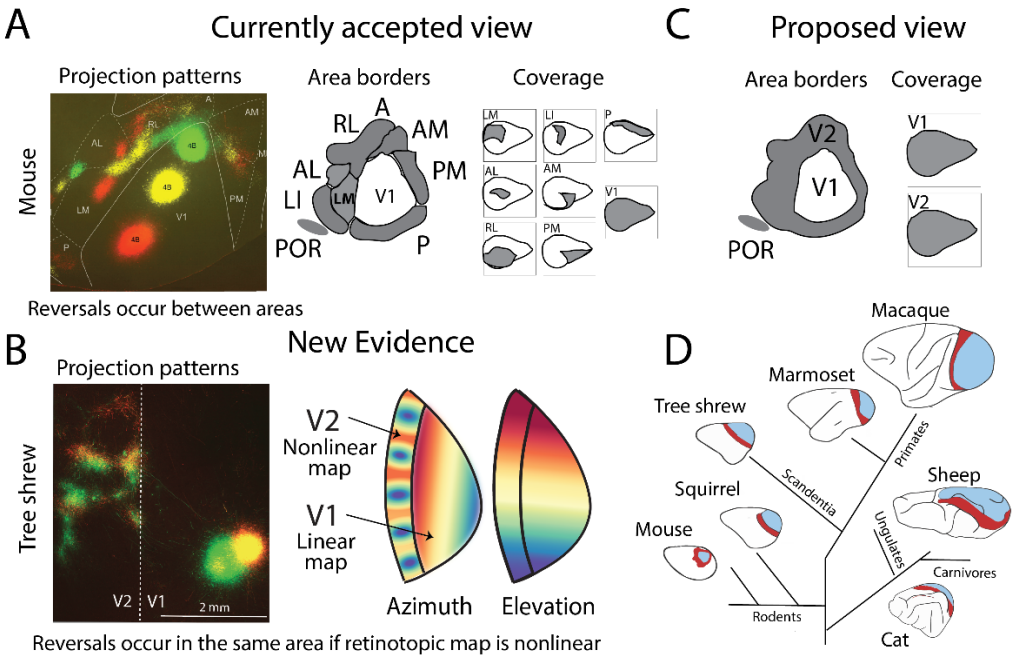

Figure 1: Higher order visual areas in the mouse may be better classified as a single area V2. A) The currently accepted organization of the mouse visual system includes multiple higher order visual areas beyond V1, defined based on reversals in the progression of the visual field, each with partial and biased coverage of the visual field. Projection pattern figure is modified from (Wang & Burkhalter, 2007b) and partial visual field coverage is modified from (Zhuang et al., 2017). **B)** New evidence of visual field reversals within single areas in the tree shrews (Sedigh-Sarvestani et al., 2021), and marmosets (H.-H. Yu et al., 2020) challenge the parcellation of higher order visual cortex in the mouse. **C)** Instead, we propose a new view supports a new view wherein a single area V2, with full coverage of the visual field, borders V1 in the mouse. **D)** This would make the organization of the mouse visual cortex like that in most other mammals, exhibiting an area V1 adjacent to a single area V2. Modified from (Rosa & Krubitzer, 1999)

Complex retinotopy within a single visual area can recapitulate the appearance of multiple higher order areas in mouse visual cortex

Until improved tracing techniques allowed anatomical mapping of visual field representations beyond V1, the region of visual cortex immediately adjacent to V1 was originally designated as simply V2 based on its cytoarchitecture (Glickfeld & Olsen, 2017). Multi-color projection studies (Wang & Burkhalter, 2007b), however, showed several reversals in progression of the visual field, similar to those observed across the border of V1 and V2 in primates. These reversals were used to delineate area boundaries in the mouse, which produced a series of higher order areas with only partial coverage of the visual field (Garrett et al., 2014b; Zhuang et al., 2017). However, as discussed above, multiple visual field reversals can be a hallmark of complex retinotopic mapping within a single area (Sedigh-Sarvestani et al., 2021; H.-H. Yu et al., 2020). We set out to explain the reversals beyond mouse V1 with an elastic net model of retinotopy, well-established for exploration of map organization in other species (Goodhill & Willshaw, 1990; Sedigh-Sarvestani et al., 2021; H.-H. Yu et al., 2020). Here, V2 is modeled using the anatomical boundaries of higher order visual cortex, and consists of point "neurons," each with a receptive field (RF) in the visual field. The objective of the algorithm is to arrange the RFs so they uniformly tile the visual field with the wiring-length constraint of preserving map "smoothness"; e.g., nearby neurons on the cortex should have nearby RFs in the visual field. The algorithm iteratively optimizes the RFs to reduce the total cost associated with visual field coverage and smoothness until a stable state is reached.

To apply the modeling techniques used in previous papers, we first needed to account for key differences in anatomy of the mouse visual cortex, including the 'tear-drop' shaped visual field and the shape of the areas in the cortical sheet (Figure 2A). This included modifying the algorithm to weight the interactions between neighbors by the inverse square of their distance in cortical space to account for non-evenly spaced nodes. In addition, we also expected a lower cost associated with the smoothness constraint due to larger receptive fields in the mouse visual system. The mouse's smaller eyes result in low spatial resolution as the visual field is projected through the pupil onto a smaller retinal surface. In V1 this results in much larger receptive fields and beyond this, allows for bigger steps in the visual field to be taken by adjacent regions of cortex while preserving an overlapping representation. Given this, we expected that a lower weight on the smoothness constraint in our model may result in a better representation of the higher order visual areas' retinotopy (Figure 2B-C).

Figure 2 shows the outcome of an example instance of the model simulating the mouse visual system beyond V1 using 640 neurons. A single elastic net model, constrained by the anatomy of the mouse visual cortex and trained to cover the mouse visual field often (but not always) creates retinotopy with reversals that align to those reported in the mouse. This implies such complex mapping, exhibiting a twisted visual field representation, is the optimal solution to smooth visual field coverage when anatomical constraints of the mouse visual cortex are accounted for. As in previous work, modifying the weights associated with smoothness and isotropy results in internal reversals, seen in alternating field sign (Sereno et al., 1994) (Figure 2C-E). The precise layout of these reversals varies somewhat with the initial random seed, but always includes multiple reversals in the upper and lower visual field representations. We note that variation also exists in the reported retinotopy of the mouse between animals (Garrett et al., 2014a; Zhuang et al., 2017). There may also be additional constraints in the mouse visual cortex that are not accounted for in our model that could result in a more robust outcome. Further work is needed to create a more reliable model, but the model as it stands clearly demonstrates the feasibility of a single mouse V2 to account for the complex retinotopic mapping, multiple visual field reversals, and the appearance of multiple visual areas under the false assumption of simple retinotopy.

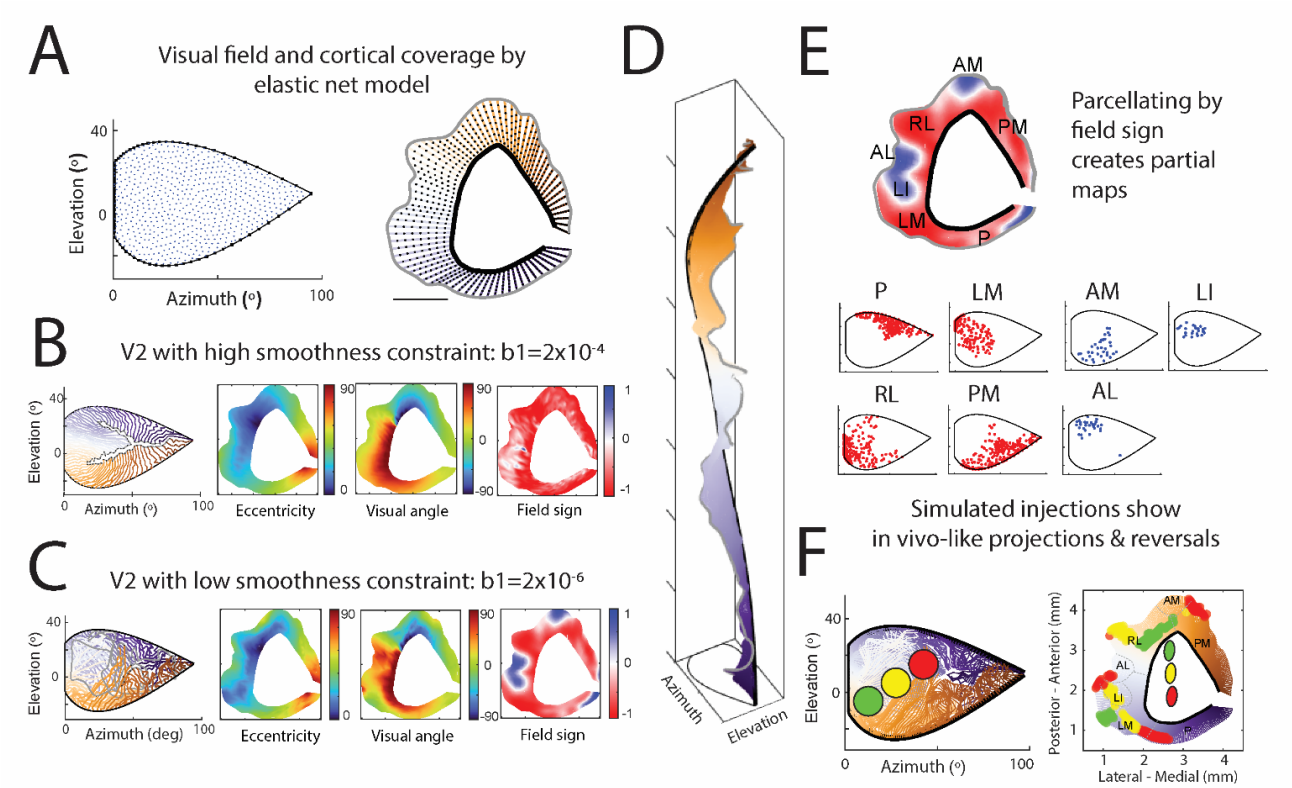

Figure 2: Retinotopic models show emergence of a single complex map of visual space beyond mouse V1. We extended the elastic net model from previous work (Sedigh-Sarvestani et al., 2020) to constrain a model of V2 to the unique structure of the mouse. **A)** Borders of cortical space were traced from (Zhuang et al., 2017) and a teardrop shaped visual field was used to approximate the full visual field covered by mouse V1. **B-C)** Modifying the constraints to smoothness and isotropy result in internal reversals, seen in alternating field sign (Sereno et al., 1994). **D)** Visualization of the visual field, azimuth & elevation planes, covered by normal lines between the V1 and higher order visual area border as in right of A. These lines are stacked on the Z-axis, and color coded, going from the caudal border of V1 in purple around the circumference of V1 to the medial edge in orange. **E)** This complex retinotopy generates, from a single continuous area, reversals that approximately match mouse higher order visual areas, showing that previously reported retinotopic maps in mouse higher order visual areas are parsimonious with a single area covering a full, but twisted, visual field. **F)** Matching points in the visual field with their locations in this single area, creates similar patterns to what has been shown in tracer studies (Wang & Burkhalter, 2007a), compare 1A.

The twisted nature of the single visual field covering higher order visual cortex can also be shown in Figure 2D, where azimuth and elevation axes are plotted against each other in X and Y coordinates at the base, and the progression along the visual field as one moves around V1 on the cortex, is plotted in the Z-axis. This complex retinotopy generates, from a single continuous area, reversals that approximately match mouse higher order visual areas (Figure 2E). In fact, we can use the same model to simulate multi-color tracer injections into V1 (Figure 2F), and show several modular projection zones, which would appear to be multiple distinct representations of the visual field without knowledge of the underlying complex transform between V1 and V2. Together, our simulation data provides strong evidence in support of the unification hypothesis and suggests that previously reported multiple higher visual areas with partial retinotopic maps can be more parsimoniously explained with a single area with a full, but twisted and complex, representation of the visual field. However, multiple differences between these areas along anatomical and functional lines have also been reported. Next, we will review and assess if a single V2 area with a warped retinotopy could account for these differences.

Reported functional property differences among higher order areas are better explained by retinotopic bias and opsin gradients

Functional feature differences are one of the main metrics used to justify areal definitions in the higher order visual system of primates and cats. For instance, area MT in primates exhibits sensitivity to global motion direction that is absent in area V2, even in identical regions of the visual field. Such hierarchical and parallel processing of overlapping parts of the visual field is thought to represent an efficient strategy to build selectivity to complex input features (Felleman & Van Essen, 1991).

While there is growing evidence of functional diversity within mouse visual cortex, most observations of diverse functional properties report relatively small and continuous changes in tuning across multiple areas, rather than robust and sharp differences between higher order areas as observed in primates (Figure 3). For instance, binocular disparity tuning (Chioma et al., 2019), color tuning (Aihara et al., 2017), and coherent motion processing (Sit & Goard, 2020) have all recently been shown to vary across the elevation axis of retinotopy (Figure 3 A). These trends are consistent with the ethological relevance of visual field locations for a low-lying animal like the mouse (Qiu et al., 2021a). Furthermore, the areas categorized into the dorsal and ventral stream of the mouse cortex also exhibit robust biases for the lower and upper visual field (Figure 3B). This further supports the major effect of retinotopy on the structure and function of the mouse visual cortex.

Functional property differences in higher order visual areas have also been reported to vary along the azimuth axis of retinotopy. For instance, receptive field size, response latency, and the degree of phase-locking to drifting gratings vary smoothly across higher order visual areas, along azimuth (Siegle et al., 2021). The effect of optogenetic inhibition of secondary visual areas also seems to exhibit a retinotopic bias, with inhibition of lateral areas producing little effect on a contrast detection task, and inhibition of the medial areas producing a robust effect (Goldbach et al., 2021; Jin & Glickfeld, 2020). However, this effect may not arise from simple stimulus-location effects but may be due to inherent differences in the contribution of different regions of the visual field to specific perceptual tasks. Finally, encoding of various behavioral task-related features was shown to vary across higher order visual areas of the mouse (Minderer et al., 2019), but as the authors point out, this variation is agnostic to higher order areal boundaries and instead follows the underlying topography smoothly (Figure 3C). In fact, the only functional discontinuities in the mouse posterior cortex were found at the major anatomical borders between V1, parietal, and retrosplenial areas.

Such observations of smooth functional property differences across mouse higher visual cortex, coupled with the fact that retinotopic locations within a single visual area often exhibit smoothly varying functional differences (Groen et al., 2021; Kanwisher, 2001; Sedigh-Sarvestani & Fitzpatrick, 2022; H. H. Yu & Rosa, 2014), leads us to a more parsimonious explanation: Functional features differences in mouse higher order cortex can be simply explained by the underlying retinotopic bias across areas. Testing this hypothesis requires careful measurements of visual field location and functional property differences in V1 and higher order visual areas. Such data sets are sparse but growing. To test our hypothesis with existing data, we reanalyzed a dataset from Han et al. (Han et al., 2022) and showed that some of the reported differences in spatial frequency (SF) and temporal frequency (TF) tuning can be accounted for by a smooth function of eccentricity and elevation (Figure 3). The relationship of tuning with eccentricity is unexpectedly inverted from what has been reported in V1 but is nonetheless still smooth.

In primate vision research ‘eccentricity’ is used to mean distance in visual degrees from the center of gaze, which is a useful metric for animals with a fovea and robust overrepresentation of the central few degrees of vision. Many functional properties scale with eccentricity within visual areas, making it a very important parameter to control for in foveal animals such as primates (Yu et al., 2015). However, in the afoveate mouse, ‘center of gaze’

is difficult to control for and typically elevation above eye level and azimuth relative to a normal through the eye are used.

While this is a reasonable approach for an animal without a fovea, it has been reported that a central region of the upper binocular visual field of the mouse is slightly overrepresented in V1 and seems to be behaviorally significant. This region was named the 'focea' (van Beest et al., 2021). Due to strong expectations that functional response properties scale with distance from this point, we will assess functional properties as a function of distance from the focea. Taking the focea as 20 degrees above resting eye level on the vertical meridian (0 degrees azimuth), 'eccentricity' (Figure 3D) is simply the Euclidean distance from this point in degrees of visual field.

There is an additional effect across retinotopy in the mouse that must be considered. The mouse retina has a gradient of cone opsins (Figure 3E) such that S-cones, sensitive to UV light, are overrepresented on the ventral surface (the upper visual field) and give way to M-cones, sensitive to green light, on the dorsal surface (the lower visual field). When a typical LCD monitor is used, M-cones but not S-cones, are partially activated (Rhim et al., 2021). This means that retina in the upper and lower visual fields are in a rod-dominated scotopic and mixed cone- and rod- mediated mesopic regime respectively. This retinal gradient is known to be preserved in the visual cortex (Rhim et al., 2017) and is thought to play an important role in predator evasion (Qiu et al., 2021b). Thus, control for the opsin gradient is crucial for accurate measurement, reporting, and comparative analysis of functional properties in mice. Specifically, the use of typical LCD monitors results in primacy of scotopic vision in the ventral retina, producing higher spatial and lower temporal frequency tuning in the upper visual field.

In Han et al. (2022) an LCD screen was used. The observed trend, albeit small, towards higher SF tuning in the areas with predominantly upper field representations (Figure 3F) suggests that the cone opsin gradient may be a factor. To account for the effects of both eccentricity from the focea and the cone opsin gradient across elevation, we fit a plane to the peak tuning as a function of these variables. The dataset includes retinotopic mapping from a clockwise circling visual stimulus, revealing reversals that were used to register data to a common map. Here, to get a more fine-grained estimate of the retinotopic locations, we further registered these to the Zhuang et al. (2017) maps for azimuth and elevation. To account for the cells that had reported tuning at the extreme edges of the range, the data was fit using expectation maximization algorithm as noisy data varying around a mean centered on a plane. The proportion of censored values was thus able to contribute to the plane fits without introducing a bias by removing them. We also excluded area P as this area wasn't separated from POR in Han et al. (2022) y. In Figure 3F-G, we show that subtracting the expected peak tuning of each cell calculated from a plane fit through eccentricity and elevation significantly reduces the functional property differences among higher order areas. This suggests that a large portion of the measured differences in spatial and temporal frequency tuning in higher order areas can be explained by their bias towards different regions of the visual field.

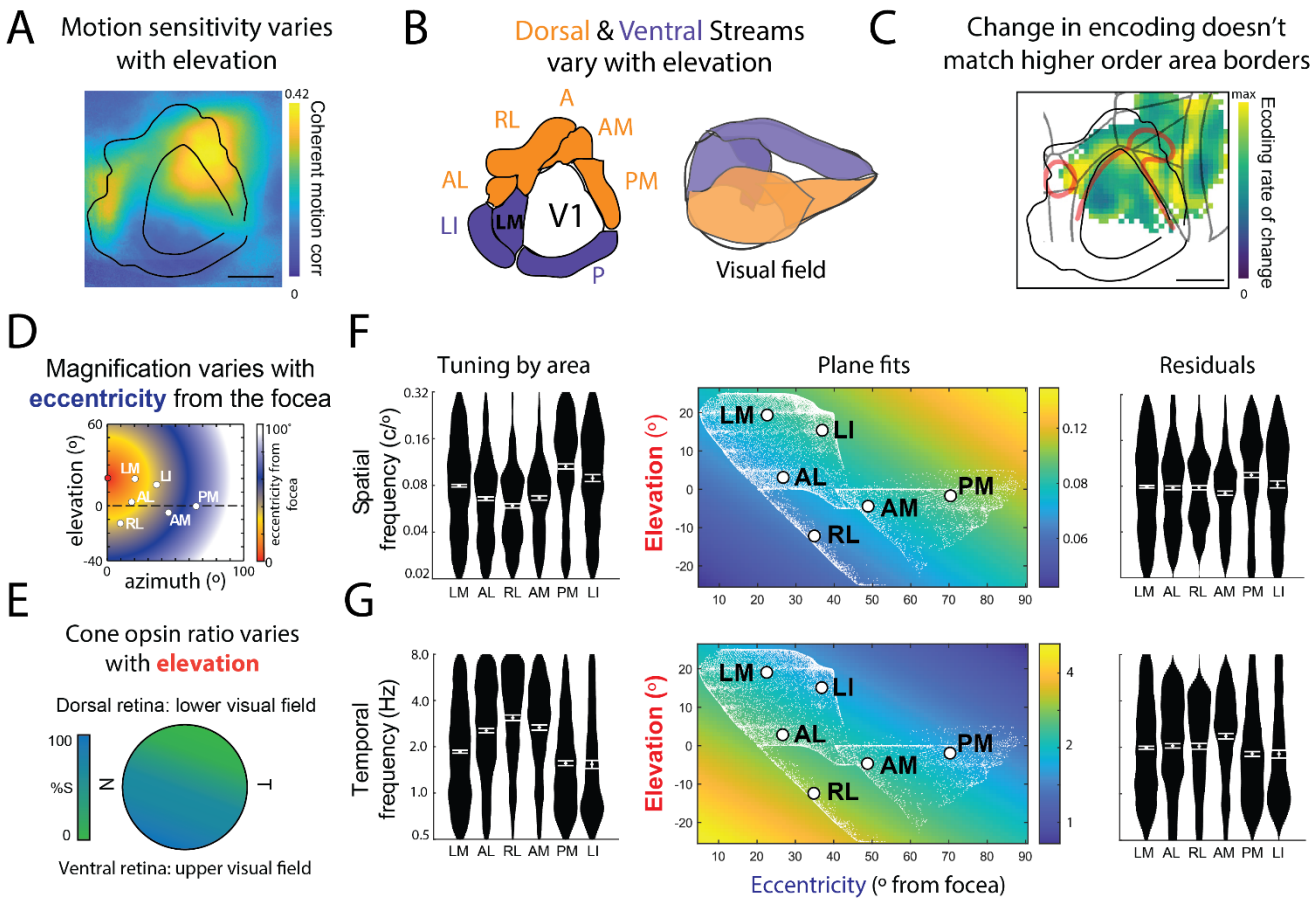

Figure 3: Retinotopy accounts for functional variations between higher order areas in mouse visual cortex. A) Map of motion sensitivity adapted from (Sit & Goard, 2020) showing higher sensitivity in the lower field representation of V1 and higher order visual areas. **B)** Dorsal and Ventral streams in the mouse containing multiple higher order visual areas have been suggested due to differences in function, however these maps closely align onto elevation axis of retinotopy. Figure made using data from (Zhuang et al., 2017) **C)** Behavioral encoding as a function of cortical space shows large change along the V1 border, but not between higher order visual areas (Minderer et al., 2019). Scale bar 1mm. **D)** Schematic of eccentricity from focea with area estimates for the data used in F&G.**E)** Schematic of retinal cone opsin gradient following (Demb & Singer, 2015). **F)** Data from (Han et al., 2022). Tuning to spatial frequency (SF) of bandpass cells in each area (left), plane fit of SF to area elevation and eccentricity from focea (middle) and the residuals (right) after subtracting a plane fit. **G)** Same for temporal frequency (TF). Area tuning violin plots show the distribution of tuning within areas with white dots for the mean and lines for 95% confidence interval.

We note that changes in spatial and temporal frequency, varying smoothly with eccentricity, have been observed in visual areas of various species including primates (Groen et al., 2021; Kanwisher, 2001; Sedigh-Sarvestani & Fitzpatrick, 2022; H. H. Yu & Rosa, 2014). However, in the case of spatial frequency, the relationship we observe in the mouse secondary visual cortex seems to be inverted from that observed in primates (Yu et al., 2015): preference for higher spatial frequencies is seen in the peripheral, rather than central vision. This has been reported in higher order visual areas of the mouse by several independent groups (Han et al., 2022; Marshel et al., 2011). However, such an inverse relationship between SF preference and eccentricity does not impact our argument that functional feature differences smoothly vary across multiple areas, rather than sharply in between higher order areas – suggesting that functional feature differences observed in the mouse do not lend support to the delineation of multiple areas. Further work is needed to explore why the neuronal preferences for spatial frequency and eccentricity seem to co-vary with opposite trends in the visual cortex of rodents and primates.

Based on this data, we believe the functional feature differences observed across the mouse higher order visual system can be explained more parsimoniously by variations in retinotopy rather than areal identity. This limits the use of functional feature diversity in justifying areal definitions. To rely on functional feature differences to assess areal identity, the confound of retinotopy must be removed. This is typically done by reporting functional feature differences across areas, in overlapping parts of the visual field representation of each area. The studies mentioned above do not carry out this important control, largely due to the fact the higher order visual areas in the mouse do not have overlapping representations of the visual field (Zhuang et al., 2017). This lack of visual field overlap across areas, is in itself, suggestive of a lack of hierarchical multi-area processing in the mouse. The lack of visual field overlap combined with the observed smooth changes in functional feature tuning strongly supports the re-classification of multiple higher order visual areas into a single area V2 (Figure 1C). Such an area would exhibit the observed functional feature differences in different parts of its visual field map, as has been observed in primates and cats. Such differences ultimately arise due to the presence of different types of ethologically relevant information in distinct parts of the visual field (Sedigh-Sarvestani et al. 2022).

Reported anatomical evidence for multiple higher order visual areas can be explained by complex retinotopy in a single area V2

Efforts to understand the organization of the mouse visual system were largely based on prior anatomical and functional measurements in primates. Early parcellations of the mouse visual cortex were made based on cytoarchitectural features including cell density and laminar distribution - leading to the delineation of two subcomponents of a single area V2 (Caviness, 1975). Future work showed boundaries in labeling of histological markers such as SMI-32 and m2ChR labeling, but such changes mostly delineated area LM/AL (Wang et al., 2011) and seemed to be correlated with the representation of the lower visual field. We now know, based on work in both mice and primates that different parts of the retinotopic map of a single visual area can exhibit different genetic and molecular markers, different cell types, different cell density, and robustly different anterograde and retrograde connections to other areas (Morimoto et al., 2021; Mundinano et al., 2019; Palmer & Rosa, 2006; H.-H. Yu et al., 2015). Therefore, observations of histological differences in higher order visual cortex, on their own, cannot be used to delineate areal boundaries.

Later parcellations of the mouse visual cortex relied, in addition to cytoarchitecture, on the pattern of anterograde connections from V1 to higher order visual cortex, as well as the pattern of callosal connections from contralateral V1 into ipsilateral higher order visual cortex. Combining these projection patterns revealed a complex set of modules in higher order visual cortex - each assumed to be a separate area (Figure 1A). We now know that both the modular mirror-map organization of anterograde projections from V1, and callosal projections from contralateral V1, can be explained by non-retinotopic mapping within a single visual area (Figure 1B), as in tree shrews (Sedigh-Sarvestani et al., 2021). The definition of a single visual area despite the appearance of multiple mirror maps, or reversals, relies on the existence of a single mapping of a visual field - with a complex transformation occurring between the retina and V2. This is precisely the case in the visual cortex of the mouse, where multiple modules (currently defined areas) combine to form a single, complex, representation of the visual field. Each module, when considered alone, represents only a subsection of the visual field, with little overlap between modules (Figure 1A). Therefore, given what we now know about complex retinotopic transforms, observations of patchy or modular organization beyond V1 cannot be used to delineate multiple areal boundaries.

In addition to cytoarchitecture and connection patterns, a third anatomical feature used to delineate the primate visual cortical hierarchy is pairwise asymmetries in feedforward and feedback connection densities and laminar distributions. Specifically, feedforward inputs tend to terminate in primate layer 4 whereas feedback inputs tend to terminate in superficial and deep layers, but not in layer 4. In the rat and mouse, the laminar distribution is less distinct between feedforward and feedback inputs, but D'Souza et al. (2022) discovered a pattern specific to the

mouse, focused on differences between Layer 1 and Layer 2-4. Feedforward inputs tend to terminate in Layers 2-4, but not in Layer 1, and feedback inputs tend to terminate in Layer 1, and less so in Layers 2-4. One can quantify this relationship using an optical density ratio (ODR) of labeling density in Layer 1, vs. all layers. An analysis based on such laminar differences easily distinguished V1 as providing feedforward input to higher order areas, with ODR values less than 0.5. Higher order areas were also easily distinguished as providing feedback inputs to V1, as evidenced by ODR values significantly greater than 0.5. However, the connections between higher order visual areas exhibited ODR values near 0.5, suggesting that these areas form neither feedforward nor feedback connections to each other, but are rather at the same level of the hierarchy. This lends further support to the unification of these higher order areas into a single V2, producing a simple 2-layer shallow hierarchy in the mouse visual cortex consisting of V1, V2, and perhaps the outlier area POR as a third layer.

Complex retinotopy beyond V1 is a common feature of secondary visual cortex in multiple species

The visual cortex beyond V1 of several species contains modular organization with multiple reversals – as in the mouse visual cortex. These include tree shrews as previously mentioned, but also ferrets (Manger et al., 2002a), and macaques (Roe & Ts'o, 1995b, 1995a). In fact, if one considers the visible portion of V1 and V2 in these species, it bears a striking resemblance to the analogous regions in the mouse visual cortex (Figure 4), with all species exhibiting simple retinotopy in V1, and complex and modular retinotopy immediately beyond V1. However, despite the presence of multiple reversals as in the mouse, the current classification of visual cortex (Figure 4, blue box) includes a single area V2 in both the tree shrew and macaque visual cortex. In the ferret visual cortex, two areas are defined: area 18 and area 19. This is contrast to the current classification of the mouse visual cortex, which includes multiple areas beyond V1, parcellated based on visual field reversals (Figure 4A). The disparity in the rules used to delineate the visual cortex of mice, vs other species is highlighted when reversals are used to delineate areas in the visual cortex of tree shrews, macaques, and ferrets (Figure 4, "Borders using reversals"). In each case, many areas would be defined beyond V1.

Given this disparity, one could argue that the current classification of the mouse visual cortex can be left intact, and the organization of the visual cortex in other species should be updated to reflect the reversal rule. This would result in common areal delineations across species. However, we believe the existing data strongly supports a single area V2 bordering V1 in all species, including mice. Below we discuss the rational for defining a single, or at most two, visual areas bordering V1 in tree shrews, ferrets and macaques.

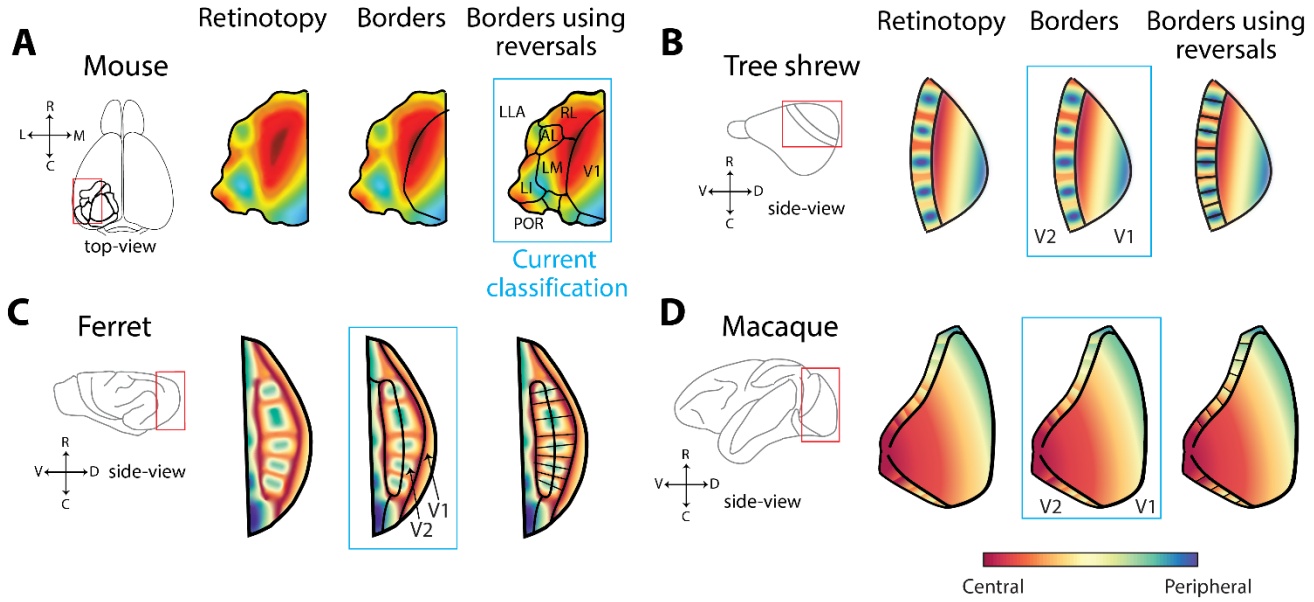

Figure 4: Complex retinotopy beyond V1 is a common feature of secondary visual cortex in multiple species. A) Retinotopy maps in mouse V1, schematics created based on data from **(Zhuang et al., 2017).** Currently accepted area delineations shown in blue box. **B)** Retinotopic maps in tree shrew visual cortex. Data from (Sedigh-Sarvestani et al., 2021). **C)** Retinotopic maps in ferret visual cortex. Data from (Manger et al., 2002a). **D)** Schematic of retinotopic maps in visible portion of macaque V1 and V2. Data from (Roe & Ts'o, 1995b; Shipp & Zeki, 2002b). Color maps are different for each species and are simply meant to indicate relatively more central or peripheral regions of the visual field.

In tree shrews (Figure 4B), the visual cortex adjacent to V1 exhibits a modular organization, with retinotopic stripes that alternate between representations of relatively more central and relatively more peripheral regions of the visual field. In the middle of each stripe lies a visual field reversal. However, a unified V2 is defined in the tree shrew which subsumes these reversals. The rational for this delineation include cytoarchitecture, projections from V1, and cross-hemispheric projections (Kaas et al., 1972; Sesma et al., 1984; Wong & Kaas, 2009). In addition, despite the modular appearance of the retinotopy map, it has been shown that there is a single visual field represented in V2 with no repeated coverage (Sedigh-Sarvestani et al., 2021). Therefore, just as in mouse visual cortex, complex retinotopy gives the appearance of multiple visual field representations where only a single representation exists. Furthermore, functional property differences observed in V2 stripes can largely be attributed to underlying retinotopic differences (Sedigh-Sarvestani et al., 2021).

In ferrets (Figure 4C), a similar modular representation was observed beyond V1, with repeated modules of crossings between more central and peripheral regions of the visual field. Within each central or peripheral module lies a visual field reversal. However, these reversals are not used to delineate multiple areas bordering V1. Instead, an area 18 (V2) and an area 19 (V3) are defined, based on cytoarchitecture, anatomy, and functional properties (Dell et al., 2019; Manger et al., 2002a, 2002b). As in tree shrews, despite the presence of multiple reversals, there is a single visual field representation across area 18 and 19, with each module covering a small portion of the visual field (Manger et al., 2002b). Similar observations have been made in the cat secondary visual cortex (Boyd & Matsubara, 1994).

A series of elegant papers in the 1980s and 1990s showed a modular, striped, organization in macaque V2 (Hubel & Livingstone, 1987; Roe & Ts'o, 1995b; Shipp & Zeki, 2002a). The stripes exhibited distinct functional feature preferences, including for color, motion, and horizontal disparity. The underlying retinotopic map has been less clearly defined, in part due to the lack of optical imaging measurements in macaque V2. Published reports

based on electrode penetrations across V2 indicate multiple reversals between relatively more foveal or peripheral regions of the visual field (Roe & Ts'o, 1995b; Shipp & Zeki, 2002b). Though these reversals were interpreted as multiple representations of the visual field, we suspect they form a single unified representation similar to tree shrews and ferrets. Nonetheless, despite the appearance of multiple representation of the visual field, a single area V2 was defined in macaques – in part because of the clear modular and repeated nature of functional property differences across the length of V2.

In summary, there appears to be a common complex organization beyond V1, exhibiting modularity, in several evolutionarily distant species. Cytoarchitecture, anatomy, and functional measurements support defining these modules into a single area V2.

Discussion:

Here we have made a case, using simulations and a critical re-analysis of published data, that many of the higher order visual areas in the mouse are actually sub-parts of a single area V2. We have shown that multiple visual field reversals, on their own, cannot be used to delineate areal boundaries. This is because complex mapping of the visual field can produce multiple reversals within a single area. We have also shown that many of the functional property differences reported between higher order areas are better explained by retinotopic bias among areas and known differences in functional feature preferences across the retinotopic map of a single visual area. We believe this evidence strongly supports redefining mouse higher order visual areas into a single area V2. What remains, is a visual system with distinct properties across its visual field - aligned with ethological needs and behaviors. This new definition produces a common set of rules for defining areal boundaries among mammals: the presence of a full visual field, homogenous cytoarchitecture and smooth functional properties.

We emphasize that our proposal goes beyond ever-green arguments on 'what is a visual area?'. Ideally, we would be able to define areal boundaries using automated, model-based, approaches (Shimaoka et al., 2024). However, we currently lack the cross-species data required to develop such models with meaningful accuracy. Until then, the least we can do is to ensure that we use the same rules to define visual areas across species, regardless of what the rules are per se. In the case of visual cortex beyond V1, applying such universal definitions for areal boundaries would bring mice into agreement with evolutionary evidence for a single area V2 in other nearby lineages (Rosa and Krubitzer, 1999).

However, there remains some evidence against the hypothesis of a single V2 in mouse visual cortex. Harris et al. (Harris et al., 2019) used the laminar density of projection patterns between different cortical and subcortical regions to give classification scores to the different higher order visual areas and found significant different hierarchy scores among these areas. However, they note that the hierarchy was much shallower than expected, particularly between these areas. Future work should assess whether hierarchy scores calculated from different regions of mouse V1 would exhibit a similar shallow network simply due to retinotopic biases in functional feature properties and laminar connection densities.

We note, again, that our argument is not novel. Rosa and Krubitzer made the same argument and plea in 1999, based on the presence of a single area V2 in a large range of mammals and non-mouse rodents (Figure 1D). We build on their argument armed with the knowledge of complex retinotopy that can explain the apparent differences in anatomy and function. More importantly, we believe the distinction of a single area into multiple areas has misled the field in both experimental design and interpretation of data collected from mouse visual cortex. Therefore, a redefinition is not merely a matter of semantics but rather necessary for improved studies of the visual system.

We believe in the value and urgent need for cross-species comparisons in neuroscience. This manuscript presents an effort on our part to align the mouse with other mammals. With a single area V2 definition, the mouse visual cortex is no longer an outlier in the evolutionary tree. This means we can continue to rely on this species to gain knowledge about the mammalian visual system. Otherwise, we should think carefully about whether what we learn in the mouse can be applied to any other mammal.

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