

What AND Where: Location-dependent feature sensitivity as a canonical organizing principle of the visual system

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Abstract: Traditionally, functional representations in early visual areas are conceived as retinotopic maps preserving ego-centric spatial location information while ensuring that other features of visual input are uniformly represented for every location in space. Higher visual areas are thought to represent features without preserving location information. Recent results challenge this framework of relatively independent encoding of location and features in the visual system, showing instead location-dependent feature sensitivity produced by specialized processing of different features in different spatial locations. Here we review the evidence for such encoding including: (1) systematic variation of functional properties within the retina and within conventional retinotopic maps in the cortex; (2) novel periodic retinotopic transforms that dramatically illustrate the tight linkage of feature sensitivity, spatial location, and cortical circuitry; and (3) species-specific retinotopic biases in functionally defined parallel streams. We propose that location-dependent feature sensitivity is a fundamental organizing principle of the visual system that achieves efficient representation of positional regularities in visual input, and reflects the evolutionary selection of sensory and motor circuits to optimally represent behaviorally relevant information. Future studies are necessary to discover mechanisms underlying joint encoding of location and functional information, how this relates to behavior, emerges during development, and varies across species.

Intro: In many parts of the brain, neurons are sensitive to changes in small parts of the visual field, sampled through the retina in the back of the eye. Often, nearby neurons in the brain signal changes in nearby visual field locations. This mapping of nearby locations on the retina onto nearby regions of the brain is referred to as retinotopic organization. Of course, neural circuits encode other aspects of visual input aside from spatial location, including many ‘functional features’ useful for different visuo-motor behaviors including identifying objects, tracking or otherwise interacting with objects, and moving through the world. The prevailing view is that these different aspects of visual information, spatial location and features, are coded independently in the visual system. Early visual areas are thought to represent features within the context of a highly-organized retinotopic map, while higher visual areas are thought to represent functional features without regard for their spatial location. When both location and features are represented in a visual area, their encoding is assumed to be independent, which would ensure uniform representation of visual features across all spatial locations.

Recent findings challenge this representational framework, showing instead a joint encoding of spatial location and features reflected in location-dependent sensitivity to functional features. Here we review the evidence for this location-dependent coding across various stages and scales of the visual system. This includes location-biased sampling of functional features in the output ganglion cell layer of the retina, systematic variation of functional properties within conventional retinotopic maps, and novel periodic retinotopic transforms that dramatically illustrate the tight linkage of feature sensitivity, spatial location, and specialized cortical circuitry. The location-dependent feature sensitivity exhibited at the cortical level appears consistent with the positional regularities in naturally experienced visual input, produced by the statistics of the environment as well as the statistics of bodily movements. Furthermore, a comparative analysis of the published literature supports a species-specific correlation between retinotopic location and functional feature processing across the parallel streams, the fundamental organizing scheme of the visual system originally defined based solely on distinct functional feature sensitivity across areas.

Based on our review and analysis of this evidence, we propose that the joint encoding of ego-centric spatial location and functional features is a canonical organizing principle of the visual system, likely reflecting evolutionary and developmental pressures that shape neural circuitry to optimally represent regularities in functionally relevant visual information. One implication of this framework is an increased need to study structural and functional properties of the developing and mature retina in order to understand the location-dependent encoding produced by specialized retinal sampling. Another implication is a need to revise experiments that investigate the representation of spatial location and functional feature sensitivities separately, since neural circuitry imposes inextricable dependencies between these features. We present other implications of this new framework and conclude with a discussion of how retinotopic specializations can be used to establish an ethological understanding of neural encoding.

Visual inputs received and relayed by the retina exhibit location-dependent statistics. The presence of a joint encoding of retino-centric location and functional features deep in the visual system suggests that these attributes may already be correlated in the retina, the first stage of visual processing and the interface between the environment and the brain. Even without specific measurements, one can safely assume that location and functional features are not independent in the retina since visual inputs are not homogeneously distributed at every retinal location and exhibit positional regularities. For instance, predators of mice regularly appear overhead in the blue sky. This produces non-uniform features with distinct statistics and behavioral salience, in the lower and upper locations of the retina. Several underlying factors (Figure 1) contribute to positional regularities in the visual input to, and visual output from, the retina that result in jointly distributed location-feature information.

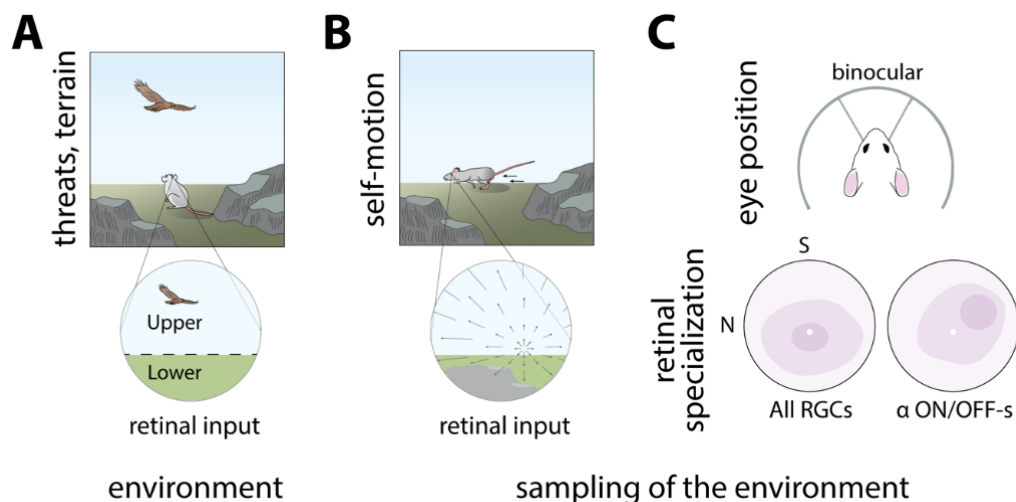


Figure 1: Visual inputs received and relayed by the retina exhibit location-dependent statistics. Correlations in visual inputs to the retina arise from **A)** non-uniform statistics of the visual environment such as predators that appear overhead, **B)** self-motion of the eyes, head, and body, and **C)** the position of the eyes in the head and the non-uniform topographic distribution of different retinal ganglion (RGC) cell sub-types that can further enhance location-feature correlations in the visual signal relayed downstream to the rest of the brain. Retinal specializations schematized from data in (Bleckert *et al.*, 2014; Heukamp, Warwick and Rivlin-Etzion, 2020a). Panel A-B modified with permission from ©2021 Dina Popovkina.

Perhaps the most obvious source of positional regularities in visual input is the environment itself, which has distinct behaviorally relevant features (Geisler, 2008) across the egocentric visual field (Figure 1A).

For instance, the upper and lower visual field of small rodents exhibit distinct color distributions (Y *et al.*, 2021) whereas the central and peripheral visual fields of social primates contain different distributions related to face recognition and communication. Other sources of non-uniform retinal input arise from self-motion (Carriot *et al.*, 2017; Bigge *et al.*, 2021) including movements of the body, the head, and the eyes (Wallace *et al.*, 2013) as well as the position of the eyes relative to the head and body (Figure 1B-C). Optic-flow related to self-motion (Angelaki and Hess, 2005) produces distinct structured patterns that can differ across regions of the retina (Bigge *et al.*, 2021). Similarly, movements of the head, especially when not compensated by opposing eye movements (Meyer, OKeefe and Poort, 2020) can produce different spatiotemporal visual inputs in different locations of each retina, and across the left and right retinæ. The position of the eyes, which are in front of the head in primates and predator animals including cats, or on the side of the head in rodents, tree shrews, and many prey animals including rabbits, influences the amount of binocular visual field. This in turn shapes the relative structure of visual input across the two retinæ with temporal regions receiving binocular information from the central visual field and nasal regions receiving monocular information from the periphery. Many prey animals also tend to have eyes close to the ground, creating differences in visual inputs between their lower and upper visual field that is more exaggerated compared to upright primates, arboreal, or flying animals.

Given that neuronal circuitry tends to utilize resources efficiently, one might expect retinal neurons to exhibit specialized processing that reflects the positional regularities present in their inputs (Kaiser *et al.*, 2019). One of the most obvious retinal specializations is the fovea, an area densely packed with photosensitive cones and retinal ganglion cells (RGCs) that provides specialized sensitivity to color and fine features used for object and face recognition, and social communication, in the most central location of the visual field of humans and most primates. The mouse retina lacks a foveal region and was long assumed to exhibit topologically uniform functional feature sensitivities, but advanced genetic approaches have revealed distinct retinal specializations in this animal (Figure 1C, (Bleckert *et al.*, 2014; El-Danaf and Huberman, 2019; Heukamp, Warwick and Rivlin-Etzion, 2020a). The best studied retinal variation concerns the non-uniform distribution of S and M opsins (Szél *et al.*, 1992; Röhlich, van Veen and Szél, 1994; Baden *et al.*, 2013b; Nadal-Nicolás *et al.*, 2020) that produces distinct color sensitivity across the upper and lower visual field (Denman *et al.*, 2018). However, topographic specializations have been discovered in several RGC subtypes with unique functional properties (Bleckert *et al.*, 2014; Heukamp, Warwick and Rivlin-Etzion, 2020b). With the exception of the primate fovea and the retinal specialization for color sensitivity in the mouse further discussed below, we do not understand the cortical and behavioral consequences of retinal specializations, although several ecological hypotheses have been formulated (Moore *et al.*, 2016; Baden, Euler and Berens, 2020). It stands to reason however that the specific sampling of visual information provided by retinal specializations should be reflected in downstream cortical representation of the retina.

Location-dependent feature sensitivity individual visual areas throughout the visual hierarchy. If functionally distinct visual information varies by spatial location in the output pathways of the retina (Figure 1), it follows that individual visual areas should reflect this organization and exhibit location-dependent sensitivity to functional features (Figure 2). In other words, different parts of the retinotopic map of a single visual area should exhibit different feature sensitivities. This is contrary to the prevailing theoretical frameworks that assume that functional feature sensitivities vary across visual areas but not within the retinotopic map of a single visual area. Such orthogonal encoding of spatial location and

visual features ensures that all locations of the visual field have equal representation of various features (Swindale *et al.*, 2000). But this would be an inefficient encoding given that visual input does not contain uniform features across all locations of the visual field. For instance, because we regularly see faces in our central visual field, there is a reduced need for specialized processing of features related to facial recognition in peripheral locations of the visual field. Here we review ample evidence in support of location-dependent feature sensitivity in individual visual areas, which has also been referred to in the published literature as ‘visual field specializations’ (Previc, 1990).

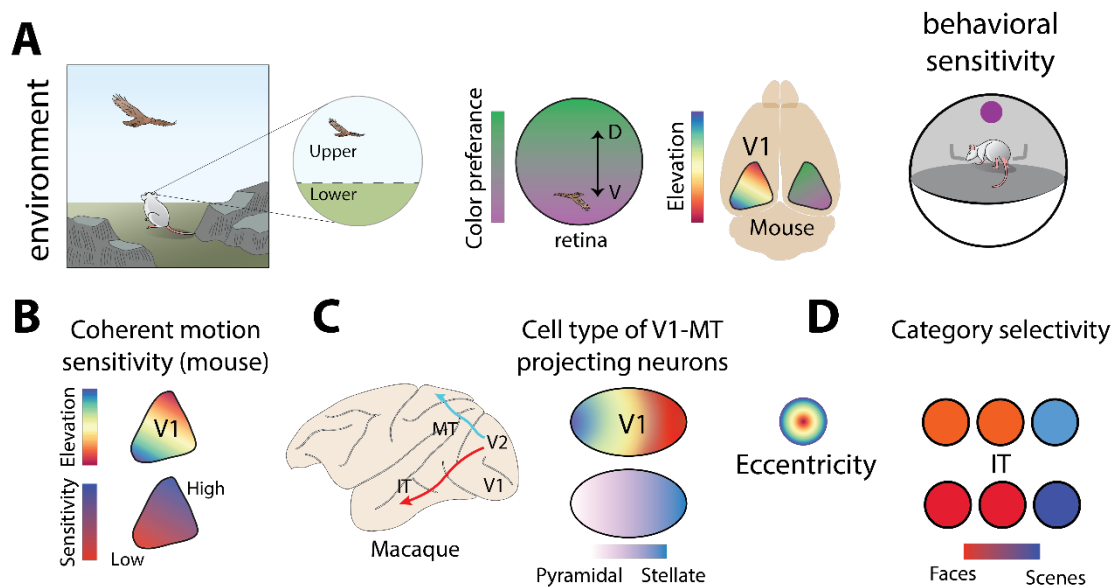


Figure 2: Location-dependent feature sensitivity in individual visual areas, and in the connection between areas. A) Distinct distribution of short and medium wavelength colors across the upper and lower visual field of mice (Y *et al.*, 2021) is reflected in the biased distribution of cones in the retina (Nadal-Nicolás *et al.*, 2020), as well as in the joint representation of elevation location and chromatic sensitivity in mouse V1 (Rhim *et al.*, 2017). Behavioral measurements of color sensitivity reflect the same bias for short-wavelength light in the upper visual field (Denman *et al.*, 2018). **B)** Sensitivity for coherent motion in mouse V1 depends on location along the elevation axis (Sit and Goard, 2020a). **C)** In marmoset V1, MT projecting neurons in layer 3C exhibit cell type variation along the central-peripheral (eccentricity) axis (Mundinano, Kwan and Bourne, 2019). **D)** In macaque IT cortex, category selective regions have biased retinotopic sensitivity that varies with their category selectivity (Levy *et al.*, 2001; Hasson *et al.*, 2002a).

As in the retina, the best-studied example of location-dependent feature encoding concerns color sensitivity (Rhim *et al.*, 2017) in mouse V1 (Figure 2A). The cortical representation of the lower visual field in V1 is more sensitive to middle (green) and the representation for the upper visual field is more sensitive to short or UV wavelengths. This specialization arises from a corresponding retinal specialization (Nadal-Nicolás *et al.*, 2020), reflects optimal sampling of environmental statistics (Baden *et al.*, 2013a; Y *et al.*, 2021), and matches behavioral chromatic sensitivity across the visual field (Denman *et al.*, 2018). Furthermore, a recent study suggests that the sensitivity of mouse V1 neurons in the upper visual field representation shifts towards shorter UV wavelengths during pupil dilations related to arousal (Franke *et al.*, 2021). This increased sensitivity may enhance detection of overhead predators during active foraging or exploration. In this series of studies, developing an ethologically contextualized understanding of a mouse-specific retinal and correlated retinotopic specialization allowed researchers to discover how pupil dilations facilitate neuronal adaptation to changing visual

input - a fundamental finding with broad relevance to other species. One can only imagine what discoveries may arise from cross-species studies of retinotopic specializations.

Several other location-dependent feature specializations were recently reported in higher order visual areas of mice, including specializations for luminance contrasts (Williams *et al.*, 2021), along the central-peripheral axis of the visual field. The representation of the lower visual field across the mouse visual system exhibits greater sensitivity to coherent motion (Sit and Goard, 2020b) (Figure 2B), as well as greater sensitivity for binocular disparity (La Chioma, Bonhoeffer and Hübener, 2019). Both location-dependent representations likely reflect natural image statistics related to visual processing in peri-personal or near visual space, which coincides with the lower field in low-lying animals like mice.

Location-dependent feature sensitivity has also been reported in other species. In primate V1, as one moves from central to peripheral locations of the retinotopic map, there are major changes in properties related to spatial acuity and binocularity (Adams, Sincich and Horton, 2007). This gradient reflects the topographical distribution of the different RGC types in primate retina as well as the position of the eyes. But specializations in cortical areas are not always simply inherited from incoming input and may develop *de novo* based on non-uniform anatomical, structural, or molecular properties of neurons in different portions of the retinotopic map. This has been nicely demonstrated in marmoset area MT, which exhibits distinct connections with other visual and non-visual areas in different parts of its retinotopic map (Figure 2C). Regions in the central representation are connected to other visual area like V1, V2, V3, and V4 whereas regions in the far peripheral representation receive inputs mainly from peripheral V1 and area prostriata in the retrosplenial cortex (Palmer and Rosa, 2006). Zooming in further, remarkable retinotopic specializations exist within the V1-MT projection (Mundinano, Kwan and Bourne, 2019). MT-projecting neurons, in layer 3C of V1, in the central regions of the retinotopic map are mostly spiny stellate whereas neurons in the peripheral representation are mostly pyramidal. Distinct connectivity between the central and peripheral representation of visual areas and the rest of the brain have also been observed in humans (Griffis *et al.*, 2017; Sims *et al.*, 2021).

Recent advances in fMRI technology have also revealed ubiquitous location-dependent functional sensitivity in higher order areas of the human visual system (Hasson *et al.*, 2002b; Groen *et al.*, 2021a). Until recently, category selective regions of the ventral stream were thought to lack representation of spatial location. High-resolution fMRI imaging highlighted multiple retinotopic maps underlying previously known functional specializations for faces, scenes and buildings (Figure 2D). Face-preferring regions overlapped with the central representation whereas scene and building-preferring regions overlapped the peripheral representation of the visual field (Levy *et al.*, 2001). A similar organization was found in the macaque (Arcaro and Livingstone, 2017). Notably, although most face-selective regions exhibited an enhanced representation of the central visual field, several regions lacked retinotopic organization of the orthogonal visual field axis or exhibited biases for the upper visual field (Silson *et al.*, 2018). This may reflect a lack of functionally distinct visual information relevant for the detection of faces in the upper and lower visual fields. In summary, precise measurements in human IT have revealed location-dependent sensitivity to functional features (Groen *et al.*, 2021b). It has been hypothesized that this encoding is anchored by general cortical architecture that becomes specifically tuned to visual experience during an animal's lifetime (Arcaro and Livingstone, 2021).

In addition to environmental statistics, positional regularities in retinal input also arise due to bodily movements (Figure 1B). As a result, one might expect to find joint encoding specializations related to

movement or navigation (Saleem, 2020). Several groups (de Malmazet, Kühn and Farrow, 2018; Li, Turan and Meister, 2020) have recently reported the joint encoding of spatial location and motion direction in the mouse superior colliculus (SC), with structures that could support the encoding of self-motion induced optic flow. However, these reports produced conflict patterns of the retinotopic specialization and corresponding encoding for optic flow. An exhaustive effort to clarify these findings (Chen *et al.*, 2021) by combining multiple measurement modalities, visual stimuli, behavioral states and sampling large regions of the retinotopic map found no evidence of correlated spatial location and motion direction encoding in mouse SC. Characterizing species-specific patterns of self-motion (Carriot *et al.*, 2017; Bigge *et al.*, 2021) or experienced optic flow would help to resolve whether positional regularities in direction of motion produced by optic-flow are represented in the visual system (Sabbah *et al.*, 2017). Recording neural activity across multiple regions of freely behaving animals will further help to determine specializations related to visual processing in the context of bodily movement.

Complex retinotopic transforms highlight location-dependent feature sensitivity. We have shown that within individual visual areas, functional feature sensitivity exhibits location-dependence in a manner that reflects efficient representation of positional regularities in visual input. In this view, there is no a priori reason why all visual areas should exhibit complete topographic representations of retinal location that preserves the planar layout of the retina. Instead, the coverage and geometry of retinotopic maps is inherently related to the functional feature encoding within a visual area. Here we review recent discoveries of retinotopic maps that deviate from conventional topographic representation of retinal location and highlight the ubiquitous location-dependent feature sensitivity in the visual system.

The conventional description of retinotopic maps is a point-to-point relationship with the retina that preserves the overall layout of the retinal image, albeit with certain deformations and exaggerations (Figure 3A). In V1 of all studied animals, retinotopic maps are simple in that they preserve the orthogonal axes of the retina. As in tree shrew V1 (Figure 3C), the azimuth or central-peripheral axis of the retina is usually mapped along the medial/lateral axis of the brain, and the orthogonal elevation axis is mapped along the orthogonal anterior/posterior cortical axis. Deviations from the conformal mapping in V1 were noted in higher visual areas of primates and cats but were often discussed in terms of a ‘discontinuity’ within an otherwise conformal map of the visual field. Our recent study (Sedigh-Sarvestani *et al.*, 2021) of the tree shrew visual system showed that retinotopic maps can exhibit all-together different transformations of the visual field that do not preserve the two-dimensional spatial layout of the retina. A recent study (Yu *et al.*, 2020) in the ‘third tier’ visual cortex of primates also reported a non-conformal map, although the particular retinotopic transform was different from our observations in tree shrew V2.

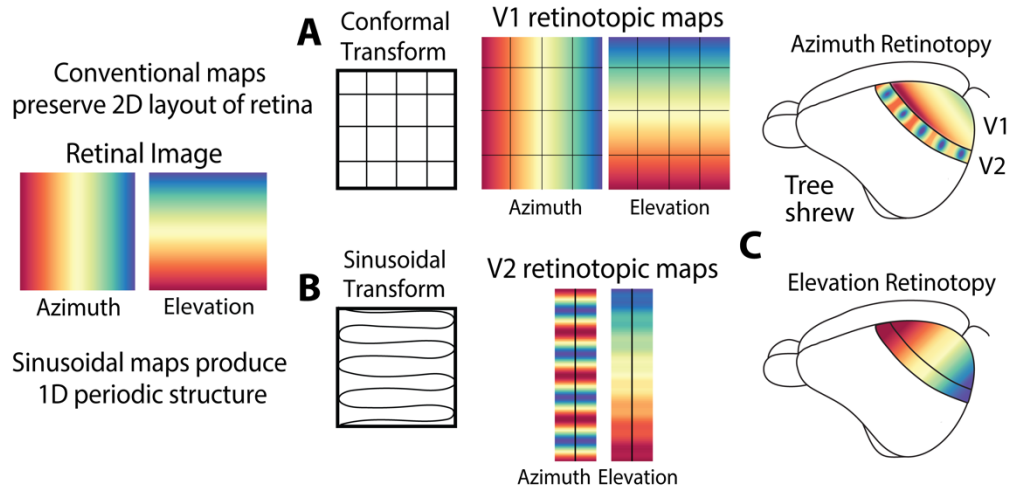


Figure 3: Retinotopic maps in the cortex can exhibit complex patterns that do not maintain the topographic layout of the retina. A) Maps of retinotopic spatial location in V1 of most animals, including tree shrews, exhibits a conformal transform that preserves 2D layout of the retina including the orthogonal relationship between azimuth and elevation. B) V2 of tree shrews exhibits a sinusoidal retinotopic transform that combines azimuth and elevation to produce a periodic structure. C) Azimuth and elevation retinotopic maps in tree shrew V1 and V2.

Unlike the conventional retinotopy in V1 of many species, the retinotopic transform in tree shrew V2 can be described as a sinusoidal transform (Figure 3C) that converts the 2D planar layout of the retina to a roughly 1D periodic structure. This transform combines elevation and azimuth by mapping them onto the same elongated axis of V2, no longer preserving their global orthogonal relationship. This produces a simple map of elevation and a periodic map of azimuth, with both maps along the length of V2.

The periodic map of retinal location oscillates between representations of the most central regions of the visual field with representation of paracentral regions separated by 10-15 visual degrees. This representation is tightly linked to enhanced sensitivity for binocularity and retinal disparity, small changes in the retinal image viewed by the two eyes that can be used to discriminate distance and depth (Figure 2C). This suggests that enhanced binocularity and disparity sensitivity are specialized for the most central regions of the visual field. Furthermore, the representation of this region of the visual field has enhanced interhemispheric connectivity. The correlated periodic pattern in visual field location and feature sensitivity is also reflected in the pattern of callosal terminals, cross-hemispheric projections which carry information about the most central regions of the visual field. Thus, the most central region of visual space specialized with enhanced binocular sensitivity also features enhanced interhemispheric connectivity, which may ensure coherence of bilateral responses in this region of visual space.

Therefore, the structured visual input produced by the position of the eyes in the head, as well as the interhemispheric connectivity, are consistent with the enhanced representation of binocular features in the the most central regions of the visual. However, as discussed in the previous sections (Figure 1), such location-dependent encoding can arise due to several other underlying factors. A remarkably similar pattern has been observed (Manger *et al.*, 2002) in secondary areas of the ferret visual cortex (Figure 4B) where the sensitivity to retinotopic location and connectivity with the opposite hemisphere vary in a periodic fashion. Future experiments will determine whether functional feature sensitivity varies in a periodic manner tightly connected to retinotopy in ferret secondary visual areas, as it does in the tree shrew (Manger *et al.*, 2002; Rosa and Manger, 2005a; Sedigh-Sarvestani *et al.*, 2021).

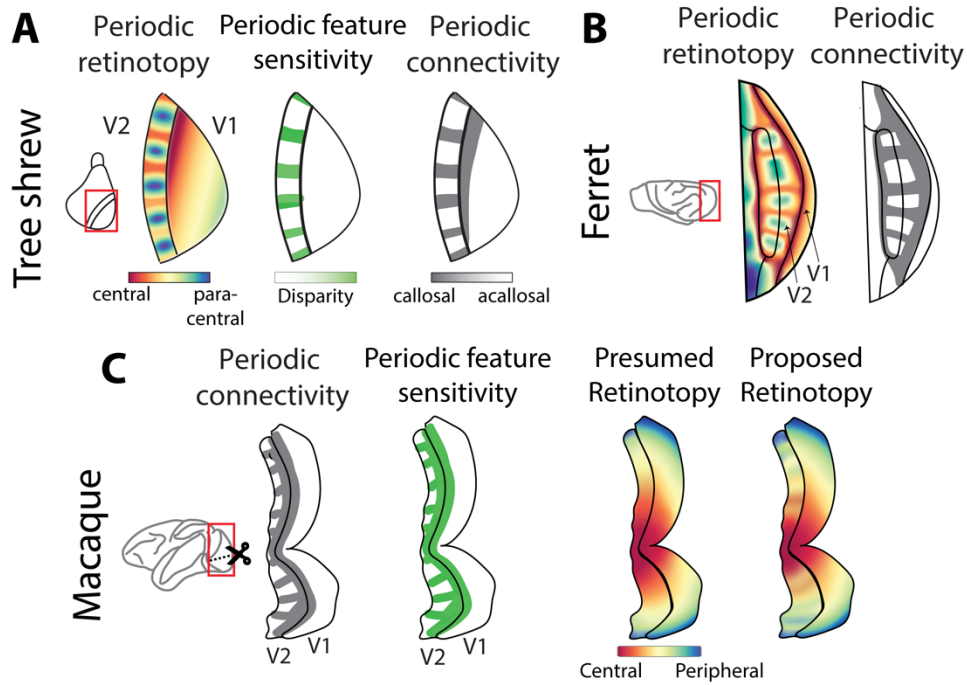


Figure 4: Complex retinotopy highlights location-dependent feature sensitivity across species. A) The complex retinotopy map in tree shrew V2 highlights the joint distribution of spatial location, disparity sensitivity, and anatomical connectivity. Regions of V2 that are sensitive to the most central regions of the binocular visual field are also sensitive to retinal disparity cues and receive callosal inputs which carry information from V1 of the opposite hemisphere (Sedigh-Sarvestani *et al.*, 2021). **B)** A similar periodic retinotopy, with corresponding periodic pattern of callosal inputs, has been observed in ferret V2 (Manger *et al.*, 2002; Rosa and Manger, 2005a). **C)** Periodic patterns of feature sensitivity, including retinal disparity, are well known in macaque V2 (Hubel and Livingstone, 1987; Hubel *et al.*, 2015; Lu, Haidong D., 2015). Callosal projections exhibit a corresponding periodicity (Olavarria and Abel, 1996), suggesting that retinotopic sensitivity may also exhibit a periodic pattern similar to that in tree shrews or ferrets. Further work is needed to test this hypothesis.

A similar periodic functional feature map exists in primate V2 (Figure 4C), where the sensitivity to binocularity, disparity, and several other features including color change in a periodic manner along the length of this region. However, it is not clear whether this functional encoding is correlated with an underlying retinotopic periodicity, although electrode recordings support the existence of periodic retinotopy at the local scale. Furthermore, since callosal projections consistently terminate near the representation of the vertical meridian, the presence of periodic bands of callosal terminals in V2/V3 of multiple species suggests a common retinotopic transform similar to that in tree shrews and ferrets (Rosa and Manger, 2005b). Although the retinotopic map in V2 is described as a conformal transform with local deviations, our prediction of periodic retinotopy in V2 is consistent with both the periodic callosal terminations in V2 and the periodic representation of visual features including disparity sensitivity (Figure 2D) and binocularity (Kaskan *et al.*, 2009). This prediction can be tested with high-resolution retinotopic mapping of V2 in small smooth-brained primates such as the marmoset.

In both tree shrews and ferrets, locations along the two axes of the retina are mapped differently. While the central-peripheral or azimuth axis is mapped in a periodic fashion, the elevation axis is mapped in the conventional smooth manner. Future work may reveal a functionally significant rationale for this mapping. Alternatively, it may be a trivial consequence of a periodic transform (Figure 3B) optimized for enhanced representation of the central visual field. More broadly, flexibility in the geometry of the

retinotopic map may enable the representation of visual information in the most functionally relevant regions of the visual field. Conversely, if parts of the visual field, or one of its two axes, are not utilized in the functional role of a brain area, the retinotopic map should reflect a correspondingly limited representation. This is the case in regions of the inferotemporal (IT) cortex involved in face recognition, where the central visual field where faces most often appear is over-represented, but there is no organized representation of the orthogonal axis of the visual field (Janssens *et al.*, 2014).

Parallel stream organization reveals species-specific joint encoding of location and feature across the entire visual system. We have discussed evidence for joint representation of retinotopic location and functional features in individual visual areas (Figure 1-4). Here we provide evidence for joint encoding of location and features across the entire visual system. The dorsal and ventral parallel streams (Figure 5) are considered the fundamental organizing scheme of the primate (Schneider, 1969; Mishkin and Ungerleider, 1982), and more recently the rodent (Wang, Gao and Burkhalter, 2011; Glickfeld and Olsen, 2017; Bennett *et al.*, 2019), visual system. Each stream is composed of multiple visual areas and is distinguished based on several factors including sensitivity to functional features, anatomical connectivity with visual and non-visual areas, and contribution to visuo-motor behaviors. We show that the parallel streams also exhibit distinct retinotopic location biases consistent with the putative functional roles attributed to each stream. Furthermore, we show that the location bias differs among species, with rodents exhibiting functional biases along the upper and lower visual field and primates exhibiting biases more pronounced along the central-peripheral visual field (Figure 5).

The study of parallel streams originated in the primate visual system with a focus on functional, not retinotopic, sensitivities. However, published data supports a central visual field bias in the primate ventral stream (Figure 5A) and more even coverage of the visual field in the dorsal stream (Yu, Chaplin and Rosa, 2015; Shetht and Young, 2016). In contrast to rodents, primate higher visual areas generally have coverage over large portions of the visual field. However, many areas exhibit a biased representation that emphasizes certain regions relative to others (Figure 5A). For instance, the ventral area V4 implicated in color processing emphasizes the central 30-40 degrees but appears to lack a representation of the far periphery (Gattass, Sousa and Gross, 1988). Neurons in IT, another area in the ventral stream tied to object and face recognition, have large receptive fields that nonetheless prefer stimuli near the fovea (Gomez *et al.*, 2018). In contrast, there is reduced emphasis on central regions in dorsal stream areas such as area MT (Rosa and Elston, 1998). Thus, the functionally distinct parallel streams of the primate visual system appear to exhibit distinct retinotopic biases consistent with their functional sensitivities.

The parallel streams in the mouse visual cortex have been largely defined by anatomical features, and seem to lack overt differences in their functional feature sensitivity, at least when compared to primates. Nonetheless, there is some evidence of developmental differences (Smith *et al.*, 2017) between areas in the dorsal and ventral stream suggesting potential functional distinctions that have yet to be discovered. Despite the lack of current evidence for robust distinction in feature sensitivity, the mouse dorsal and ventral streams exhibit clear and pronounced retinotopic bias (Figure 5B). Areas in the dorsal stream collectively tile the lower visual field whereas areas in the ventral stream tile the upper visual field. This retinotopic bias is consistent with the joint encoding of spatial location and functional features in visual areas of the mouse (Figure 2A-B), which largely occur along the elevation axis.

Therefore, retinotopic separation of functionally distinct visual circuits appears to be the major organizational scheme of the visual system of both primates and rodents.

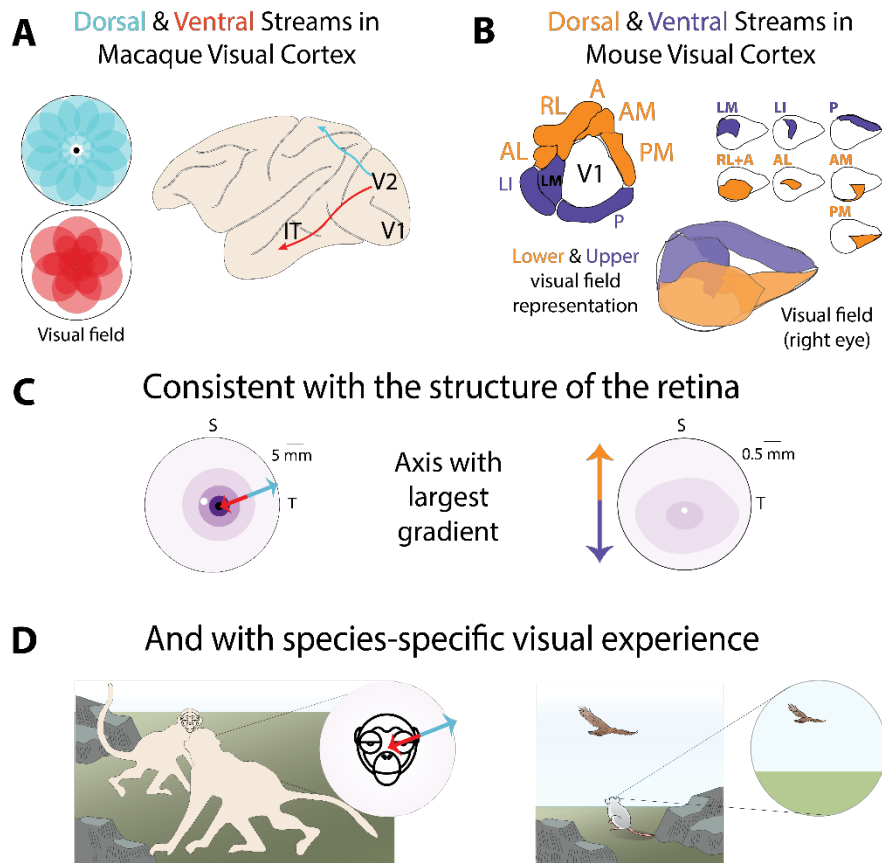


Figure 5: Parallel stream organization reveals species-specific joint encoding of location and features across the entire visual system. **A)** The macaque functional parallel streams exhibit distinct biases along the central-peripheral axis of the visual field (Yu, Chaplin and Rosa, 2015; Sheth and Young, 2016). **B)** The mouse functional parallel streams exhibit distinct biases along the elevation axis of the visual field (Garrett et al., 2014; Zhuang et al., 2017). **C)** Topographical distribution of RGCs in the macaque and mouse retina exhibit their largest variance along different axes (Heukamp, Warwick and Rivlin-Etzion, 2020b). Darker colors indicate higher density. White dots are optic disc. **D)** The visual behaviors of macaques and mice are broadly consistent with distinct functional relevance of central-peripheral or upper-lower visual fields. Panel D modified with permission from ©2021 Dina Popovkina.

But why does the main axis of this joint location-feature encoding differ between species? First, it reflects the main axis of change in the topographical distribution of RGCs in the retina (Figure 5C). Whereas the foveal specialization in macaques exhibits a gradient largely along the central-peripheral axis, the RGC distribution in the mouse retina has a larger deviation along the elevation axis. More importantly, these axes in the retina and cortex are consistent with the visual environment and behaviors of each animal (Figure 5D). The egocentric visual world of a ground-dwelling prey animal contains distinct functionally relevant information, environmental statistics (Y *et al.*, 2021), and distance to objects (La Chioma, Bonhoeffer and Hübener, 2019), compared to the upper visual field. On the other hand, the egocentric visual world of the upstanding and social primate contains detailed cues relevant

for social communication and order. Therefore, the organization of the visual system of each species reflects the geometry and positional regularities of their behaviorally relevant visual experience.

Implications for future studies of the visual system. The evidence highlighted so far demonstrates a new framework for the organization of the visual system where information about spatial location and functional features are jointly encoded throughout the visual system, in a manner that reflects the specific visual experience of different species. In this view, the geometric distribution of functionally relevant information in the egocentric visual field shapes sensory encoding in the retina and throughout the visual system. A major implication is that our understanding of the structure and function of the visual system is constrained by our understanding of the structural and functional properties of the retina in the context of species-specific visual experience. In the past two decades, several groups have contributed to a growing understanding of the properties of the mouse retina, how these properties reflect the visual experience of mice, and how functionally relevant retinal sampling is communicated to the rest of the visual system. Similar knowledge in other model organisms used in systems-level visual neuroscience pales in comparison. This is partially due to the suite of genetic tools available in mice, but it also reflects a prevailing assumption that functionally simple visual inputs gain complexity only through discrete transitions across each area of the visual cortical hierarchy. Our framework dispels this notion and suggests instead that visual information is already functionally specific at the retinal stage and gains further complexity not only across hierarchical areas but also within each area. Consequently, we believe there is an immediate need for outside-in characterization of the visual experience and retinal properties of tree shrews, ferrets, cats, primates, and other model organisms used in vision research.

Specifically, additional research is needed to determine the role of internal and externally driven visual experience in development of retinal specializations. In this review we suggest that retinal specializations, such as topographic biases in the density of specific functional classes of RGC cells, are specific to and consistent with the visual experience of animals. However, we do not actually know if visual experience plays any causal role in the formation of retinal specializations in mice or in any other species. A further complication is spontaneously generated ‘visual experience’. Even before the onset of visual experience during development, activity in different locations of the retina exhibits distinct properties due to the presence of spatiotemporally structured spontaneous activity referred to as ‘retinal waves’. It has been suggested (Pratt, Hiramoto and Cline, 2016; Ge *et al.*, 2021) that retinal waves act as a simulacrum of future structured visual experience and serve to scaffold optimal visual circuitry. Cross-species measurement and manipulation of retinal waves will produce further insight into the causal role of this source of early activity in the species-specific organization of the visual system.

A second implication is that retinotopic maps can and should be utilized to elucidate the functional properties of visual areas. Most circuit-level studies of the visual system utilize retinotopic measurements primarily for practical matters such as delineating area borders or determining regions of interest for neural recording. However, the retinotopic map itself is rarely considered in attempts to decipher neural computation. Furthermore, many studies report neural encoding in a limited part of the retinotopic representation of a visual area. This practice is problematic in light of retinotopic specializations that exhibit distinct functional encoding, structural connectivity, anatomical, and molecular properties across the retinotopic map of the same visual area. A poor understanding of the retinotopic map, or reliance on measurements from only a single region of the map, could mask potential specializations and produce conflicting reports attributed to a particular cortical region.

Furthermore, even at scales far smaller than an entire visual area, neural encoding for location and features need to be studied together since there is no way to untangle their inherent joint processing in the brain. For instance, the visual signal received by subcortical and cortical areas will contain correlated information about spatial location and functional features due to non-uniform retinal sampling, even when the externally controlled visual input has uniform features at all locations of the display monitor.

Conclusion: In summary, we have presented evidence for location-dependent feature sensitivity as an organizing principle of the entire visual system. This joint encoding framework contrasts with prevailing views that distinguish between information related to the location ('where') and identity ('what') of objects in the visual field. Instead, it suggests that these properties are encoded together by the same neuronal circuits, reflecting their inseparable existence in the visual field. We suggest that this principle reflects the evolutionary selection of sensory and motor circuits to optimally represent behaviorally relevant information suited to an animal's unique sensory-motor demands. Future studies are necessary to discover mechanisms underlying joint encoding of location and functional information, how this relates to behavior, emerges during development, and varies across species.

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