Symposium

Development of Higher-Level Vision: A Network Perspective

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Most studies on the development of the visual system have focused on the mechanisms shaping early visual stages up to the level of primary visual cortex (V1). Much less is known about the development of the stages after V1 that handle the higher visual functions fundamental to everyday life. The standard model for the maturation of these areas is that it occurs sequentially, according to the positions of areas in the adult hierarchy. Yet, the existing literature reviewed here paints a different picture, one in which the adult configuration emerges through a sequence of unique network configurations that are not mere partial versions of the adult hierarchy. In addition to studying higher visual development per se to fill major gaps in knowledge, it will be crucial to adopt a network-level perspective in future investigations to unravel normal developmental mechanisms, identify vulnerabilities to developmental disorders, and eventually devise treatments for these disorders.

Introduction

Vision is a key sense for our interactions with the world, and higher visual functions—such as object recognition and spatial vision—are an important reason why. These functions rely on the processing power of the full visual system from retina to the highest visual stages (and beyond), with its feedforward and feedback connectivity that links areas within and across pathways. Many of these components are immature at birth across species, and their development is shaped by complex interactions between genetic cues, spontaneous activity patterns, and visual experience (see below for details and references). The outcome of these processes can have fundamental consequences for everyday life. Research to date provides a detailed characterization of the development of the initial stages of the visual system, from the retina to primary visual cortex (V1). Much less is known about the development of the higher stages of the visual hierarchy, especially at the neural level. The existing data, however, show a gradual, protracted emergence of the different higher visual functions.

It would be tempting to capture this phase of development as a bottom-up emergence of the visual hierarchy, a feedforward sweep in which one visual area after the next comes online according to their position in the hierarchy (see Fig. 1*A* for an illustration of this idea). In this view, the development of V1 would represent a major bottleneck, and higher areas would add on to an existing network by refining their inputs and internal circuity (without significant adjustments in preceding stages). While this model is appealing because of its simplicity, it still needs to accurately describe visual cortex development based on the currently available data. These data show that in addition to general differences in the developmental timelines of the dorsal and ventral stream, areas can develop "out of order", earlier than predicted by a strictly feedforward sequence (again, see below for details and references). Further factoring in developmental changes in connectivity between areas and in each area's cell type composition, it is much more accurate to think of the visual system's development as a sequence of unique networks, rather than partial, gradually more complete, versions of the adult hierarchy (Fig. 1*B*). Consequently, deriving accurate models of visual development will require studying development not just area by area, but at the network level. Adopting this more global, network-level perspective also promises to deliver novel, important insights into the causes and effects of developmental disorders. In this review, we will support these ideas by discussing recent findings and open questions regarding the development of

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higher-level vision. We will conclude by highlighting opportunities for future research, partly enabled by advances in tools and the inclusion of a diverse set of model systems. Throughout the review, we have limited our discussion to work performed in nonhuman primates, humans, and carnivores. Research in rodents has led to fundamental insights into developmental processes, such as the identification of factors responsible for the opening and closing of the critical period for ocular dominance (Crowley and Katz, 2002; Hensch, 2005; Sale et al., 2010). At the same time, we currently know most about higher visual areas and their functions in nonhuman primates and primates, followed by carnivores. Additionally, the organization of higher visual areas share significant similarities in these species, so that results can be compared across them. Since the focus of this review is on the development of higher visual functions, we have restricted its scope in terms of species accordingly. However, it should be noted that recent studies investigating the development of higher visual areas in the mouse similarly point to the importance of a network-level approach, e.g., by demonstrating that changes in ocular dominance in these higher areas are not simply inherited from V1 (Craddock et al., 2023) and that higher areas show systematic differences in their developmental time courses (I. T. Smith et al., 2017).

Development of the Visual Hierarchy: Anatomy

The hierarchical theory of cortical development posits that basic functional properties and anatomical circuits mature before more complex, downstream ones. This concept dates back to early studies by Flechsig (1901) on human brain myelination, which showed a progression from primary sensory areas to association cortices. Recent research provides a much more nuanced view at least for the development of the marmoset's visual system (Bourne and Rosa, 2006; Mundinano et al., 2015). These studies demonstrate a sequential development of visual areas, with a systematic relationship between cortical hierarchy and maturational timing. However, ventral stream development lags behind that of the dorsal stream. Thus, dorsal and ventral stream areas that occupy similar hierarchical levels in the adult brain will be at different developmental states in immature brains, a fundamentally different network configuration.

An equally important observation that emerges from these studies is that dorsal stream area MT, in adults considered a higher order motion area, develops as early as V1 and before V1-adjacent areas (Flechsig, 1901; Condé et al., 1996; Bourne and Rosa, 2006; Warner et al., 2012; Mundinano et al., 2015). This has motivated the "molecular anchors" theory, which proposes that V1 and MT are the primary nodes for the subsequent

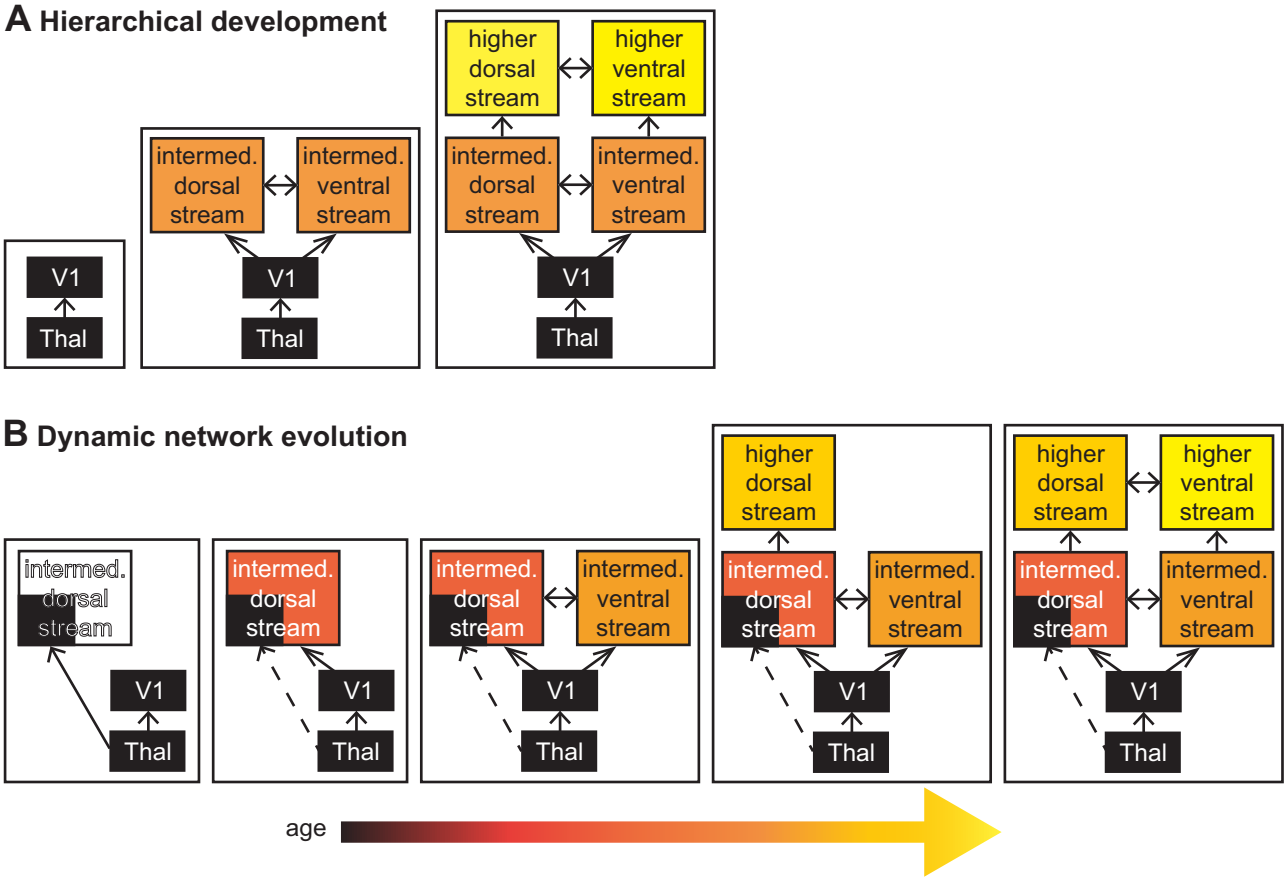

Figure 1. Schematic overview over the two developmental models contrasted in the review. ***A***, In the hierarchical development model, the adult network slowly emerges from lower to higher stages in a feedforward sweep. Areas of the same hierarchical level develop at the same time, as "add-on" to the existing hierarchy, so that at each age the network essentially resembles a partial version of the adult network. In this model, V1 would be a major bottleneck for the development of the entire system. ***B***, In the dynamic network model, the visual system instead steps through a sequence of unique networks that are not partial versions of the adult network but can differ in fundamental ways. Connectivity at young ages does not necessarily match the adult, and areas that ultimately occupy similar hierarchical levels develop at different times. In the model, alternative starting points for development exist beyond V1. Note that for clarity only the network components most relevant for the review are shown in this summary (Thal: thalamus, both first- and second-order nuclei. The dashed versus solid line in ***B*** indicates a change in strength of a connection).

ventral (occipitotemporal) and dorsal (occipitoparietal) stream development, respectively (Bourne and Rosa, 2006). Indeed, marmosets who received a MT lesion early in life showed lasting goal-orientated reach and grasp behavior deficits and changes in the cytoarchitecture throughout dorsal stream areas (Kwan et al., 2021). V1 direction selectivity was also impacted, meaning developmental lesion effects can spread to earlier areas (at least when referencing the hierarchical positions in adult brains).

In adults, V1 is thought to seed processing in both streams. This picture obviously needs to be revised with respect to development to incorporate the early maturation of MT and its possible role as a primary area. This is even more important as differences in network configuration between immature and mature brains extend beyond the relative role of V1 and MT. In adult marmosets, the medial portion of the inferior pulvinar (PIm) relays retinal input directly to MT (Warner et al., 2010; Kwan et al., 2019), in addition to other inputs arising from areas such as the lateral geniculate nucleus (LGN) and V1 (Sincich et al., 2004; Nassi and Callaway, 2006; Warner et al., 2012). Intriguingly, the MT input originating in PIm is more dominant in early postnatal life and is pruned once MT receives direct input from V1 (Warner et al., 2012). A series of lesion studies confirms the importance of this transient input: Early-life ablation of V1, before the direct V1-MT projection is established (Warner et al., 2015), results in a sustained increase in the retina-pulvinar-MT pathway and continued maturation of MT and adjacent cortices into adulthood. On the contrary, early-life lesions of PIm result in deficits in the anatomical maturation of MT and interconnected regions (Mundinano et al., 2018). Thus, the pulvinar may serve as a crucial developmental scaffold for extrastriate areas like MT, underscoring the importance of considering multiple pathways of influence in cortical development, even those that may appear to be weak in adults.

In general, combining data from multiple anatomical markers (e.g., different calcium-binding proteins) reveals that developmental profiles can be quite heterogeneous across areas, likely necessary for correct circuit establishment (Elston, 2002; Oga et al., 2013; Elston and Fujita, 2014). Some evidence is clearly consistent with the hypothesis of a sequential development: In primates, feedforward pathways mature earlier, often prenatally, while feedback pathways undergo extensive remodeling postnatally (Barone et al., 1995; Batardiere et al., 1998). Other data, however, is not consistent with this hypothesis, such as the observation that synaptogenesis and pruning can occur concurrently in cortical regions distributed throughout the brain (Rakic et al., 1986), including in visual areas at different hierarchy levels (Mundinano et al., 2015). These findings suggest that the maturation of the visual system involves a complex interplay of sequential and concurrent processes. Fully capturing these mechanisms will require further detailed, systematic comparisons of the relative timelines of different areas, combined with quantifying inter- and intra-areal connectivity patterns as a function of age.

Development of the Visual Hierarchy: Function

At least based on behavioral metrics, visual functions largely develop from simple to complex, with behavioral functions such as global motion sensitivity and contour integration showing a more protracted developmental timeline than orientation discrimination or contrast sensitivity (for a recent review, see Kiorpes, 2016). This might suggest that the higher areas responsible for these functions develop more slowly than lower stages. The behavioral data also point to differences between dorsal and ventral stream consistent with the anatomical findings discussed above, as sensitivity to global motion can be detected earlier than sensitivity to global form (Braddick et al., 2003; Kiorpes et al., 2012).

Unfortunately, supporting functional data, especially recordings of neural tuning functions across areas and ages, remain sparse. Still, the available studies suggest a picture as complex and dynamic as the one emerging from the anatomical data. Remarkably, functional neuroimaging (fMRI) studies have demonstrated adult-like organization of lower visual areas V1–V3 as early as 4 months in human infants (Ellis et al., 2021) and in neonatal monkeys (M. J. Arcaro and Livingstone, 2017). This includes the observation that a retinotopic, hierarchical organization of visual cortex is present at birth and distinguishes dorsal and ventral visual pathways in neonate macaques (M. J. Arcaro and Livingstone, 2017), along with a third, lateral, pathway in neonate humans (M. Arcaro, 2023). In contrast, higher-order areas in both the ventral and dorsal stream remain immature for several months (Distler et al., 1996; Grootel et al., 2017). For example, in both humans (Deen et al., 2017; Kosakowski et al., 2022, 2024) and macaques (Rodman et al., 1993; Livingstone et al., 2017), face selectivity in ventral visual cortex emerge within the first several months postnatally and, in humans, have been shown to mature throughout adolescence (Golarai et al., 2007).

All of the above studies indicate that functions develop sequentially according to the visual hierarchy. There is also evidence that functions develop from simple to complex, at least within the same area: For example, in ferret PMLS (a higher visual motion area similar to primate MT; Lempel and Nielsen, 2019), global motion integration develops after basic direction selectivity has matured. Motion integration also shows a protracted development occurring over weeks in primate MT (Kiorpes and Movshon, 2014). Similarly, surround interactions develop in V2 after responses to stimuli at the center of the receptive field (Zhang et al., 2005).

However, not all data conform with the sequential model. Instead, at the minimum, they again point to an early emergence of MT. Recent fMRI studies, e.g., show that the major cortical areas serving motion processing in adults are operative by 5 weeks of age (Biagi et al., 2015, 2023). Specifically, the MT complex and other motion associative areas, like V6 and PIVC, show strong selectivity to flow motion as in adults, despite an underdeveloped and poorly responsive V1 and immature functional connectivity between V1 and motion associative areas (Biagi et al., 2015, 2023). Perhaps most surprising is the evidence that young infants may integrate visual motion with vestibular information, a circuit that in adults subserves the sense of vection. Yet, it should be noted that sensitivity for motion coherence continues to mature gradually over the first year in humans (Wattam-Bell et al., 2010; Blumenthal et al., 2013), attaining adult levels after 10 years of life for very fine displacements (Meier and Giaschi, 2017). Consequently, despite the differences in onset, there is strong overlap in the development of global form sensitivity and global motion sensitivity (Braddick et al., 2003; Kiorpes et al., 2012).

These overlapping developmental time windows mean that the impact of cross-talk between higher and lower areas and between both streams needs to be seriously considered in developmental models, not just the feedforward propagation of maturation. There are other examples that support this claim: Direction selectivity develops during the same time window in V1 and PMLS in ferrets and cats, for example (Price et al., 1988; Lempel and Nielsen, 2021). In monkeys, the maturation

of center/surround interactions, and temporal frequency tuning, occurs during overlapping time windows in V1 and V2 (Zhang et al., 2005; Zheng et al., 2007). Finally, direct evidence for the impact of higher areas on lower ones comes from the ferret, in which the development of motion integration in PMLS comes with a transient increase in motion integration in V1 due to PMLS feedback (Lempel and Nielsen, 2021). Thus, as for the anatomical data, both concurrent and sequential processes—across areas and across streams—need to be considered in generating models for functional development. Crucially, deriving these models will require substantial additional neural data across species, ages and areas.

Role of Visual Experience in Shaping Development of Higher Visual Cortex

A fundamental question regarding the development of any part of the nervous system is to what degree it is intrinsically specified and follows a predetermined program, versus responsive to the impact of external cues such as the available visual experience. The latter covers both cases in which the input plays a permissive or an instructive role, i.e., cases in which it is required to drive sufficient activity levels, or directly molds the maturing circuits. As mentioned above, primate extrastriate cortex is organized into a series of topographic maps at birth. The persistence of retinotopic organization in congenitally blind humans (Butt et al., 2013; Striem-Amit et al., 2015) and in monkeys reared without form vision (M. Arcaro et al., 2018) further attests that visual input is not required for the formation of these maps. Combined with the remarkable consistency in the number and relative positioning of extrastriate areas across individuals within a species (at least for the species discussed here), this raises the intriguing question whether extrastriate areas are genetically predetermined like the primary cortical areas (Rakic, 1988). Recent computational modeling employing activity-based self-organizing dynamics that encourage the clustering of inputs with similar activity patterns can generate mirror-symmetric maps akin to extrastriate cortex (Imam and Finlay, 2020) when anchored to the map of primary cortex (Rosa, 2002). These data suggest that the formation of extrastriate areas could emerge from general principles of neural organization rather than genetic predetermination.

Some clustering of functionally similar inputs within extrastriate cortex begins to take shape prior to substantial experience, with the internal organization of primate V2, including thick and thin stripes, forming late in gestation (Coogan and Van Essen, 1996). The extent to which such clustering is established prenatally in higher visual areas in primates, such as V4, still needs to be determined. However, clustering of face selectivity, a prominent feature of adult inferotemporal cortex (IT), requires visual experience to form (M. J. Arcaro et al., 2017, see also below). Interestingly, anatomical connectivity (Saygin et al., 2016; Cabral et al., 2022) and cortical morphology (M. J. Arcaro et al., 2020) present in neonates predict where such category-selective visual clusters develop later. One possible explanation is that the clustering of functionally similar inputs is heavily constrained by the intrinsic architecture of visual cortex (M. J. Arcaro and Livingstone, 2021). The topographic representation of visual space would then effectively function as a fundamental organizing principle that scaffolds the subsequent development of visual cortex, by guiding the sampling from the environment to allow for efficient adaptation to the specific visual statistics encountered.

Indeed, although much of the architecture of visual cortex is established prior to substantial experience with the external world, the environment plays a crucial role in shaping visual circuits, demonstrating the potential for plasticity of intrinsic developmental programs and the resulting architecture. In extrastriate cortex, visual experience has been found to impact tuning functions ranging from simple to complex. Strobe rearing, for example, results in a loss of basic direction selectivity in cat PMLS (Spear et al., 1985). For complex motion functions, the amount of visual experience (measured in days since eye opening) is correlated with the developmental state of motion integration in ferret PMLS (Lempel and Nielsen, 2021). Dark rearing cats impairs perceptual motion integration thresholds (Mitchell et al., 2009), and humans with bilateral cataracts early in life have impaired global motion vision (Ellemberg et al., 2002). Amblyopia—caused by severe mismatch of input from the two eyes during a critical period of development—also impacts the processing of global motion in humans (Hamm et al., 2014) and monkeys (Kiorpes et al., 2006; El-Shamayleh et al., 2010). Importantly, MT responses to global motion stimuli show matching deficits in amblyopic monkeys (El-Shamayleh et al., 2010). The impact of visual experience on higher visual development is not limited to motion vision. Appropriate visual experience is required for face- (M. J. Arcaro et al., 2017) and word-selective (Dehaene-Lambertz et al., 2018) clusters to emerge in ventral visual cortex, and amblyopia causes deficits in global form perception (Kozma and Kiorpes, 2003; Hamm et al., 2014). These findings suggest that higher visual functions are sensitive to visual experience. How much of the effects can be explained by alterations in V1 "propagating up" and causing deficits downstream, versus selective impacts on higher visual circuits themselves, is an important question for future research, one that needs to be resolved to identify efficient treatments for conditions like amblyopia.

Developmental Disorders and Higher-Level Vision

A thorough understanding of the dynamic evolution of the visual hierarchy will also be paramount for identifying the causes underlying developmental vision disorders. Intriguingly, motion vision appears to be impacted by developmental disorders at perinatal ages much stronger than form vision, leading to the hypothesis of a particular vulnerability of the dorsal stream (reviewed in Atkinson, 2017). Considering the earlier development of dorsal versus ventral stream discussed above, a possible explanation might be that areas developing early are at higher risk for developmental disorders. It should be noted that ventral stream functions can also be impacted by developmental disorders, e.g., Williams syndrome and autism (Golarai et al., 2006; Landau et al., 2006; Braddick and Atkinson, 2011), in conjunction with abnormal or delayed dorsal pathway development (Atkinson et al., 1997, 2006).

One example of the vulnerability of the dorsal stream is the observation that premature and very low weight babies have consistent deficits in visual motion perception (MacKay et al., 2005; Birtles et al., 2007; Weinstein et al., 2010) but not in ventral stream functions (Atkinson, 2017). In preterms, hypoxic-ischemic damage of the periventricular (PVL) white matter causes lesions, usually occurring at the beginning of the third trimester of gestation (Volpe, 2001) and typically affecting the dorsal pathways (Guzzetta et al., 2009), but also the ventral pathways in a subset of subjects (Perez-Roche et al., 2017; Castaldi et al., 2018). The motion deficit is present in all preterm children, regardless of brain lesions. Interestingly, not all motion perception properties are equally affected in PVL, and some patients have paradoxical and very specific abnormal perception. For example, Morrone et al.

(2008) observed PVL children with normal contrast sensitivity to motion, normal rotational or expansional motion coherence thresholds, but consistently reporting the opposite direction of translating motion. fMRI in these PVL children showed abnormal responses in the MT complex, suggesting malfunction of some basic mechanism of motion processing. Again, taking into account the very early development of MT, this malfunction may be a consequence of fast developmental processes that are sensitive to damage early in life and/or do not allow for the establishment of compensatory circuity in the critical period window. At the same time, the effects of PVL lesions cannot be purely explained by the effects on MT, as the motion deficits correlate well with V1 thickness, but not with MT thickness (Bhat et al., 2021). It seems likely that the complex interplay of sequential and concurrent developmental processes discussed above results in a change in V1 input to MT, which in turn limits motion coherence sensitivity attainable in adulthood.

Identifying the mechanisms underlying developmental disorders will generally require knowledge of age-dependent changes in circuit configuration. In a subject with neonatal unilateral resection of the optic radiation, e.g., no major visual deficits occurred despite the large V1 deafferentation (Mikellidou et al., 2019). One possible explanation is an early, strong, and direct thalamic projection to MT, as discussed above, which becomes stabilized after V1 lesions and could provide a V1 bypass. Indeed, the same subject showed massive reorganization of the visual circuits in the damaged hemisphere. Interestingly, the reorganized circuits could support good form vision, but motion perception was impaired, as if MT function was altered (possibly in support of other functions). A similar observation was made in a patient with a congenital lesion involving the complete thalamus in one hemisphere (Bhat et al., 2022). Despite the lesion, the subject had nearly complete vision, but reduced motion sensitivity, suggesting again that rerouting vision through MT comes at a cost in functionality. In summary, as these examples highlight, identification not just of sources of vulnerability, but also of sources of plasticity, will require studying visual development at the network level.

Opportunities: Tools and Data Sets

The sections above highlight the conceptual advances to be made by studying the development of higher-level vision with a particular focus on the network level. Several recently developed tools offer exciting opportunities in this context, a few of which will be highlighted below. First, animal experiments will continue to be fundamental for resolving the mechanisms guiding neural circuit development, using the kinds of neural recordings and manipulations only possible in animals. In terms of manipulations, the use of optogenetics (Deisseroth, 2015) and designer receptors exclusively activated by designer drugs (DREADDs, K. S. Smith et al., 2016) continue to hold great promise because they enable precise circuit manipulations. In terms of neural recordings, exciting new opportunities for developmental research arise from techniques that enable massively parallel sampling of large populations of neurons, ideally over longer periods of time, like acute or chronic Neuropixels (Juavinett et al., 2019; Steinmetz et al., 2021; Bimbard et al., 2024) or flexible polymer probes (Zhao et al., 2023). Similarly, the advent of large-scale, rapid sequencing tools promises to provide a much more nuanced understanding of the developmental timeline of different circuit elements in different areas (see Özel et al., 2021, for a recent application of this idea in the developing fly brain).

Second, there currently is a severe lack of data—especially pronounced for the youngest age groups—on human brain development using approaches with high spatial resolution like fMRI. A major bottleneck in addressing this issue are the practical difficulties encountered when trying to characterize developing neural representations. Experiments in young participants are often by necessity short, and the data collected are consequently only a fraction of that in adults, with limitations both in the amount of data (e.g., trials) and the amount of conditions (e.g., visual stimuli). Two possible solutions to this problem take inspiration from recent developments in visual neuroscience in adults. The first opportunity lies in the use of advanced analysis techniques that have proven to have high sensitivity in adults but are not commonly used in infants (Aslin, 2007). One such analysis approach is the use of multivariate pattern analysis (Kriegeskorte, 2011; Haynes, 2015) to establish statistical dependencies between experimental conditions and patterns of brain activity (Bayet et al., 2020; Ashton et al., 2022; Xie et al., 2022). Another approach is to characterize the representational geometry of neural activity and relate it to behavior (Spriet et al., 2022), computational models (Xie et al., 2022), and adult brains (Bayet et al., 2020; Spriet et al., 2022; Xie et al., 2022). The second opportunity lies in optimizing strategies to increase the available data. In adults, large-scale efforts and deep sampling of single participants (Naselaris et al., 2021; Allen et al., 2022) have enabled analyses not possible in standard experiments that map brain activation in a few participants (often <20) in a limited way (often 1–2 sessions). To apply the same concept to infant research, a paradigm shift in acquisition and/or large-scale collaborations will be required to increase sampling per participant (by calling the same subject back repeatedly) and to increase the breadth of sampling across participants (e.g., akin to ManyBabies initiative, Frank, 2016; Byers-Heinlein et al., 2020). The feasibility of this approach hinges on adapting recording techniques to the behavior and specifics of infants, and work to this effect is already under way (Ellis et al., 2020; Yates et al., 2021; Kosakowski et al., 2022; Turk-Browne and Aslin, 2024). These efforts will also be able to take advantage of recent large-scale neuroimaging initiatives like the Developing Human Connectome Project (Edwards et al., 2022) and the Lifespan Human Connectome Project in Development (Somerville et al., 2018), which provide unprecedented access to functional and anatomical imaging data from large cohorts, albeit outside of the context of a task and without longitudinal assessments within individual subjects.

Two additional opportunities for both human and animal research need to be mentioned at least briefly: One is the use of eye and head trackers, combined with head-mounted cameras and tools for automatic extraction of behaviors such as DeepLabCut (Mathis et al., 2018) or SLEAP (Pereira et al., 2022), to determine the "visual diet" at different ages as thoroughly as possible (L. B. Smith et al., 2018; Sullivan et al., 2021). Second, there is clear synergy to be exploited between computational work on deep neural networks for vision and developmental research. It is generally agreed that development harbors insights useful for modeling of human vision and engineering of artificial vision (Vogelsang et al., 2018; Zaadnoordijk et al., 2020; Jang and Tong, 2021; Turk-Browne and Aslin, 2024). On the flip side, deep networks could be powerful tools for generating testable hypotheses for network-level development of visual cortex: Not only are they currently the best models for visual cortex function (Yamins and DiCarlo, 2016; Cichy and Kaiser, 2019; Doerig et al., 2023), their inherent network nature,

the gradual emergence of tuning functions with training (Blauch et al., 2022), and the impact of the chosen training set on network properties (Dobs et al., 2022) all could be leveraged for developmental research.

Opportunities: Diverse Species

In addition to optimizing the available tools, it is increasingly recognized that neuroscience benefits from using as many different species as possible to distinguish between shared principles and species-specific properties, and developmental research is no exception. In the context of studying the development of higher level vision, nonhuman primates and humans are obviously highly important because of the complexity of visual function found in both. Indeed, much of the data reviewed so far arise from either nonhuman or human primates. For developmental research in nonhuman primates, it is important to note the value of studying marmosets in addition to macaques (Homman-Ludiye and Bourne, 2020). Marmosets generally have twins or triplets (rather than a single offspring like macaques) twice a year, and sexual maturity is reached at 18 months of age (compared with ∼3–4 years for rhesus monkeys). Thus, not only are larger cohort sizes for developmental studies more easily feasible, age-matched siblings can be used as controls for developmental manipulations. Furthermore, marmosets are born relatively immature compared with macaques and humans, so that interventions performed perinatally are comparable with late in utero stages in humans (Homman-Ludiye and Bourne, 2020).

However, primates are not the only animal model suitable for studying higher visual development. We will highlight two additional animal models here because of their unique advantages. The first animal model is ferrets, carnivores like cats. Following groundbreaking work by Chapman and Stryker (Chapman and Stryker, 1993), research in ferrets has significantly contributed to our understanding of the development of early visual stages up to V1 (Sharma and Sur, 2014). Ferrets are generally uniquely suited for developmental research because of early parturition, which allows easy experimental access to developmental stages that occur in utero in other species. Additionally, they have relatively large litter sizes (on average ∼10 kits), useful for capturing developmental variability and providing control data. In terms of visual processing, important similarities have been identified between the early visual stages of ferrets, cats, and primates (Sharma and Sur, 2014). Much less is currently known about the properties of higher visual areas, but there is evidence for significant additional processing of visual information beyond V1. Anatomically, a total of 19 visual areas have been identified to date (Homman-Ludiye et al., 2010). Behaviorally, ferrets are capable of performing shape and motion tasks in the laboratory (Doty et al., 1967; Hupfeld et al., 2007; Dunn-Weiss et al., 2019). This suggests that dedicated higher visual areas for form and motion might exist in the ferret. Indeed, as mentioned above, ferret PMLS mirrors primate MT in integrating local V1 motion signals into a global motion signal (Lempel and Nielsen, 2019), making ferrets a valuable animal model for studying the development of higher-level motion vision.

The second animal model of interest is the tree shrew, a small diurnal mammal of the order Scandentia that is considered a prototype of early prosimian primates (Petry and Bickford, 2019). Tree shrew visual cortex shares a number of features with primates, in particular with respect to LGN and V1 organization (Petry and Bickford, 2019; Savier et al., 2021 for recent reviews). Their lissencephalic brain means they are, like marmosets, especially suitable for imaging studies. Additionally, their large superior colliculus and pulvinar provide opportunities for studying the contribution of those structures to visual function (Petry and Bickford, 2019). As in ferrets, higher visual areas have received little attention so far, but a number of higher visual areas have been identified anatomically (Wong and Kaas, 2009). Of these, area TD appears similar to MT in terms of relative location, myelination, and V1 input (Wong and Kaas, 2009). Behaviorally, tree shrews show capacity for color, form, and motion vision (Petry and Bickford, 2019; Savier et al., 2021), supporting the notion that tree shrews, like ferrets, could be used to investigate higher visual functions. Tree shrews have a short breeding cycle and are born relatively immaturely (Drenhaus et al., 2006), which previous studies have taken advantage of to investigate the development of V1 (Drenhaus et al., 2006), and to test the impact of visual experience manipulations, including using tree shrews as a model for developmental myopia (Norton, 1990). Taken together, these findings make tree shrews a promising model for developmental research focused on areas beyond V1.

Finally, while we have limited this review to nonrodent species, it should be reiterated that research in rodents has contributed much to our understanding of developmental processes and will continue to do so, especially because the genetic dissection of circuits is much more feasible in rodents than in larger species. In the context of this review, developmental research in mice focusing on a broad range of functions beyond ocular dominance, and on areas outside of V1, would provide exciting opportunities for cross-species comparisons.

Outlook

We have collectively just begun to scratch the surface of visual development, especially that of higher visual functions. Systematic research is needed to clarify anatomical and functional development of the entire visual hierarchy, taking into consideration that the whole network configuration might well be changing between ages and that the adult network configuration is a poor proxy for networks during development. We also need to recognize that development of higher areas cannot be approximated by exclusively focusing on V1 but that different areas follow unique timelines and have their own set of vulnerabilities. Addressing these questions does not just promise insights into fundamental developmental mechanisms shaping one of our most important senses; it also is a necessary step to develop treatments for developmental disorders that cause vision impairments.

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