

# 99 Neural Limitations on Visual Development in Primates: Beyond Striate Cortex

LYNNE KIORPES AND J. ANTHONY MOVSHON

Since the pioneering work of Wiesel and Hubel in the 1960s and 1970s, we have known that the primary visual cortex shows evidence of postnatal development and is susceptible to effects of visual experience during an early critical period. It was therefore widely assumed that the maturation of striate cortex presented an important limit on the development of visual function (Wiesel, 1982). However, despite substantial investigation over the past 50 years into the anatomical and physiological processes that take place postnatally in the primate visual system, it remains unclear what neural mechanisms limit the development of vision. In nonhuman primates, where we have the strongest data across levels of analysis—from cellular to behavioral—it is clear that early postnatal changes at the level of the retina pose no important limit on performance (Kiorpes et al., 2003). Similarly, for spatial vision, development of neuronal response properties at the level of the lateral geniculate nucleus (LGN) and striate cortex are insufficient to account for behavioral development of spatial resolution and contrast sensitivity (Kiorpes & Movshon, 2004a; Movshon et al., 2005; Zheng et al., 2007). Conversely, temporal resolution, as represented by the high temporal frequency cutoff of the temporal modulation transfer function, is well matched to the temporal frequency response properties of magnocellular LGN neurons (Stavros & Kiorpes, 2008). Thus, although the striate cortex has long been thought to be the likely site of limitations on vision in infants, development of neuronal response properties at this level of the visual system does not seem to account for behaviorally measured visual function (Kiorpes & Movshon, 2004a). This chapter will evaluate the idea that later, hierarchical development of extrastriate visual areas is permitting the progress of visual development and will address additional hypotheses regarding the quality of information available to the behavioral output in infants.

It is well accepted that the cortical visual system is organized in a hierarchical fashion, with dominant extrastriate pathways emerging from primary visual cortex (Felleman & Van Essen, 1991; see chapter 17, this volume) and with higher-level visual areas involved in ever more complex visual processing. Although there is good evidence to suggest that the brain develops hierarchically as well (Guillery, 2005), with subcortical development preceding cortical, and primary sensory cortices preceding secondary and higher areas, there has to date been no full analysis of this process at the functional level. The basic organization of striate cortex is laid down prenatally, with ocular dominance and orientation domains essentially adult-like at birth in nonhuman primates (Blasdel, Obermayer, & Kiorpes, 1995; Horton & Hocking, 1996; Wiesel & Hubel, 1974). Cytochrome oxidase organization—blobs, patches, and stripes—is also quite mature in areas V1 and V2 in neonatal macaques (Baldwin et al., 2012; Horton & Hocking, 1996) and humans (Burkhalter, Bernardo, & Charles, 1993). Visual experience is not required for this organization to develop although abnormal visual experience can disrupt its maintenance (Horton & Hocking, 1996, 1997; Wiesel & Hubel, 1974). As reviewed by Kennedy and Burkhalter (2004), the organization of feedforward and feedback interareal connections is also largely laid down prenatally, linking areas that are hierarchically related in the adult monkey. Topographic specificity of feedforward projections is relatively adult-like near birth and undergoes relatively little refinement postnatally. Feedback projections are in general more diffuse and exuberant initially and require substantial postnatal refinement. Nevertheless, they are apparently fully mature by 2–4 months after birth (Baldwin et al., 2012; Kennedy & Burkhalter, 2004). A similar pattern of cortical maturation is found in human visual cortex although in humans refinement of feedback projections continues until 18–24 months

(Burkhalter, 1993). The types of changes described at the anatomical level could support a modest decrease in the size of receptive field centers and more substantial development or reorganization of receptive field surround mechanisms, similar to what has been reported previously based on electrophysiology in V1 and V2 of macaques (Baldwin et al., 2012; Chino et al., 1997; Kiorpes & Movshon, 2004a; Zheng et al., 2007). However, even basic visual functions measured behaviorally are still quite immature in nonhuman primates at 16 weeks when these structural and electrophysiological processes are found to be completely mature. This suggests that the important limitations lie downstream from V1 and V2. Therefore it is of interest to evaluate the development of visual functions that may depend on higher-level visual areas.

A number of higher-order visual functions have been studied in young macaques. These more complex visual functions are generally integrative in nature, requiring combination of information across space or space-time to yield a coherent or global percept. Some integrative functions are thought to reflect the processing of particular extrastriate visual areas. For example, the middle temporal area MT/V5 in the dorsal stream is well-known to be involved in the processing of global motion stimuli and provides signals that support the perception of motion (Britten et al., 1992; Newsome & Pare, 1988). On the other hand, perception of static global form stimuli, such as Glass patterns, and figure-ground segmentation tasks are thought to depend on processing in ventral stream areas like V4 or lateral occipital complex (Altmann, Bülthoff, & Kourtzi, 2003; Ostwald et al., 2008). Thus, examination of the development of sensitivity to integrative stimuli should provide a window into the role of extrastriate areas in the vision of young primates.

One of the best-documented correlations between neuronal activity and perception is that of the electrophysiological properties of neurons in area MT and the perception of motion. In adult macaques and human patients, damage to area MT results in changes in perception of global motion (Newsome & Pare, 1988; Rudolph & Pasternak, 1999; Shipp et al., 1994; Vaina et al., 2005). Also, electrical stimulation of selected populations of MT neurons biases perceived motion direction in a predictable fashion (Salzman et al., 1992). Naturally, then, one would expect a close correlation between the development of neural function in this area and development of motion sensitivity. Behavioral development of motion sensitivity has been described in infant macaques (Hall-Haro & Kiorpes, 2008; Kiorpes & Movshon, 2004b; Kiorpes et al., 2012; Mikami & Fujita, 1992). With either 1-D grating stimuli or

integrative motion stimuli based on random dot kinematograms (RDKs), infant macaques are able to detect visual motion and discriminate its direction shortly after birth. However, motion sensitivity in infants is substantially reduced compared with that in adults and improves over a long, slow developmental time course that comprises the first 2–3 years after birth (see figure 99.1A). Interestingly, the perception of 2-D pattern motion diverges from this profile. Perception of coherent motion of a plaid pattern develops comparatively late. Infants under the age of 12 weeks failed to identify the direction of plaid motion while they had no difficulty discriminating the direction of 1-D grating motion on a comparable task (Hall-Haro & Kiorpes, 2008). This ability was evident in all animals by 18 weeks after birth and, although individuals varied greatly in absolute sensitivity, pattern motion sensitivity reached asymptotic levels around the end of the first postnatal year (see figure 99.1B). Clearly the developmental time course for motion perception depends on the type of motion under test, and the neural processes supporting perception of motion in RDKs and plaids are not the same.

To investigate the relative maturity of neurons in area MT of infant macaques, our group recorded single-neuron response properties in 1-, 4-, and 16-week-old infants and in adults (Movshon et al., 2003). We found infant MT neurons to be well tuned for speed and direction of 1-D motion similar to those of adults. However, there were some immaturities. As noted in earlier cortical areas (V1 and V2) (see Kiorpes & Movshon, 2004a; Zheng et al., 2007), infant MT neurons were comparatively weakly responsive with longer latencies and lower spike rates than found in those of adults. Unlike earlier cortical areas, these properties were not fully adult in MT at 16 weeks. One striking difference between infant and adult MT was a dearth of pattern direction selective (PDS) neurons, those that signal the direction of motion of complex patterns, such as plaid patterns (Movshon et al., 1985; Rodman & Albright, 1989). PDS responses emerge from the elaboration of specific feed-forward projections from cells in V1 to MT, and the late development of these cells may reflect the delayed refinement of that pattern of connections (Rust et al., 2006). The proportion of PDS cells in 16-week-olds was only one-half that of adults and was substantially smaller at younger ages (see figure 99.1C). While it is not straightforward to make a direct comparison between behavioral and electrophysiological results, these neural data suggest that infant macaques have the neural machinery to detect and discriminate simple motion but, based on the dearth of PDS cells, the youngest infants may not have the ability to appreciate complex pattern motion. These predictions are borne out by the

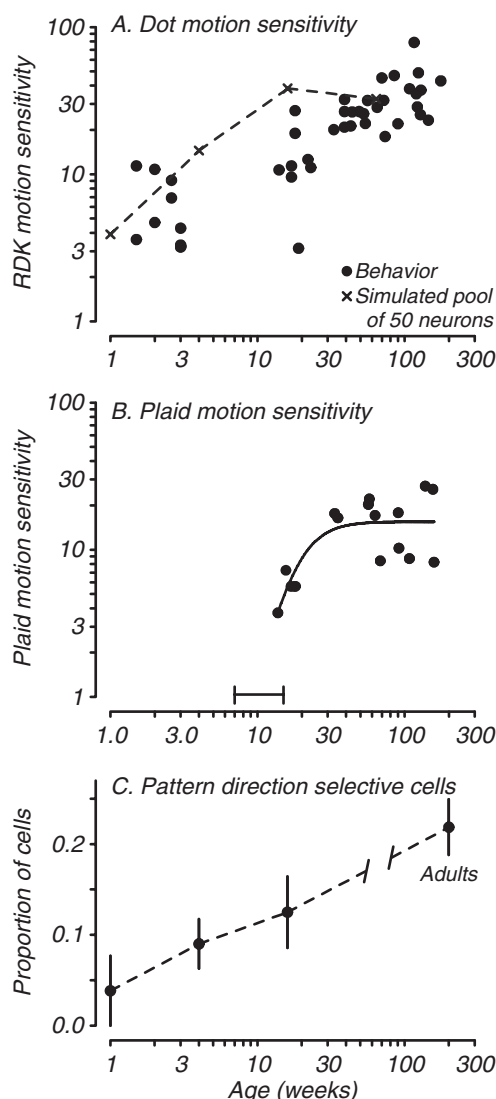


FIGURE 99.1 Development of “dorsal stream” motion mechanisms. (A) Development of sensitivity to random dot motion. Coherence represents the strength of the motion signal in the random dot kinematogram (RDK) stimulus. Filled symbols are data from individual infant monkeys plotted as a function of age (data from Kiorpes & Movshon, 2004b). The Xs and dashed line show the estimated sensitivity of the population of middle temporal visual cortex (MT) neurons recorded at each age, based on a pool size of 50 neurons. (B) Development of sensitivity to the direction plaid pattern motion. The filled symbols are data from individual monkeys plotted as a function of age. The horizontal bar along the abscissa delimits the range of ages over which infants failed to demonstrate the perception of plaid motion. The line fit to the data is a Michaelis-Menton function which captures the rate of development and the age at which sensitivity reaches 50% of adults levels (after Hall-Haro & Kiorpes, 2008). (C) Proportion of pattern direction cells in MT recorded at each age (mean  $\pm$  SE).

behavioral data (see figure 99.1A, B) showing early onset of RDK motion discrimination but delayed development of pattern motion discrimination. What then explains the comparatively poor performance of infants shown in figure 99.1A and the extended developmental profile? As mentioned above, although MT neurons are well tuned in the youngest infants, they are only weakly responsive, and overall responsivity changes with age. To capture neuronal coherence thresholds as a function of age, we performed a pooling analysis similar to that used by Shadlen et al. (1996). An estimate of population-level coherence sensitivity at each age revealed parallel improvement between neuronal sensitivity and behavior up to 16 weeks when adult-level neuronal sensitivity was reached (Xs and dashed line in figure 99.1A). The correlation between neural and behavioral development at the early ages is appealing although this leaves the remaining extended developmental period for RDK motion sensitivity unexplained.

A variety of visual abilities that are thought to rely on ventral stream function have been studied in young macaques. Ventral stream function is characterized by perceptual challenges such as organization of static elements into a coherent form, figure-ground segmentation, object recognition, and object invariance, all of which rely on global form perception. To segment elements of a scene into objects and background, it is necessary to distinguish contours and textures that define their boundaries. Orientation and texture perception are apparent quite early in monkeys and humans (Atkinson & Braddick, 1992; El-Shamayleh, Movshon, & Kiorpes, 2010; Sireteanu & Rieth, 1992). Orientation and texture discrimination ability are evident in macaques as early as 5–6 weeks after birth (El-Shamayleh, Movshon, & Kiorpes, 2010). Interestingly, the ability to discriminate patterns based solely on second-order textures cues matured *earlier* than first-order spatial contrast sensitivity (see figure 99.2A, B). Thus the building blocks for global form perception develop quite early.

A canonical measure of global form perception is the ability to appreciate global structure in Glass patterns (Glass, 1969). Glass patterns are composed of oriented dipoles, the global structure of which is perceptible only by integration of dipole patterns across space. We studied the development of sensitivity to Glass pattern structure and found comparatively late onset of this ability, which was followed by an extended developmental time course that was reminiscent of that for global motion perception (see figure 99.2C) (Kiorpes et al., 2012). Few monkeys were able to discriminate Glass pattern structure from incoherent control patterns before about 15 weeks; adult levels of sensitivity were

approached 2–3 years after birth. This profile seems to be fairly general for global form perception. Contour integration requires both perceptual organization and figure–ground segmentation skills. It is typically measured by the ability to link Gabor patches or other discrete elements together to extract a global shape from a background of randomly arrayed noise elements (Field, Hayes, & Hess, 1993). This ability also develops quite late compared to spatial contrast sensitivity, which is measureable near birth in macaques and approaches adult levels near the end of the first postnatal year (see figure 99.2A) (El-Shamayleh, Movshon, & Kiorpes, 2010; Stavros & Kiorpes, 2008). Kiorpes and Bassin (2003) reported a failure of contour integration ability prior to about 16 weeks in young macaques followed by development to adult levels over at least the succeeding year (see figure 99.2D). Late development of contour integration ability has been reported in human children as well, with onset after 3 years of age and improvement continuing into the teenage years (Kovács et al., 1999). Consistent with psychophysical measures of global form development, several studies of object concepts in young macaques show development over the

first 4 or more months after birth (Diamond, 1990; Ha, Kimpo, & Sackett, 1997; Hall-Haro et al., 2008).

The neural processes underlying global form perception in adults are a matter of ongoing debate. Second-order orientation-defined texture discrimination of the kind tested by El-Shamayleh, Movshon, and Kiorpes (2010) is correlated with activity both in and downstream of early visual areas V1 and V2 in human visual cortex (Larsson, Landy, & Heeger, 2006). Consistent with that report, El-Shamayleh and Movshon (2011) failed to find evidence for second-order texture coding by neurons in macaque V2. Other studies have identified neural correlates of shape and texture processing at the level of V4 (De Weerd, Desimone, & Ungerleider, 1996; Huxlin et al., 2000; Schiller, 1995). The ability to extract a coherent percept from integration of elements imbedded in noise, as required for contour integration, appears to involve higher occipitotemporal areas as well as contextual interactions in early visual cortex (Altmann, Bühlhoff, & Kourtzi, 2003; Kourtzi et al., 2003; Li, Piëch, & Gilbert, 2006, 2008). The onset of contour integration ability in macaques coincides with maturation of feedback projections to V1 and V2

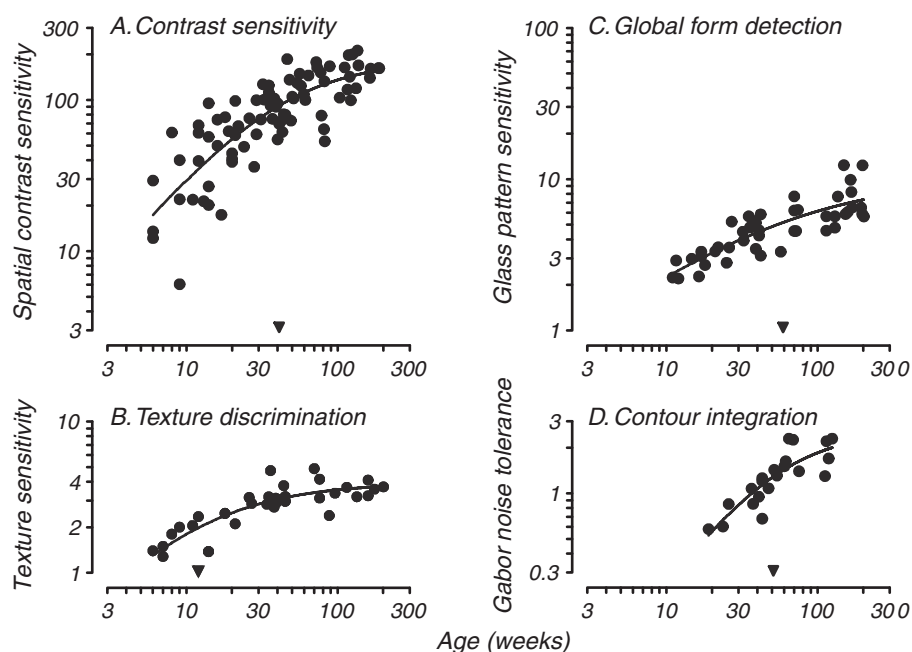


FIGURE 99.2 Development of “ventral stream” form mechanisms. (A) Development of peak spatial contrast sensitivity (data from Stavros & Kiorpes, 2008). (B) Development of sensitivity to second-order orientation defined texture (data from El-Shamayleh, Movshon, & Kiorpes, 2010). (C) Development of sensitivity to global structure in concentric Glass patterns (data from Kiorpes et al., 2012). (D) Development of contour integration ability (data from Kiorpes & Bassin, 2003). Filled symbols in each panel are data from individual infant monkeys plotted as a function of age. The line fit to the data in each panel is a Michaelis–Menton function which captures the rate of development and the age at which sensitivity reaches 50% of adults’ levels (indicated by the filled triangles along the abscissa).



and the subsequent reorganization of receptive field surrounds as described by Baldwin et al. (2012). Extraction of global form in Glass patterns seems to rely on activity in higher-order extrastriate areas (Ostwald et al., 2008); activity in early visual cortex in the presence of Glass patterns can be attributed to local orientation signals (Smith, Bair, & Movshon, 2002; Smith, Kohn, & Movshon, 2007). Together with a preponderance of evidence for shape processing in inferotemporal visual areas, it is likely that global form perception depends on the function of areas beyond V2. Unfortunately little is known about the development of neuronal response properties in areas beyond V2. Rodman and colleagues recorded from inferior temporal (IT) neurons in macaques ranging in age from 5 weeks to adult (Rodman, Scalaidhe, & Gross, 1993). They found dramatically reduced responsiveness of IT neurons compared with MT neurons recorded under the same conditions in the same animals. However, IT neurons that were responsive in young monkeys (6–8 weeks of age) showed typical tuning for shapes, patterns, and faces. It is important to note that they encountered a substantially higher proportion of responsive neurons in awake infant recordings compared with anesthetized preparations, a distinction that was not found for MT. As reported by Movshon et al. (2003) for MT neurons, infant IT neurons were less responsive overall and responded with longer latency compared with those of adults regardless of state. These results suggest that ventral stream areas may be somewhat less mature in young monkeys than dorsal stream areas, which is consistent with metabolic assays of maturation (Distler et al., 1996). However they leave the late onset of global form perception and its long developmental time course unexplained.

Taken together, electrophysiological data on neuronal response properties and anatomical studies of cortical organization show that visual brain areas linked with higher-order perception in adults are substantially more mature than would be expected based on behavioral assessment of visual function in infants. Therefore, stimulus information is available to the infant—encoded with reasonable fidelity—that is not being used or is not sufficient to support appropriate behavior. A number of possibilities exist to explain the comparatively poor performance of infants. One obvious candidate is a limitation on the behavior itself or on the ability of the animal to understand the task. These explanations are unlikely since behavioral ability has been clearly demonstrated by success on tests of basic visual function at very young ages (e.g., Kiorpes & Bassin, 2003; Stavros & Kiorpes, 2008) or under comparable task demands (Hall-Haro & Kiorpes, 2008). Another possibility is the

weak responsiveness of infant neurons: Although the tuning properties of most infant neurons appear to be adult-like at very young ages, they respond at quite low rates, with long latency. The weaker responses could translate to lower signal-to-noise ratio in infants or greater response variability. Curiously, an analysis of the reliability of infant V1 neurons concluded that in fact their responses are *more* reliable, not less so (Rust, Schultz, & Movshon, 2002). However, there is good evidence that the infant visual system is “noisier” than that of the adult and that developmental changes in contrast sensitivity parallel a decrease in signal-to-noise ratio which may reflect improved signaling by cortical neurons (Brown, 1994; Kiorpes & Movshon, 1998; Norcia, 2004).

Up to this point, we have primarily considered the maturation of single-neuron properties as a substrate for visual development. As we have seen, those properties provide a partial account of the changes during visual development, but not a complete one. Of course, it is unlikely that behavioral performance depends on the output of individual neurons; rather it must reflect the activity of a large number of neurons active together. Thus, it is instructive to consider how the properties of infant neurons might impact the response of the population. The rather weak responses of infant neurons combined with their broader latency distribution (as noted in MT and IT) might result in a less coherent population output from extrastriate areas to their downstream targets, even though individual neuron responses reflect stimulus attributes quite well. As responsivity increases and the latency distribution narrows with age, the population of neurons in a given area would generate a stronger and more coherent readout pattern of activity for downstream areas to decode, allowing performance on visual tasks to improve disproportionately more than the properties of individual neurons. Equally plausible, it might be the rules for how neuronal responses are combined to formulate a population response—such as pool size or identity of neurons in the pool—that change with development. Changes in pooling rules could result in a population response that becomes stronger with maturation, driving an improvement in the quality of information available to the behavioral output.

We know that the tuning properties of infant neurons are quite mature, so let's suppose that the population output from midlevel extrastriate areas in fact faithfully represents the encoded visual stimulus. If so, then it may be that the neural “decoder”—the downstream process responsible for translating this encoded information into a perceptual decision—is untuned or inefficient in young infants. For instance, an accurate

readout from an upstream visual area may be incorrectly interpreted or inappropriately weighted by the decision process, with the result that behavioral performance is poor. In this case, the developmental time course reflected by behavioral assay might be defined by a process of “tuning” or learning by the decoder to correctly interpret the sensory readout rather than by a refinement of neuronal response properties. One can imagine a developmental process that is analogous to perceptual learning in the adult, but on a more dramatic scale. Law and Gold (2008) recorded simultaneously from MT and lateral intraparietal area (LIP) while adult monkeys practiced a motion direction discrimination, with an eye movement as the behavioral output. They found substantial modification of responses in LIP with extended practice but observed no concurrent changes in MT. Their interpretation was that improvement in the animals’ performance was related to more efficient decoding of the upstream information. A similar change might take place during normal development as the animal interacted with the visual world.

In reality, the processes by which downstream areas decode their inputs to form perceptual decisions may not in fact differ from those used to combine inputs for the creation of more elaborate receptive field properties. The construction of linear likelihood-based decoders for the output of MT as used in motion discrimination tasks reveals that a feedforward pattern of connections

involving summation of signals from nearby directions and suppression by signals from remote directions is optimal for coarse discrimination tasks like the ones we study (Graf et al., 2011; Jazayeri & Movshon, 2006). This decoding theory also provides a very accurate account of the perceptual learning results of Law and Gold (2008). Consider figure 99.3. On the left is the deduced pattern of output connections from a population of V1 neurons inferred by a likelihood decoding model from the recordings of Graf et al. (2011). This is an optimal connection pattern for identifying orientation on the basis of V1 activity. Note the excitatory feedforward output from neurons tuned near the direction of choice and the suppressive output from neurons tuned to more remote directions. On the right is shown the connectational architecture deduced by Rust et al. (2006) for the computation of pattern motion by MT neurons. According to this account, pattern selective responses emerge in large part from the particular pattern of feedforward connections. The similarity of that pattern to the architecture required for decoding is obvious. Thus it may be that the connections that are responsible for the computation of a more elaborate response property—for example, one that permits the analysis of higher-order motion signals—are the same ones needed for the computation of sensory decision variables. Perhaps these can be achieved in the same type of cortical circuits using the same algorithms. Note also that,

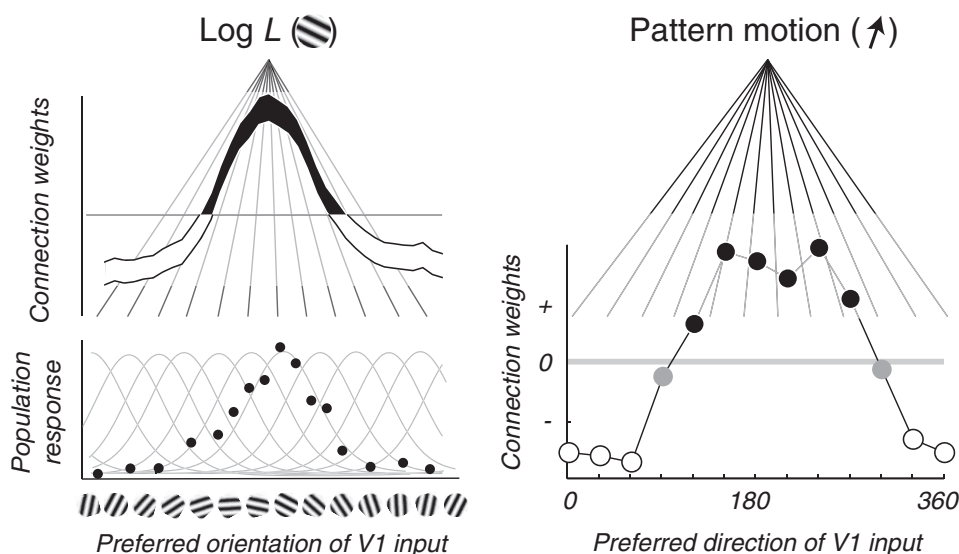


FIGURE 99.3 Computing an optimal linear decoder may involve the same circuits and computations as higher-order receptive field properties. The left panel shows results from Graf et al. (2011), showing the average connection weights (top) for the optimal estimation of orientation from a population response of V1 neurons (schematically illustrated at the bottom); mean positive weights for one set of data ( $\pm 1$  SEM) are shown in the solid black band and negative weights as an open band. The right panel shows the feedforward connectational architecture inferred by Rust et al. (2006) for the V1 inputs to an example pattern selective neuron in MT. Positive weights are again filled, negative ones open. The pattern of connections for decoding orientation (left) is essentially identical to that for encoding pattern motion (right) ( $x$  axes in degrees).

as shown above, the computation of pattern motion by MT neurons develops relatively late (see figure 99.1); similarly the delayed onset of performance at integrative visual tasks suggests that the precision of V1 decoding might also develop late.

A parsimonious account of a large amount of data is that visual development depends on two separate processes: The age of onset of a particular visual function may reflect the maturation of a limiting underlying neural substrate while the subsequent development to adult levels may reflect the learning or tuning of a perceptual template by the decoder. These two processes are intertwined and can be achieved by the same architecture. The delayed development of higher-order stimulus selectivity in downstream cortical areas could be the result of the late establishment of this pattern of functional connections, and as a consequence performance—which depends on optimal decoding—might be similarly delayed even though the signals carried by input neurons are quite adult-like. Substantiation of these ideas will require a combination of population-level assessment of neural activity at multiple stages of the visual system hierarchy and direct evaluation of decoding principles in play during development.

#### ACKNOWLEDGMENTS

The research from our laboratories described in this chapter was supported primarily by National Institutes of Health grants EY05864, EY04440, and EY2017 and Center grant RR00166 to the Washington National Primate Research Center. We are grateful to many individual students and colleagues for their contributions as well as excellent animal care and oversight by Michael Gorman and the NYU Office of Veterinary Resources.

#### REFERENCES

Altmann, C. F., Bülthoff, H. H., & Kourtzi, Z. (2003). Perceptual organization of local elements into global shapes in the human visual cortex. *Current Biology*, *13*, 342–349.

Atkinson, J., & Braddick, O. (1992). Visual segmentation of oriented textures by infants. *Behavioural Brain Research*, *49*, 123–131.

Baldwin, M. K., Kaskan, P. M., Zhang, B., Chino, Y. M., & Kaas, J. H. (2012). Cortical and subcortical connections of V1 and V2 in early postnatal macaque monkeys. *Journal of Comparative Neurology*, *520*, 544–569.

Blasdel, G., Obermayer, K., & Kiorpes, L. (1995). Organization of ocular dominance and orientation columns in the striate cortex of neonatal macaque monkeys. *Visual Neuroscience*, *12*, 589–603.

Britten, K. H., Shadlen, M. N., Newsome, W. T., & Movshon, J. A. (1992). The analysis of visual motion: A comparison of neuronal and psychophysical performance. *Journal of Neuroscience*, *12*, 4745–4765.

Brown, A. M. (1994). Intrinsic contrast noise and infant visual contrast discrimination. *Vision Research*, *34*, 1947–1964. doi:10.1016/0042-6989(94)90025-6.

Burkhalter, A. (1993). Development of forward and feedback connections between areas V1 and V2 of human visual cortex. *Cerebral Cortex*, *3*, 476–487.

Burkhalter, A., Bernardo, K. L., & Charles, V. (1993). Development of local circuits in human visual cortex. *Journal of Neuroscience*, *13*, 1916–1931.

Chino, Y. M., Smith, E. L., III, Hatta, S., & Cheng, H. (1997). Postnatal development of binocular disparity sensitivity in neurons of the primate visual cortex. *Journal of Neuroscience*, *17*, 296–307.

De Weerd, P., Desimone, R., & Ungerleider, L. G. (1996). Cue-dependent deficits in grating orientation discrimination after V4 lesions in macaques. *Visual Neuroscience*, *13*, 529–538.

Diamond, A. (1990). The development and neural bases of memory functions as indexed by the AB and delayed response tasks in human infants and infant monkeys. *Annals of the New York Academy of Sciences*, *608*, 267–317.

Distler, C., Bachevalier, J., Kennedy, C., Mishkin, M., & Ungerleider, L. G. (1996). Functional development of the corticocortical pathway for motion analysis in the macaque monkey, a 14C–2-deoxyglucose study. *Cerebral Cortex*, *6*, 184–195.

El-Shamayleh, Y., & Movshon, J. A. (2011). Neuronal responses to texture-defined form in macaque visual area V2. *Journal of Neuroscience*, *31*, 8543–8555.

El-Shamayleh, Y., Movshon, J. A., & Kiorpes, L. (2010). Development of sensitivity to visual texture modulation in macaque monkeys. *Journal of Vision*, *10*, 1–12. doi:10.1167/10.11.11.

Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, *1*, 1–47. doi:10.1093/cercor/1.1.1-a.

Field, D. J., Hayes, A., & Hess, R. F. (1993). Contour integration by the human visual system: Evidence for a local “association field.” *Vision Research*, *33*, 173–193.

Glass, L. (1969). Moiré effect from random dots. *Nature*, *223*, 578–580.

Graf, A. B., Kohn, A., Jazayeri, M., & Movshon, J. A. (2011). Decoding the activity of neuronal populations in macaque primary visual cortex. *Nature Neuroscience*, *14*, 239–245.

Guillery, R. W. (2005). Is postnatal neocortical maturation hierarchical? *Trends in Neurosciences*, *28*, 512–517. doi:10.1016/j.tins.2005.08.006.

Ha, J. C., Kimpo, C. L., & Sackett, G. P. (1997). Multiple-spell, discrete-time survival analysis of developmental data: Object concept in pigtailed macaques. *Developmental Psychology*, *33*, 1054–1059.

Hall-Haro, C., Johnson, S. P., Price, T. A., Vance, J. A., & Kiorpes, L. (2008). Development of object concepts in macaque monkeys. *Developmental Psychobiology*, *50*, 278–287.

Hall-Haro, C., & Kiorpes, L. (2008). Normal development of pattern motion sensitivity in macaque monkeys. *Visual Neuroscience*, *25*, 675–684.

Horton, J. C., & Hocking, D. R. (1996). An adult-like pattern of ocular dominance columns in striate cortex of newborn monkeys prior to visual experience. *Journal of Neuroscience*, *16*, 1791–1807.

- Horton, J. C., & Hocking, D. R. (1997). Timing of the critical period for plasticity of ocular dominance columns in macaque striate cortex. *Journal of Neuroscience*, 17, 3684–3709.
- Huxlin, K. R., Saunders, R. C., Marchionini, D., Pham, H. A., & Merigan, W. H. (2000). Perceptual deficits after lesions of inferotemporal cortex in macaques. *Cerebral Cortex*, 10, 671–683.
- Jazayeri, M., & Movshon, J. A. (2006). Optimal representation of sensory information by neural populations. *Nature Neuroscience*, 9, 690–696.
- Kennedy, H., & Burkhalter, A. (2004). Ontogenesis of cortical connectivity. In L. M. Chalupa & J. S. Werner (Eds.), *The visual neurosciences* (pp. 146–158). Cambridge, MA: MIT Press.
- Kiorpes, L., & Bassin, S. A. (2003). Development of contour integration in macaque monkeys. *Visual Neuroscience*, 20, 567–575.
- Kiorpes, L., & Movshon, J. A. (1998). Peripheral and central factors limiting the development of contrast sensitivity in macaque monkeys. *Vision Research*, 38, 61–70.
- Kiorpes, L., & Movshon, J. A. (2004a). Neural limitations on visual development in primates. In L. M. Chalupa & J. S. Werner (Eds.), *The visual neurosciences* (pp. 159–173). Cambridge, MA: MIT Press.
- Kiorpes, L., & Movshon, J. A. (2004b). Development of sensitivity to visual motion in macaque monkeys. *Visual Neuroscience*, 21, 851–859.
- Kiorpes, L., Price, T., Hall-Haro, C., & Movshon, J. A. (2012). Development of sensitivity to global form and motion in macaque monkeys (*Macaca nemestrina*). *Vision Research*, 63, 34. doi:10.1016/j.visres.2012.04.018.
- Kiorpes, L., Tang, C., Hawken, M. J., & Movshon, J. A. (2003). Ideal observer analysis of the development of spatial contrast sensitivity in macaque monkeys. *Journal of Vision*, 3(10), 630–641. doi:10.1167/3.10.6.
- Kourtzi, Z., Tolias, A. S., Altmann, C. F., Augath, M., & Logothetis, N. K. (2003). Integration of local features into global shapes: Monkey and human fMRI studies. *Neuron*, 37, 333–346.
- Kovács, I., Kozma, P., Fehér, A., & Benedek, G. (1999). Late maturation of visual spatial integration in humans. *Proceedings of the National Academy of Sciences of the United States of America*, 96, 12204–12209. doi:10.1073/pnas.96.21.12204.
- Larsson, J., Landy, M. S., & Heeger, D. J. (2006). Orientation-selective adaptation to first- and second-order patterns in human visual cortex. *Journal of Neurophysiology*, 95, 862–881.
- Law, C., & Gold, J. I. (2008). Neural correlates of perceptual learning in a sensory-motor, but not a sensory, cortical area. *Nature Neuroscience*, 11, 505–513.
- Li, W., Piéch, V., & Gilbert, C. D. (2006). Contour saliency in primary visual cortex. *Neuron*, 50, 951–962.
- Li, W., Piéch, V., & Gilbert, C. D. (2008). Learning to link visual contours. *Neuron*, 57, 442–451.
- Mikami, A., & Fujita, K. (1992). Development of the ability to detect visual motion in infant macaque monkeys. *Developmental Psychobiology*, 25, 345–354.
- Movshon, J. A., Adelson, E. H., Gizzi, M. S., & Newsome, W. T. (1985). The analysis of moving visual patterns. In C. Chagas, R. Gattass, & C. Gross (Eds.), *Pattern recognition mechanisms* (pp. 117–151). Rome: Vatican Press.
- Movshon, J. A., Kiorpes, L., Hawken, J. A., & Cavanaugh, J. R. (2005). Functional maturation of the macaque's lateral geniculate nucleus. *Journal of Neuroscience*, 25, 2712–2722.
- Movshon, J. A., Rust, N. C., Kohn, A., Kiorpes, L., & Hawken, M. J. (2003). Receptive field properties of MT neurons in infant macaques. *Perception*, 33, ECVF Abstract Supplement. doi:10.1068/v040593.
- Newsome, W. T., & Pare, E. B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *Journal of Neuroscience*, 8, 2201–2211.
- Norcia, A. M. (2004). Development of spatial selectivity and response timing in humans. In L. M. Chalupa & J. S. Werner (Eds.), *The visual neurosciences* (pp. 174–188). Cambridge, MA: MIT Press.
- Ostwald, D., Lam, J. M., Li, S., & Kourtzi, Z. (2008). Neural coding of global form in the human visual cortex. *Journal of Neurophysiology*, 99, 2456–2469.
- Rodman, H. R., & Albright, T. D. (1989). Single-unit analysis of pattern-motion selective properties in the middle temporal visual area (MT). *Experimental Brain Research*, 75, 53–64.
- Rodman, H. R., Scalaidhe, S. P., & Gross, C. G. (1993). Response properties of neurons in temporal cortical visual areas of infant monkeys. *Journal of Neurophysiology*, 70, 1115–1136.
- Rudolph, K., & Pasternak, T. (1999). Transient and permanent deficits in motion perception after lesions of cortical areas MT and MST in the macaque monkey. *Cerebral Cortex*, 9, 90–100.
- Rust, N. C., Mante, V., Simoncelli, E. P., & Movshon, J. A. (2006). How MT cells analyze the motion of visual patterns. *Nature Neuroscience*, 9, 1421–1431.
- Rust, N. C., Schultz, S. R., & Movshon, J. A. (2002). A reciprocal relationship between reliability and responsiveness in developing visual cortical neurons. *Journal of Neuroscience*, 22, 10519–10523.
- Salzman, C. D., Murasugi, C. M., Britten, K. H., & Newsome, W. T. (1992). Microstimulation in visual area MT: Effects on direction discrimination performance. *Journal of Neuroscience*, 12, 2331–2355.
- Shadlen, M. N., Britten, K. H., Newsome, W. T., & Movshon, J. A. (1996). A computational analysis of the relationship between neuronal and behavioral responses to visual motion. *Journal of Neuroscience*, 16, 1486–1510.
- Schiller, P. H. (1995). Effect of lesions in visual cortical area V4 on the recognition of transformed objects. *Nature*, 376, 342–344.
- Shipp, S., de Jong, B. M., Zihl, J., Frackowiak, R. S., & Zeki, S. (1994). The brain activity related to residual motion vision in a patient with bilateral lesions of V5. *Brain*, 117, 1023–1038.
- Sireteanu, R., & Rieth, C. (1992). Texture segregation in infants and children. *Behavioural Brain Research*, 49, 133–139.
- Smith, M. A., Bair, W., & Movshon, J. A. (2002). Signals in macaque striate cortical neurons that support the perception of Glass patterns. *Journal of Neuroscience*, 22, 8334–8345.
- Smith, M. A., Kohn, A., & Movshon, J. A. (2007). Glass pattern responses in macaque V2 neurons. *Journal of Vision*, 7(3), 5. doi:10.1167/7.3.5.



- Stavros, K. A., & Kiorpes, L. (2008). Behavioral measurements of temporal contrast sensitivity development in macaque monkeys (*Macaca nemestrina*). *Vision Research*, 48, 1335–1344. doi:10.1016/j.visres.2008.01.031.
- Vaina, L. M., Cowey, A., Jakab, M., & Kikinis, R. (2005). Deficits of motion integration and segregation in patients with unilateral extrastriate lesions. *Brain*, 128, 2134–2145.
- Wiesel, T. N. (1982). Postnatal development of the visual cortex and the influence of environment. *Nature*, 299, 583–591.
- Wiesel, T. N., & Hubel, D. H. (1974). Ordered arrangement of orientation columns in monkeys lacking visual experience. *Journal of Comparative Neurology*, 158, 307–318.
- Zheng, J., Zhang, B., Bi, H., Maruko, I., Watanabe, I., Nakatsuka, C., et al. (2007). Development of temporal response properties and contrast sensitivity of V1 and V2 neurons in macaque monkeys. *Journal of Neurophysiology*, 97, 3905–3916.

