6 Visual Development

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Newborns can see – but only if they are awake with an object right in front of them that is large with elements of high contrast against the background, like the mother's face. Improvements come rapidly after birth with the maturation of the retina and the visual cortex to which it connects, allowing better input to higher visual areas that underlie the perception of whole objects and their movement. Nevertheless, missing visual input near birth because of dense cataracts in one or both eyes alters the developmental trajectory, even when treatment occurs within the first few months of life. Thus, the early visual input, despite its limitations, is critical for setting up the neural architecture for later refinement.

This chapter begins with a description of the limitations on the newborn's visual world and their source in immaturities in the retina and visual cortex. Variations in diet affect the postnatal development of the retina and hence lead to cross-cultural variations in the quality of visual input. Although the long-term consequences of these cross-cultural differences are unknown, we do know that when input is more seriously limited by visual deprivation, deficits in both low-level (acuity, peripheral vision) and high-level (motion, faces) processing emerge later. Those effects will be illustrated by using motion and face perception as examples of how changing neural limitations alter the effective visual world of the baby and of how, in turn, environmental variations ranging from complete visual deprivation to culturally biased visual input, can affect that neural development.

6.1 Newborns' Visual Perception: Low-Level Vision

6.1.1 Acuity

To assess an adult's vision, the adult is asked to read letters of decreasing size and the measure of acuity is the smallest letters the adult can recognize accurately. To measure newborns' vision, the test is adapted to take advantage of infants' preference to look at something patterned over something plain (Fantz, 1963; Fantz, Ordy, & Udelf, 1962): the baby is shown a gray field with a gray patch to one side (to the right or left) and a patch of black-and-white stripes to the other side. When the stripes are large, the baby rapidly orients toward and fixates them. As the stripes get smaller, the looking preference – for stripes sometimes on the right and sometimes on the left – diminishes until the baby responds randomly. The measure of vision is the smallest size of stripe for which the baby shows a reliable preference. Newborns respond to stripes only if they are about 40 times larger than the limit for adults with normal vision, a size larger than the top line of most eye charts. Over the next 6 months there is a rapid 8-fold improvement, so that the baby responds to lines like those forming the 20/100 line of an adult eye chart. Over the next 6–7 years, there is gradual improvement to adult thresholds for detecting thinner lines and for the harder task of recognizing them when they form a letter surrounded by other letters (Ellemberg, Lewis, Liu, & Maurer, 1999; Mayer et al., 1995). The implication is that initially only large objects will be visible to the baby, and within them, only large details.

6.1.2 Contrast Sensitivity

Not only must the details be large, they must also be of high contrast. Newborns' sensitivity to contrast has been tested with a method similar to the acuity test, but now, during each block, the stripes remain the same size over trials, but their contrast is systematically reduced. Then in another block, the same test is performed with stripes of a different size. For each size of stripe, the measure is the lowest contrast at which the baby reliably fixates the stripes (Brown, Lindsey, Cammenga, Giannone, & Stenger, 2015; Brown, Opoku, & Stenger, 2018). For the large sizes of stripe to which the newborn responds, contrast has to be more than 100 times greater than in adults with normal vision (Brown et al., 2015). Over the next few months, babies begin to respond to thinner stripes and to lower contrasts but adult-like sensitivity is not achieved until around age 7 (Banks & Salapatek, 1978; Drover, Earle, Courage, & Adams, 2002; Ellemberg et al., 1999). The implication is that infants can see only high-contrast features of objects, such as the eyes and hairline of a face, but not its nose, and likely the mouth only if its contrast is heightened by showing the teeth or the application of makeup.

The initially poor vision of the newborn arises largely from an immature retina. In adults, the perception of fine detail and low contrast is mediated by the fovea, the central region of the retina that is densely packed with cones that efficiently transmit light. In newborns, the transmission is estimated to be 350 times less efficient than in adults (Banks & Bennett, 1988) because the foveal cones are wider and shorter and, therefore, spaced further apart, preventing the resolution of fine detail and efficient light transmission from their inner to outer segments; they are also intermingled with, and covered by, outer ganglion cells that block light transmission. Computational modeling indicates that retinal immaturities account for much, but not all, of newborns' limited acuity and contrast sensitivity (Banks & Bennett, 1988; Candy, Crowell, & Banks, 1998).

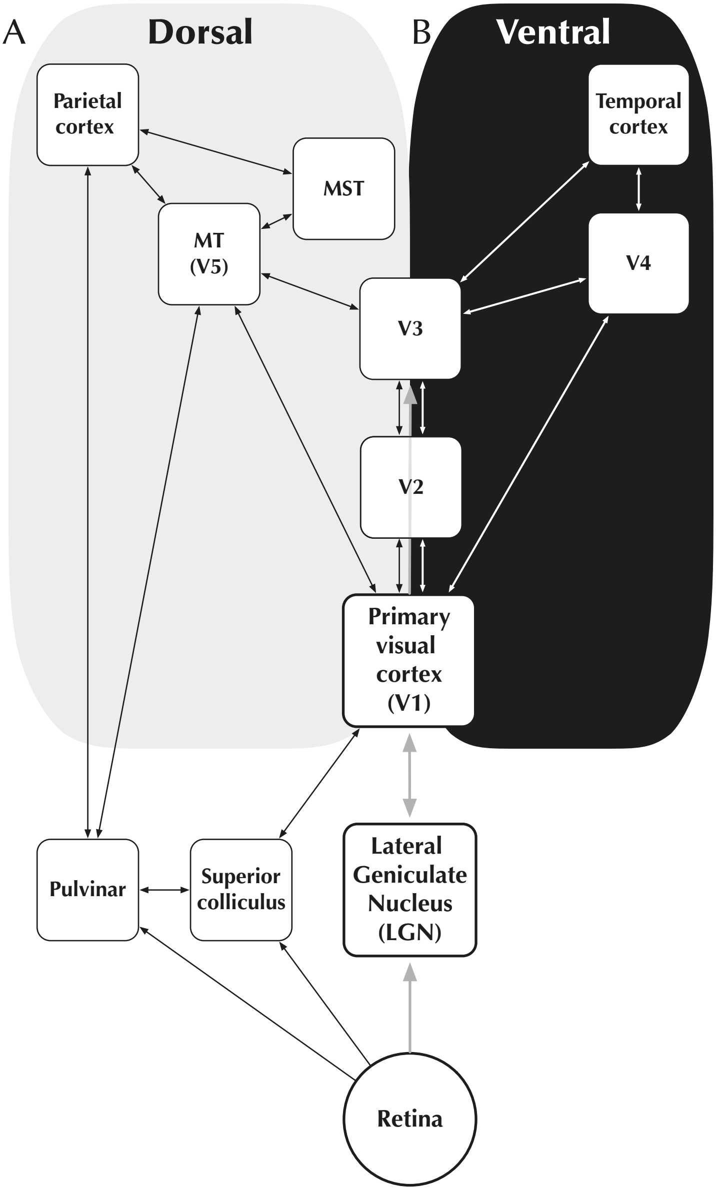

Figure 6.1. *The most principal pathways from the retina to the visual cortices.*

The remaining limitations likely arise from immaturities in the pathway from the retina through the lateral geniculate nucleus to the primary visual cortex (V1) (see Figure 6.1): neurons in the lateral geniculate nucleus and the primary visual cortex are less sensitive than in adults, at least in the monkey (Blakemore, 1990; Blakemore & Vital-Durand, 1986; Kiorpes, 2016; Movshon & Kiorpes, 1993), and synaptic density in the human primary visual cortex continues to increase until about 8 months after birth (Huttenlocher, 1990), later to be pruned back to adult levels, presumably based on experience. Underlying these changes are shifts in the predominance of different types of cortical receptors that mediate excitatory versus inhibitory responses (Siu & Murphy, 2018).

6.1.3 Peripheral Vision and Stereopsis

Newborns' peripheral vision is also limited. When shown a large (6°) flashing light in the periphery, newborns orient toward it only out to 30° while adults can detect it past 100° (Lewis & Maurer, 1992). Over the next 4 months, the visual field expands rapidly to reach nearly adult extent for such large stimuli. However, sensitivity to smaller and dimmer stimuli continues to improve into middle childhood (Bowering, Maurer, Lewis, Brent, & Riedel, 1996). Moreover, throughout infancy, babies respond to peripheral stimuli much less frequently if the stimulus is static rather than flickering (Delaney, Dobson, Mohan, Harvey, & Harvey, 2004), if they are already attending to something in the central visual field ("sticky fixation": Hood & Atkinson, 1993), or if they are viewing monocularly while the stimulus is in their nasal visual field (across the nose) (Lewis & Maurer, 1992). The consequence is that newborns are mainly aware of objects only if they are large and in a tunnel in front of either the right or left eye. These limitations in peripheral vision arise, at least in part, from immaturities between the primary visual cortex and the networks controlling eye movements (Maurer & Lewis, 1998). Only objects dead ahead functionally stimulate both eyes – and initially those two eyes work independently. It is not until several months after birth that the inputs from the two eyes fuse into a binocular image (3 months) and begin to mediate the perception of three-dimensional depth (4 months: stereopsis) (E. E. Birch, Gwiazda, & Held, 1982; Braddick, Wattam-Bell, Day, & Atkinson, 1983; Gwiazda, Bauer, & Held, 1989). Mom's face is processed independently by each eye as she leans over her newborn's crib but out of sight once she moves even a little bit off to the side.

6.2 Importance of Early Visual Experience for the Development of Low-Level Vision

Despite these limitations, early visual experience is critical for later visual development. The clearest evidence comes from children who were born with cataracts in both eyes that blocked all patterned visual input until the cataracts were removed surgically and the eyes fit with compensatory contact lenses (Maurer, Lewis, Brent, & Levin, 1999). At the time that the treated infants can first see, their acuity is like that of a normal newborn, even when treatment occurs 2–8 months after birth. Thus, the rapid improvement in babies with normal eyes immediately after birth must depend on visual experience: it fails to occur when that experience is missing because of cataracts. Treated infants show rapid recovery that normalizes visual acuity by 12 months of age (Lewis, Maurer, & Brent, 1995). Nevertheless, deficits in all aspects of low-level vision emerge later: Adults treated during infancy for bilateral congenital cataracts later have abnormal acuity, contrast sensitivity, peripheral vision, and stereopsis, even when treatment occurred before 2 months of age (E. E. Birch, Cheng, Stager, Weakley, & Stager, 2009; Bowering, Maurer, Lewis, & Brent, 1993; Bowering et al., 1996; Ellemberg, Lewis, Maurer, Lui, & Brent, 1999; Tytla, Lewis, Maurer, & Brent, 1993). These "sleeper effects" that emerge later (Maurer, Mondloch, & Lewis, 2007) indicate that early visual experience – at a time when infants' vision is poor – is, nevertheless, critical for setting up the visual neural architecture for later refinement.

The outcome is worse when the baby was born with a cataract in only one eye. Vision in the treated eye – acuity, contrast sensitivity, and peripheral vision – are worse than in eyes treated for bilateral congenital cataracts, unless there had been extensive patching of the "good" eye throughout early childhood (Lewis & Maurer, 2009). This pattern indicates that during infancy the two eyes – which begin by functioning independently – compete for cortical connections, and when one eye sends better input – because it is a normal eye – and the other eye sends weaker input – because there is no patterned input before removal of a cataract and then less sharp input after treatment – one eye will develop better vision at the expense of the affected eye. However, even the good eyes in children treated for monocular congenital cataract later have subtle deficits in acuity (Lewis, Maurer, Tytla, Bowering, & Brent, 1992). Thus, visual experience in the perinatal period that is balanced between eyes is critical if the child is to later develop normal vision in both eyes. When the input is monocular, both the deprived eye and the "normal" eye fail to develop optimal vision.

On the other hand, extra-visual experience because of premature birth does not lead to any advantage: Acuity and binocular vision develop based on gestational age, rather than the number of months of postnatal experience (Weinacht, Kind, Mönting, & Gottlob, 1999). On many measures, premature babies even lag behind, especially if they were born very early, for example, before 30 weeks gestation (Hou et al., 2011). The overall pattern suggests that the visual cortex is experience-expectant after 40 weeks of gestation – that the cortex evolved to profit from visual experience during a critical period near birth, when many types of neurotransmitter have become functional (Siu & Murphy, 2018).

6.3 Cultural Variations: Effect of Diet on the Development of Low-Level Vision

Cultural variations in diet may influence the baby's visual development because of the influence of long-chain polyunsaturated fatty acids in the mother's diet during pregnancy, in the mother's breast milk, or included as an additive to the baby’s formula. Critical are docosahexaenoic acid (DHA) and arachidonic acid (ARA). These fatty acids support neural development during the last trimester of pregnancy and the early months of development, greatly increasing their concentration in gray matter over this period (E. E. Birch et al., 2007; Hoffman, Boettcher, & Diersen-Schade, 2009). DHA has an especially high concentration in retinal photoreceptors and appears to affect both myelination and synaptic formation throughout the nervous system. Infants cannot generate adequate DHA and ARA endogenously and must obtain it from breast milk or from supplemented formula, supplementation that became common only after 2002. Preterm infants fed formula containing long-chain fatty acids show better retinal development (as indexed by the electroretinogram) (D. G. Birch, Birch, Hoffman, & Uauy, 1992) and better visual acuity (especially when indexed by visually evoked responses) than preterm babies fed unsupplemented formula (E. E. Birch, Birch, Hoffman, & Uauy, 1992). Even full-term babies fed supplemented formula have visual acuity that is better than that of age-matched babies fed formula without the supplement and as good as babies fed human breast milk (Hoffman et al., 2009). Comparisons of groups fed in different ways postnatally reveal differences in visual acuity as late as 4 years after birth (E. E. Birch et al., 2007). Although these differences are small and there is considerable overlap in acuity between groups, in animal (rodent) models the changes effected in neurotransmitters from inadequate diets are not reversible after weaning (Kodas et al., 2004).

The levels of ARA and DHA in breast milk vary cross-culturally over a 4-fold and 18-fold range, respectively (Brenna et al., 2007). Levels are higher in societies where fish is a regular part of the diet (e.g., Japan, Canadian Arctic, Philippines) than in societies where eating fish is rare (e.g., Pakistan, Europe, the United States, and the rest of Canada). A causal relation is suggested by the finding that the concentration of DHA in maternal blood is directly related to the amount of oily fish that she consumes (Williams, Birch, Emett, & Northstone, 2001). Moreover, maternal consumption of oily fish during the pregnancy is related to the infant’s later visual development, presumably through fetal exposure to DHA: Children 3.5 years old whose mothers ate oily fish at least once every 2 weeks during pregnancy had better stereo (3-D) vision than those whose mothers never ate oily fish, even after controlling for postnatal diet (Williams et al., 2001).

Together, the evidence on the effect of diet suggests that there may be considerable variation cross-culturally in retinal and visual cortical development and the fine visual resolution they come to mediate. Newborns are known to differ in the quality of the visual input they receive with which to build their cortical circuitry – the quality is lower for babies born preterm or with peripheral visual perturbations like cataracts. Additional differences may arise from variations in provision of ARA and DHA through the maternal diet prenatally, breast milk postnatally, and/or the composition of formula. Not only will such variation influence the initial visual input made available through retinal processing but it may affect the ultimate acuity achieved: One can speculate that the distribution of visual acuities (with any necessary optical correction) may be shifted toward finer values in cohorts living in countries where the eating of oily fish during pregnancy and breast-feeding have always been common (e.g., high Canadian Arctic, Philippines) than in cohorts where this is uncommon and/or formulas had not yet been supplemented with fatty acids. Although this pattern has been documented for stereoacuity at 3.5 years of age (see above), the prediction about the distribution of adult acuities is speculative because there has been no study that compared the distributions in different geographic regions or across different time periods.

6.4 Higher-Level Vision: Motion Processing

6.4.1 Newborns' (In)Sensitivity to Direction of Motion

Newborns fail most tests of sensitivity to motion, whether tested for sensitivity to the direction of motion with visually evoked potentials or with preferential looking. For example, when shown a stimulus with uniformly moving dots versus a stimulus in which a form is defined by dots moving in a direction opposite the background, infants show no preference to look at the motion-defined form before 7 weeks of age and then do so only for a restricted range of velocities, namely, dots moving about 5–10 deg/second (Wattam-Bell, 1996b). This is the same age at which sensitivity to direction of motion is first evident in visually evoked potentials (Braddick, Birtles, Wattam-Bell, & Atkinson, 2005; Wattam-Bell, 1991). Even so, babies do not show evidence of discriminating between two directions of uniform motion until after 9–12 weeks of age (Armstrong, Maurer, Ellemberg, & Lewis, 2011; Wattam-Bell, 1996a): after habituation to one direction of motion, before that age they do not show renewed interest when the direction is shifted by 180°. Newborns' preference for moving over stationary stimuli, therefore, likely is a preference for the flicker induced by the moving stimuli when the infant maintains fixation on a selective part of it. The slow development of sensitivity to direction of motion contrasts with the earlier development of sensitivity to the orientation of stationary stimuli, whether measured with habituation/dishabituation (Maurer & Martello, 1980) or visually evoked potentials (Braddick et al., 2005). The limitations in sensitivity to motion likely reflect immaturities in the primary visual cortex and the retinal input it receives (see above) since it is the first cortical way station where individual neurons are tuned to direction.

6.4.2 Surprising Exceptions: Sensitivity to Evolutionarily Important Global Patterns of Movement

Despite apparent insensitivity to direction of motion, from birth infants prefer to look at certain overall patterns of movement, specifically those signaling that an object is going to strike the baby's face and those signaling that the movement comes from a biological organism. For example, they fixate a video of a striped ball moving toward them in preference to one moving away or one on a trajectory that will miss the face (Orioli, Filippetti, Gerbino, Dragovic, & Farroni, 2018). The sensitivity to collision is likely based on sensitivity to the optical expansion of a stimulus as it approaches the face, filling more and more of the visual field, modulated by sensitivity to whether the expansion is symmetrical (as it will be if the object is on a trajectory colliding with the face) or not (as it will be if the trajectory will miss the face).

Another exception is sensitivity to *biological motion*, the special trajectories of motion formed by the joints of biological organisms, which is commonly tested by point light displays in which the baby sees only the movement trajectories of lights affixed to those joints. From birth, babies look longer at a pattern of dots moving like a biological organism (such as a walking hen) than a pattern with the same dots moving in random directions or inverted, or a pattern of rigid nonbiological motion (a rotating object) (Bardi, Regolin, & Simion, 2011; Simion, Regolin, & Bulf, 2008). However, the preference disappears if the biologically moving display is pitted against a display with the dots scrambled spatially (Bardi et al., 2011) or against randomly moving dots following the same pattern of translation (e.g., moving sideways to the left) (Bidet-Ildei, Kitromilides, Orliaguet, Pavlova, & Gentaz, 2014). Both results suggest that the initial preference is based on some innate sensitivity to certain patterns of movement that are present in moving human organisms but that are not human-specific.

What this means for the newborn's perception is that modulation attracts attention – the flickering input on the retina induced by limited scanning (Salapatek & Kessen, 1966) of moving stimuli – with special sensitivity to modulation coming toward the baby's face or from a biological organism. Initially the baby will perceive local motion within an object – such as moving lips as the mother talks or changes her facial expression – only as change, not as movement in a particular direction. Nevertheless, the change will attract the baby's attention and hence bias the baby's visual experience. The initial sensitivities ensure that young infants will preferentially attend to human adults over inanimate objects in their environment because adults frequently move into the baby's field of view and do so with the signature movement patterns of a biological organism, enhanced by being on an approaching trajectory.

When 7-week-old infants are shown dots moving coherently in a pattern of expansion (looming, signaling collision), or spiraling inward or outward compared to randomly moving dots, there is selective fMRI activation for the coherent motion in areas active under the same conditions in adults, namely throughout the dorsal stream, including likely areas V3 and MT and their projections to the parietal cortex (see Figure 6.1; Biagi, Crespi, Tosetti, & Morrone, 2015). One possibility is that during early infancy, input reaches these higher cortical areas not via V1 as it does in adults, but mainly via the retinal-pulvinar pathway, as has been documented anatomically in the developing marmoset (Warner, Kwan, & Bourne, 2012). With age, the pulvinar input to the marmoset's MT diminishes as V1 input increases in magnitude. That type of reorganization is supported by evidence in humans that the topography of visually evoked potentials induced by global motion is different at 4–5 months of age from that shown in adults (Wattam-Bell et al., 2010).

Similarly, the early preferences for biological motion may be mediated by pathways that largely bypass the primary visual cortex yet innervate higher motion processing systems, including MT/MST and STS (biological motion). (See Figure 6.1 for a schematic drawing of the motion visual pathways; STS is a more central hub receiving input from several dozen structures, including MT and MST.) Later sensitivity may reflect the increased influence of input through the primary visual cortex to these higher cortical areas. Just such a reorganization is suggested by research on newborns' preference to look at upright biological motion over an inverted version with the frames in reverse order. Unlike newborns (Simion et al., 2008), 2-month-olds fail to show a looking preference for the upright version, with the preference re-emerging from 3 months of age (Sifre et al., 2018). This apparently U-shaped developmental trajectory may represent early sensitivity mediated by an early experience-expectant mechanism that is largely subcortical (Sifre et al., 2018) and biased for certain patterns of local motion typically made by moving limbs (Bardi et al., 2011), without any sensitivity to the biological form itself (Chang & Troje, 2009). Only later may an experience-dependent and cortically mediated mechanism emerge that is sensitive to those configural cues and affected by learning (Chang & Troje, 2009).

6.5 Importance of Early Visual Experience for the Development of Motion Processing

Children who missed early visual input because of dense cataracts in one or both eyes later have only small deficits in processing the direction of motion in sine wave gratings when local cues are sufficient and no global integration is required (Ellemberg et al., 2005). However, when global integration is required because only some dots are moving coherently in the same direction while the rest move randomly (e.g., in a random dot kinematogram testing sensitivity to the direction of global motion), adults treated for congenital cataract have significant deficits even when the deprivation began at birth and lasted only a few months. When tested as adults, those treated for bilateral congenital cataracts have greatly elevated thresholds, such that roughly 50% of the dots have to move coherently for them to detect the direction while adults with normal vision can do so with fewer than 10% of the dots moving coherently. This is another example of a sleeper effect (Maurer et al., 2007): Visual deprivation early in life – before the capability is manifest in babies with normal eyes – prevents *later* normal development of processing of global motion. No such deficit is evident in patients treated for dense bilateral cataracts that developed postnatally between 1 and 10 years of age: Despite acuity deficits secondary to the visual deprivation, their sensitivity to global motion is completely normal (Ellemberg, Lewis, Maurer, Brar, & Brent, 2002; see also Fine et al., 2003). This pattern supports the hypothesis that some aspects of sensitivity to global motion depend on postnatal experience, as does visual acuity, but that the timing of the needed experience varies from a short critical period for global motion to a much longer one for visual acuity. Similar tests of sensitivity to global form also reveal deficits, although they are smaller than the deficits for global motion (Lewis et al., 2002), suggesting more damage to the dorsal pathway (Figure 6.1A) than the ventral pathway (Figure 6.1B).

Despite the deficits in sensitivity to global motion, patients treated for bilateral congenital cataracts are normal at detecting the presence of biological motion (compared to motion with the trajectories spatially scrambled), even when moving masking dots are superimposed on the stimulus (Hadad, Maurer, & Lewis, 2012). Like adults with normal vision, they can still detect which of two patterns contains the biological motion when more than 70 masking dots are superimposed (Hadad et al., 2012). Similar to the findings on normal development, this pattern suggests that more than one mechanism is at work: an early developing experience-expectant mechanism that allows the newborn to pick out biological motion and that continues to be able to mediate that behavior after early visual deprivation, and two later developing experience-dependent mechanisms that mediate sensitivity to the *direction* of global motion and the *form* of the moving organism. The first mechanism is evident at birth and even after early visual deprivation, dependent only on there having been normal development in the womb without the necessity of *visual* experience; the second are manifest only postnatally and only when there has been patterned visual input. Unclear from these experiments is whether the visual experience must involve exposure to moving stimuli (for global motion) and pattern elements (for global form). However, studies of kittens raised without exposure to moving stimuli – because the environment was lit by stroboscopic light – suggest that experience with moving stimuli may be necessary. After strobe rearing, cats have normal sensitivity to orientation but can discriminate opposite directions of motion only at high contrast and they have fewer cortical neurons tuned to direction (Humphrey & Saul, 1998; Pasternak & Leinen, 1986).

Further insights arise from comparisons to children treated for unilateral congenital cataracts who, as described above, have larger deficits than patients treated for bilateral congenital cataracts in basic visual capabilities like acuity, contrast sensitivity, and peripheral vision. They, too, manifest deficits in integrating local signals into a global perception of motion or of form, but, unlike bilateral patients, their thresholds are only slightly elevated compared to adults with normal eyes (Ellemberg et al., 2002; Lewis et al., 2002). Thus, the integrative processes mediated by the dorsal pathway (see Figure 6.1A) for motion processing and by the ventral pathway for form processing (see Figure 6.1B) can develop almost normally when there was normal visual input through one eye throughout life. Neurons in the visual cortical pathway in areas beyond the primary visual cortex are predominantly binocular, with larger receptive fields than in primary visual cortex and less spatial resolution. The consequence is that input from just one eye before treatment and from a second eye with poor acuity after treatment may be sufficient to induce nearly normal development for these higher visual areas but be inadequate for tuning the neurons in primary visual cortex that mediate basic low-level visual capabilities.

What goes wrong in children treated for bilateral congenital cataract that prevents such recovery, especially in dorsal stream areas? One possibility is that, in the absence of visual input, those areas start responding to input from other sensory modalities, as happens in the congenitally blind (Renier, de Volder, & Rauschecker, 2014), and continue to do so after treatment. Indeed, as in the congenitally blind, there is activation in the dorsal *visual* cortex, around area V3, when adults treated for bilateral congenital cataracts do *auditory* processing (Collignon et al., 2015). Unlike adults with normal vision, in such patients, a motion aftereffect induced by sound transfers to vision (Guerreiro, Putzar, & Röder, 2016): After hearing a sound that increases in loudness to simulate an approaching object, adults treated for bilateral congenital cataracts, unlike controls, perceived a pattern of squares to be increasing in size as if they were approaching the face. That transfer suggests that the auditory input to the visual cortex may be functional. Input from one eye during the period of deprivation may be sufficient to prevent such rewiring in children treated for unilateral congenital cataract. If this interpretation is correct, then during normal development, visual input during infancy is not only setting up the visual cortical architecture for later refinement, it is also preserving the dorsal visual pathway as a visual processor.

Getting this visual experience early – because of premature birth, however, is not beneficial. Even in the absence of any detectable neurological problems, during infancy, such children show delays in developing visually evoked potentials to changes in the direction of motion (Birtles, Braddick, Wattam-Bell, Wilkinson, & Atkinson, 2007) and, during middle childhood, they have elevated thresholds for seeing global motion (Taylor, Jakobson, Maurer, & Lewis, 2009). Enhancing the diet of preterm babies promotes better neurological growth, including white matter growth, and normalizes the directionally selected visually evoked potential recorded at 5 months corrected age (Blakstad et al., 2015). The deficits in motion processing contrast with normal visually evoked potentials to changes in orientation during infancy (Birtles et al., 2007) and, in middle childhood, normal thresholds for discriminating changes in orientation (MacKay et al., 2005) and in seeing static global form (Taylor et al., 2009). The pattern is consistent with "dorsal vulnerability" (Atkinson et al., 1999), that is, especial vulnerability of the dorsal pathway through the primary visual cortex to areas V3 and V5 (MT/MST; see Figure 6.1) that mediates the processing of motion compared to less vulnerability of the ventral pathway to the ventral extrastriate cortex (e.g., V4 and fusiform face area in temporal cortex; see Figure 6.1) that mediates the processing of form and its properties. When some abnormality affects the development of higher levels of the visual cortex, be it visual deprivation, prematurity, brain damage, or genetic disorders like fragile X or Williams syndrome, it is the dorsal stream that is more likely to be affected adversely (Braddick & Atkinson, 2011). Nevertheless, the pattern of deficits is not hierarchical – they do not increase monotonically from lower to higher cortical areas or from low-level to higher-level visual processing: Like children treated for bilateral congenital cataracts, babies born premature have (almost) normal sensitivity to biological motion, a capability that requires integration of form and motion information (Taylor et al., 2009) and that is mediated by a complex network of dorsal and ventral pathway structures, including the superior temporal sulcus (STS; Giese & Poggio, 2003).

6.6 Higher-Level Vision: Face Processing

6.6.1 Detecting Faces

The immaturities in newborns' acuity and contrast sensitivity result in severe limits on the information they can perceive in a face, especially if it is more than a foot away. One simulation (von Hofsten et al., 2014) shows faces at that distance preserve the shape of the head framed by hair, but very few details about the internal features, which look merely like dark blobs. At 2 feet, even the dark blobs begin to disappear. Picking up information about the internal features is further limited by the newborn's bias to scan the external contour of the face (the dark transition from face to hair) (Hainline, 1978; Haith, Bergman, & Moore, 1977), rarely looking at the internal features. Nevertheless, already at birth, or perhaps even during the last trimester of pregnancy (Reid et al., 2017), infants have some sensitivity to face-like properties in the arrangement of the internal features. Within the first hour after birth, they look preferentially toward faces over other visual stimuli with the same amount of visible energy (Johnson, Dziurawiec, Ellis, & Morton, 1991; Mondloch et al., 1999), especially if the face is oriented frontally with direct gaze (Farroni, Menon, & Johnson, 2006). The preference is based only on very low spatial frequencies (de Heering et al., 2008) and may be mediated in part by peripheral vision (Morton & Johnson, 1991; Johnson, Senju, & Tomalski, 2015).

Newborns' preference to look at face-like stimuli does not appear be an attraction specifically to faces but rather an attraction to stimulus properties like being top-heavy (having more elements in the top half), having congruent structure (the outer contour is widest where the internal features are also widest), and having positive polarity (black elements on a white background) (Cassia, Turati, & Simion, 2004; Simion & Giorgio, 2015). A looking preference is manifest whenever a schematic drawing containing these properties is pitted against other drawings without them and the preference may be mediated subcortically through the superior colliculus (see Figure 6.1; Johnson, 2005; Johnson et al., 2015), rather than the ventral cortical pathway that will come to mediate face processing (see Figure 6.1). The looking preference generalizes to nonface-like schematic drawings (Cassia et al., 2004) and to monkey faces (Di Giorgio, Leo, Pascalis, & Simion, 2012). Regardless of the basis for the preference, however, it assures that the newborn infant is biased to attend to faces over other stimuli in the environment and will prefer to look at an upright human face rather than an inverted face because only the former has the requisite properties.

6.6.2 Learning About Individual Faces

Already at birth, newborns can learn about faces they encounter repeatedly, like those of their parents. When tested with habituation in the lab, after repeated exposure to the face of one unfamiliar woman, they show recovered interest for a different unfamiliar woman and can do so even after sleeping for 2 hours (Cecchini et al., 2017) and even when required to generalize from *en face* to 3/4 view (Turati, Bulf, & Simion, 2008). Not surprisingly, they show evidence of recognizing the mother's face within a few days after birth (Pascalis, de Schonen, Morton, Deruelle, & Fabre-Gremet, 1995), even when the cumulative exposure is just a few hours (Bushnell, 2001), at least if it has been accompanied by the mother's voice (Sai, 2005). Newborns' recognition of individual faces is likely to be based on scanning the external features of the face (Haith et al., 1977) and noting something about very blurry internal features from peripheral vision: When the images of mom and the contrasting stranger wear identical scarves, evidence of recognition disappears (Pascalis et al., 1995; see Turati, Macchi Cassia, Simion, & Leo, 2006 for similar results for the discrimination of two strangers' faces). Nevertheless, information about individual faces is fed into developing cortical pathways.

By 3 months of age, acuity and contrast sensitivity have improved sufficiently to allow many more details of faces to be visible. Perhaps as a consequence, babies now scan the internal features of faces, shifting among them rapidly, with a bias to come back repeatedly to the eyes (Haith et al., 1977; Maurer & Salapatek, 1976). By 3 months, the baby has also developed the cognitive ability to average faces across presentations to form a prototype to which future encounters are compared (de Haan, Johnson, Maurer, & Perrett, 2001).

Forming a prototype is a prerequisite for the formation of the multidimensional face space that underlies adults' efficient processing of faces (Rhodes & Jeffery, 2006). The possibly related ability to process faces holistically, rather than piecemeal, develops at the same age (Turati, Di Giorgio, Bardi, & Simion, 2010). The consequence of these developments is that babies' accumulating experience can be organized across viewpoints and facial expressions. At the same time, the baby develops more complex face preferences, looking preferentially at faces with more face-like structure even when the comparison stimuli are matched on the originally preferred basic structural properties like top-heaviness (Turati, Valenza, Leo, & Simion, 2005).

6.7 Cultural Biases in the Tuning of Early Face Processing

6.7.1 Face Input

The face input that tunes infants' face processing is not a representative sample of the world, but rather restricted initially to people who resemble the baby's mother. Those faces are predominantly female, own race, and of adult age, even in a city as multicultural as Toronto (Sugden, Mohamed-Ali, & Moulson, 2014). Cameras mounted on the heads of young infants indicate that they see faces more often than objects, that the faces are usually upright and facing them at a close distance, and that a small handful of faces are present repeatedly and for a relatively long duration (Jayaraman & Smith, 2018; Sugden et al., 2014; Sugden & Moulson, 2017). This biased experience combines with the infant's attentional bias toward face-like structure to guarantee that developing cortical systems receive upright face input and that the input promotes learning to recognize a few individual faces. After the first 3 months, the exposure changes to more often involve hands or other body parts, rather than the face, such that face exposure when a person is present decreases by a factor of 3 between 3 and 18 months of age (Jayaraman, Fausey, & Smith, 2017).

Given the female bias (70% of faces overall in Sugden et al., 2014), it is not surprising the infants' face processing at 3 months is more discriminating for female than male faces, unless the baby is being reared by a male rather than female caretaker (Quinn, Yahr, Kuhn, Slater, & Pascalils, 2002). This difference for male and female faces emerges by 3 months of age but only for same-race faces, that is, faces of the type to which the baby has been exposed (Quinn et al., 2008). At this age, infants show a looking preference for both female and for own-race faces over male and other-race faces (Bar-Haim, Ziv, Lamy, & Hodes, 2006; Kelly et al., 2005; Kelly, Liu et al., 2007; Quinn et al., 2002). At 3 months, babies do not yet seem to integrate the processing of internal and external features of faces (Cashon & Cohen, 2004) or to be sensitive to differences in the spacing of the internal features (Bhatt, Bertin, Hayden, & Reed, 2005), both of which are fundamental components of adults' expertise in face processing (Maurer, Le Grand, &

Mondloch, 2002). These skills are only evident by 4–6 months of age (Ferguson, Kulkofsky, Cashon, & Casasola, 2009; Hayden, Bhatt, Reed, Corbly, & Joseph, 2007), initially for all faces, be they upright or inverted, own or other race.

6.7.2 Perceptual Narrowing: Tuning to Human Species and Own Race

Over the first year of life, babies' face processing improves (see previous section) but at the same time becomes specialized for the categories of faces that are most commonly seen, namely, upright human faces matching the baby's ethnicity. This phenomenon – termed perceptual narrowing – has been well documented for both species (human vs. nonhuman primate) and for ethnicity (matching that of the baby or not).

6.7.3 Species

At birth, babies have no looking preference for human over monkey faces (Di Giorgio et al., 2012) and as late as 6 months, babies can discriminate as readily between two monkey faces as between two human faces (Pascalis, de Haan, & Nelson, 2002). At 9–12 months, however, babies fail to show discrimination between monkey faces when tested with the same paradigm, while continuing to "pass" for human faces (Fair, Flom, Jones, & Martin, 2012; Pascalis et al., 2002; Pascalis et al., 2005). A similar pattern has been documented for sheep faces (Simpson, Varga, Frick, & Fragaszy, 2011). Evidence of discrimination can be recovered by extending the exposure time (Fair et al., 2012) or by giving the baby experience looking at individually named pictures of monkeys (Pascalis et al., 2005; Scott & Monesson, 2009). Nevertheless, it is evident that toward the end of the first year of life, biased exposure to human faces leads babies to improve their skill at individuating human faces while their skill at doing so for nonhuman faces is attenuated.

6.7.4 Race

At birth, babies have no looking preference for faces matching their own ethnicity (and hence the ethnicity of the faces to which they are most likely to be exposed), but by 3 months they already have a looking preference for "own-race" faces, unless they are being raised in an environment in which they are exposed to both the "own" and the "other" category on which they are tested (Bar-Haim et al., 2006; Kelly, Liu et al., 2007). As with monkey faces, initially babies can discriminate as readily between other-race as own-race faces but by 9 months they fail the same tests with other-race faces (Heron-Delaney et al., 2011; Kelly, Quinn et al., 2007; Kelly et al., 2009; Sugden & Marquis, 2017; Vogel, Monesson, & Scott, 2012). As with species, the other-race discrimination failures can be overcome by encouraging babies to attend to their features by, for example, exposing the baby to named individuals of the rarely encountered race (Anzures et al., 2012; Heron-Delaney et al., 2011) or using spatial cuing to encourage babies to attend to the location where the other-race face appears (Markant, Oakes, & Amso, 2016).

6.7.5 Other Domains

Perceptual narrowing occurs across a number of domains over the first year of life (Maurer & Werker, 2014) in each case biasing the baby's discriminations to the categories the baby has experienced. This happens for speech distinctions in the language the baby hears versus other languages; for human versus animal voices; and for matching talking faces to the accompanying sound track. Although the timing of the narrowing may differ across domains, they have in common the attunement of the baby's perceptual categories to stimuli emanating from his/her own cultural group. The baby learns to recognize members of his/her own "tribe" and to treat members of other groups simply as "other." In fact, by 6 months, babies match the sound of a nonnative language with an other-race face (Uttley et al., 2013).

6.8 Importance of Early Visual Experience for the Development of Face Processing

Perceptual narrowing provides evidence that changes in face processing are driven by the statistics of the faces that the baby encounters during the first year of life. When the baby fails to see any faces during early infancy – because bilateral congenital cataracts block all patterned input to both eyes – developmental changes in face processing fail to occur both during infancy and later in development. When the babies can first see after the cataracts are removed and the eyes given corrective contact lenses, they select face-like patterns matching the preferences of normal newborns, rather than age mates with postnatal visual experience (Mondloch, Lewis, Levin, & Maurer, 2013), just as is the case with their visual acuity (Maurer et al., 1999). In other words, neither more complex face preferences nor better acuity emerge in the absence of visual input. Unlike acuity, the improvements in face preferences after treatment are not accelerated but take the normal number of months of visual experience: for example, only after 3 months of visual experience do face preferences begin to match those of 3-month-old babies with normal eyes (Mondloch, Lewis et al., 2013). By late infancy, the ability of infants treated for bilateral congenital cataracts to detect facial structure appears to be normal and this normality is corroborated when they are tested as adults: They have normal accuracy and response times to distinguish intact and scrambled facial structure (Mondloch, Segalowitz et al., 2013). Nevertheless, event-related potentials reveal that the neural network underlying this normal adult performance is altered: The adults deprived of visual experience in infancy demonstrate the normally larger N170 to a face than to a scrambled image but its amplitude is roughly double that of controls and it occurs after a significantly longer latency. A similarly increased amplitude is evident for the P100 and the response to scrambled faces. The amplified response to photographs of faces is correlated with the duration of the initial deprivation. Thus, normal visual experience is necessary for the postnatal changes in face preferences *and* for their normal efficient neural processing.

Patients treated for bilateral congenital cataract show later deficits in other aspects of face processing. When asked to indicate whether or not two faces are the same, they are as good as controls when the faces differ only in the shape of the external contour or only in the shape of the eyes and mouth, but make more errors than controls when the only difference is the location of the eyes and mouth, a cue termed "spacing" or "second-order relations" (Le Grand, Mondloch, Maurer, & Brent, 2001; Mondloch, Le Grand, & Maurer, 2003; Mondloch, Robbins, & Maurer, 2010).This is the condition in which adults with normal eyes are experts – as long as faces are upright, that is, as long as they match the condition to which experience is biased from early infancy (Maurer et al., 2002). When the accuracy plummets for adults with normal vision because the faces are inverted or the same spacing differences are introduced into monkey faces, adults treated for bilateral congenital cataracts perform normally (Maurer et al., 2002; Robbins, Nishimura, Mondloch, Lewis, & Maurer, 2010. Thus, early visual experience appears to be necessary to set up the neural circuitry for later refinement of sensitivity to spacing specifically in upright human faces, an ability that normally emerges during infancy (Bhatt et al., 2005) and improves into middle childhood (Mondloch, Le Grand, & Maurer, 2002). Studies of adults treated for unilateral congenital cataract suggest that it is early input to the right hemisphere that is especially important (Le Grand, Mondloch, Maurer, & Brent, 2003). fMRI data suggest that it is connectivity within the extended face network centered in the temporal cortex (see Figure 6.1) that is altered by early visual deprivation (Grady, Mondloch, Lewis, & Maurer, 2014).

The difficulty of adults treated for bilateral congenital cataract in perceiving subtle differences in the spacing of the features of upright human faces may be related to their piecemeal processing of facial features, unlike the more holistic processing of adults with normal vision. A sensitive test of holistic processing is the "composite face effect": The task is to decide whether the top halves of two faces are the same while ignoring their different bottom halves. Holistic processing makes it difficult – unless it is broken by misaligning the top and bottom halves or inverting the face (Mondloch & Maurer, 2008; Young, Hellawell, & Hay, 2013). Adults treated for bilateral congenital cataracts, however, are good at the task even with upright aligned faces: their superior accuracy to controls indicates that they do not process faces holistically (de Heering & Maurer, 2014; Le Grand, Mondloch, Maurer, & Brent, 2004). Thus, even though holistic face processing normally emerges postnatally (Nakato, Kanazawa, & Yamaguchi, 2018; Turati et al., 2010), it fails to emerge in babies who missed early experience with faces because of congenital cataracts – another sleeper effect (Maurer et al., 2007). Critical to the difference between babies with normal eyes and those treated for congenital cataracts may be the timing of first exposure to faces (different neurotransmitters present when exposure is delayed by treatment for cataracts), the initial density of faces as the learning takes place (higher in early infancy than later after treatment because parents' behavior changes), and/or the blurriness of the input as the initial representations are formed (blurred in newborns with normal eyes and poor acuity vs. rapidly improving acuity in treated infants) (Jayaraman et al., 2017; Vogelsang et al., 2018).

Babies whose visual experience with faces is altered by being born premature also follow an abnormal developmental trajectory. At birth, they do not show the standard preferences for face-like stimuli (Pereira et al., 2017) and at 6–10 months corrected age, the brain's response to the mother's face is smaller in the right frontotemporal cortex than in controls and not normally differentiated from the response to a stranger's face (Frie, Padilla, Ådén, Lagercrantz, & Bartocci, 2016). Thus, extra exposure to faces in the preterm nursery at an earlier-than-normal time appears not to be beneficial and may even interfere with the normal development of face processing.

6.9 Summary and Policy Implications

Newborns' vision is limited to large stimuli of high contrast in the central visual field. Nevertheless, that type of visual input is necessary for the system to be refined later for low-level visual sensitivity (acuity, contrast sensitivity, and peripheral vision), as well as for higher-level integrative perceptual processing (of global motion, global form, and facial identity). In the absence of visual input, development, at least of acuity and of face processing, the only two tested longitudinally, appears to be in stasis and the input received after treatment is not sufficient to offset the delay. One reason may be the encroachment of input from other sensory modalities during the visual deprivation, input that forms functional synapses that remain after the cataracts are removed. When the deprivation is monocular rather than binocular, such encroachment may be prevented. When the perturbation is premature birth, the extra and early visual experience appears not to aid visual development.

In the child with normal eyes, patterned visual input near the time of normal birth appears to be critical to set up the neural pathways for later refinement. Delayed input is inadequate, as is the mistimed input in the preterm nursery. The timing may be so critical because of changes in excitatory versus inhibitory neurotransmitters and their balance, as well as in myelination, which make experiential effects more likely at certain points in development (Hensch & Quinlan, 2018; Siu & Murphy, 2018).

The implication of these findings is that any condition or treatment that blocks early visual input is to be avoided when possible. If it is necessary – like patching an eye after surgery or covering the eyes during photo treatment for jaundice – the period of deprivation should be as short as medically allowed and relieved, when possible, by periods of visual stimulation (e.g., a 2-hour break from jaundice treatment with the blindfold off). When visual input cannot be normal, it would be wise to begin therapeutic compensation during infancy, rather than wait until deficits emerge later in development.

The evidence on perceptual narrowing indicates that early visual experience affects the tuning of every baby's visual processing to match the characteristics of faces and speech most often experienced. That experience appears almost always to be biased toward the baby's own ethnic group. By the end of the first year of life, the baby has improved ability to discriminate among speech sounds and faces from the own-race group but has begun to process speech and faces from other groups at the categorical ("speech" or "face") level, no longer processing enough details to make individual discriminations. This perceptual bias may form the basis for, or at least contribute to, later prejudice. It can be overcome by exposure to individuated other-race faces. Although such individuated training is effective even later in development (Sangrigoli, Pallier, Argenti, Ventureyra, & de Schonen, 2005; Ventureyra, Pallier, & Yoo, 2004), retuning during infancy may be easier and might be more durable.

There is reason to suspect that there are other cross-cultural differences in visual processing that arise from variations in the mother's diet during the pregnancy and breastfeeding and in the composition of any formula. Such differences have been documented for certain polyunsaturated fats but possible differences arising from mineral or vitamin deficiencies, maternal malnutrition, vegetarian versus paleo diets, etc. have not been investigated. Any such effects could lead to generational as well as cross-cultural differences in visual processing. They are likely to be subtle – showing up as small changes in distributions, such as more adults with 20/10 vision when the early diet included substance X – and hence may easily go unnoticed. They could be manifest not only as cross-cultural differences but also differences within a country where the diet varies across geographical regions (e.g., coastal vs. inland, plains vs. mountains).

In summary, the newborn baby emerges from the womb able to see the stimuli right in from of him/her that are large and of high contrast: the mother's face usually first and foremost. Her face continues to dominate the baby's experience over the next few months, along with the faces of the father and close relatives and friends. Because these are usually of the same ethnicity as the baby and mother, the baby's processing begins to be tuned to upright, human faces that are female and own race. As the baby begins to see more details and the visual field expands, the baby picks up more information from faces and other objects in the environment. Still, he/she is learning to recognize “my tribe” and by the end of the first year of life, treats faces and speech that are less often encountered as “other.” Underlying this attunement are cortical changes that support more complex visual processing acting on the types of experience the baby encounters. Through this process, the baby’s acculturation begins.

If the process is altered by mistiming from premature birth or visual deprivation, the cortical changes do not proceed normally, preventing the later development of normal low-level and high-level vision. More subtle changes may be induced by variations in the nutrients to which the baby’s developing cortical system is exposed. Combined, these alterations indicate that we have evolved so that visual experience at the expected time, when the right stew of neurochemicals are active, will tune cortical pathways to allow the optimal refinement of vision and its adaptation to our particular visual environment.

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