Normal development of pattern motion sensitivity in macaque monkeys

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Abstract

We studied the development of sensitivity to complex motion using plaid patterns. We hypothesized, based on neurophysiological data showing a dearth of pattern direction–selective (PDS) cells in area medial temporal (MT) of infant macaques, that sensitivity to pattern motion would develop later than other forms of global motion sensitivity. We tested 10 macaque monkeys (*Macaca nemestrina*) ranging in age from 7 weeks to 109–160 weeks (adult). The monkeys discriminated horizontal from vertical pattern motion; sensitivity for one-dimensional (1D) direction discrimination and detection were tested as control tasks. The results show that pattern motion discrimination ability develops relatively late, between 10 and 18 weeks, while performance on the 1D control tasks was excellent at the earliest test ages. Plaid discrimination performance depends on both the speed and spatial scale of the underlying patterns. However, development is not limited by contrast sensitivity. These results support the idea that pattern motion perception and are consistent with the idea that the representation of PDS neurons in MT may limit the development of complex motion perception.

Keywords: Pattern motion, Plaid, Visual development, Monkey, MT

Introduction

There is much evidence showing that vision is immature at birth in primates and that extensive development occurs postnatally over the first several years of life (Teller, 1997; Kiorpes & Movshon, 2004a). Furthermore, it is clear that different visual functions develop over different time courses, with more complex perceptual abilities developing later than more basic ones. For example, acuity and spatial contrast sensitivity, which are standard metrics for visual development, are not mature at birth and develop to adult levels over the course of the first 3-7 postnatal years in humans (Teller, 1997; Ellemberg et al., 1999). However, contour integration performance is substantially poorer in young children compared with adults, and performance continues to mature until adolescence is reached (Kovacs et al., 1999; Kovacs, 2000). Similarly, in nonhuman primates, spatial contrast sensitivity and acuity show rapid development over the first 10-20 postnatal weeks and reach adult levels by 1 year of age (Boothe et al., 1988; Kiorpes, 1992), but contour integration only begins to develop around 16 weeks and continues maturation up to 18 months of age or more (Kiorpes & Bassin, 2003). These data illustrate that, in humans and macaque monkeys, even when basic spatial vision is fully developed, other more global perceptual functions are not.

Several global perceptual abilities have been studied developmentally, particularly in an effort to characterize the relative maturation of the form and motion pathways. Research in humans suggests that sensitivity to global form and motion mature at different rates although in neither case has the full time course been described (Braddick et al., 2003; Ellemberg et al., 2004; Lewis et al., 2004; Parrish et al., 2005). Motion sensitivity is the best-studied global ability. Many psychophysical studies have shown sensitivity to direction of motion within the first 3 postnatal months in humans (Banton & Bertenthal, 1997; Braddick et al., 2003). In a series of studies by Wattam-Bell, 3- to 5-week-old human infants did not show evidence of motion direction discrimination when presented with a uniform random-dot kinematogram (RDK) versus a segregated one. Infants started to discriminate direction of motion at about 6-8 weeks of age (Wattam-Bell, 1996a). Similarly, Banton et al. (2001) showed that infants did not discriminate motion direction at 6 weeks but were able to do so at 12 weeks. Interestingly, infants as young as 1 month old were able to detect coherent motion (as different from random), but they were apparently not yet able to discriminate direction cues (Wattam-Bell, 1996b). Even at 3 months, sensitivity to direction of motion in human infants is poorer than typical adult sensitivity. Three-month-olds need a level of signal strength 10-20 times higher than adults to render equivalent performance (Wattam-Bell, 1994; Banton et al., 2001).

Two longitudinal studies of motion sensitivity have been conducted in macaque monkeys. Mikami and Fujita (1992) measured speed thresholds in infant macaques. They found that speed thresholds for detection of moving gratings versus static ones improved with age in a consistent manner over the first several postnatal weeks. They reported a 4.2-fold improvement in

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speed thresholds over the first 100 days of life. The monkeys in this study did not reach adult levels by the oldest test age, though, implying that the ability to detect visual motion must continue to develop after the first 3 months. Kiorpes and Movshon (2004*b*) showed that motion sensitivity in macaque monkeys improves far beyond the first year of life. In this study, monkeys between the ages of 10 days and 3 years discriminated the direction of translational motion in RDKs with varying degrees of coherence. Their results show that although direction discrimination was possible as early as 2 weeks of age, it was apparent only for fast dot speeds and sensitivity was quite low. Motion sensitivity improved steadily over the first year and in fact continued to develop over the first 3 years.

Electrophysiological studies in monkeys suggest that perception of coherent motion in RDKs depends on brain areas downstream of the primary visual cortex, such as the medial temporal (MT) and medial superior temporal (MST) areas (Newsome & Pare, 1988). Physiological studies reveal that MT neurons are not only selective for direction of motion of one-dimensional (1D) grating stimuli and RDK motion but a percentage of them are also selective for the true motion of complex patterns. Pattern direction-selective (PDS) cells respond to the motion of a twodimensional (2D) pattern as a whole and not to the motion of the components comprising the pattern (Movshon et al., 1985; Rodman & Albright, 1989). Perceptually, patterns formed by superimposing two moving sinusoidal gratings of different orientations (plaid patterns) appear to move coherently in a direction that is different from either moving component. Under certain circumstances, though, the components seem to slide transparently on top of each other. Many have hypothesized that PDS cells in MT mediate the perception of coherent motion in plaids (Movshon et al., 1985; Rodman & Albright, 1989). For example, Stoner and Albright (1992) showed that when PDS cells in macaque MT were stimulated with plaids that did not render a coherent motion percept to human observers, their responses became more similar to the response of those MT cells that are selective for direction of motion of 1D stimuli (i.e., more component-like). Interestingly, an electrophysiological study in infant macaque monkeys has shown that while most MT cells are directionally selective at very young ages (1 week old), PDS cells are very scarce. This study showed that the proportion of PDS cells encountered increased with age, but by 16 postnatal weeks, when most properties of MT cells adult-like, PDS neurons were still only half as frequent as in adult monkeys (Movshon et al., 2004; Kiorpes et al., 2007).

Taking these results together with the notion that PDS cells in MT mediate perception of coherent pattern motion, one would expect relatively late development of this visual function. In other words, if pattern motion perception indeed depends on the existence (or number) of functional PDS cells, then its development should track with, or perhaps be limited by, the development of pattern-selective cells in MT. We investigated this hypothesis by studying the development of sensitivity to pattern motion in infant macaque monkeys.

A few studies have investigated sensitivity to pattern motion in human infants by measuring the subjects' ability to track direction of motion of plaid stimuli using eye movements. Manny and Fern (1990) found that 1-month-old infants exhibited optokinetic nystagmus (OKN) in a direction consistent with coherent pattern motion in an eight-alternative design. They also found that the percentage of trials in which this was the case was similar in 1-, 2-, and 3-month-old infants. However, adults demonstrated a higher percentage of trials with agreement between OKN and coherent motion, so it is possible that this function continued to improve with age. Similarly, Dobkins et al. (2004) investigated the development of infants' ability to track pattern motion. In this study, 2-, 3-, 4-, and 5-month-old infants showed evidence for pattern motion integration; however, in this case performance *decreased* with age. These studies suggest that pattern motion perception develops very early, earlier than one would expect from studies of direction sensitivity using simple 1D stimuli or uniform global motion stimuli. Since these studies used OKN rather than a behavioral response, it is possible that the measured performance represents the function of subcortical visual structures rather than cortical areas like MT (Distler & Hoffmann, 2003). Thus, the link to perception remains unclear.

It is widely accepted that macaque monkeys are a good model for the human visual system, in general, and for visual development in particular (Teller & Boothe, 1979; Boothe et al., 1985; Teller, 1997). Monkeys are excellent subjects for developmental studies because they can be tested at virtually any age in quantitative psychophysical tasks and individuals can be followed throughout development. In this study, we documented the developmental time course for pattern motion sensitivity in macaque monkeys using 2D plaid patterns as stimuli. We measured the ability of macaque monkeys of various ages to discriminate horizontal versus vertical plaid motion. Human psychophysical studies have shown that the probability of perceiving coherent motion declines as the characteristics of the components are made less similar (Adelson & Movshon, 1982; Delicato & Derrington, 2005). Therefore, we varied similarity-using contrast as the dimension-of the components to manipulate motion signal strength and obtained psychometric functions for a range of signal strengths. We found that young infant monkeys, younger than about 10 weeks, do not show evidence of complex motion perception. However, this ability develops rapidly with age to become adultlike near the end of the first postnatal year.

Materials and Methods

Subjects

Ten visually normal pigtailed macaque monkeys (Macaca nemestrina) ranging in age from 6 weeks to 3 years participated in this study. All of them were born at the Washington National Primate Research Center, were separated from their mothers at birth, and were hand-reared in the nursery facility of the Visual Neuroscience Laboratory at New York University. Experimental procedures and animal care were in accordance with the NIH Guide for the Care and Use of Laboratory Animals and the guidelines of the Society for Neuroscience and were approved by the New York University Animal Care and Use Committee. Two monkeys (LU and LW) were tested longitudinally spanning the first postnatal year, two additional monkeys (QI and QJ) were tested longitudinally during only the first 4 postnatal months, and two monkeys (KF and KG) were tested at two older ages during the second postnatal year. For comparison, four monkeys (FT, GM, GL, and JK) were each tested once as adults (age range 109-160 weeks).

Stimuli

Stimuli consisted of drifting sinusoidal gratings generated by a Dell Optiflex GX1 computer via a CRS video card (VSG 2/3). The stimuli were presented on a 21-inch EIZO FlexScan FXE8 monitor with a gray background; the mean luminance was 40 cd/m^2 , and the

frame rate was 100 Hz. The horizontal extent of the display subtended 54.2 deg of visual angle at 50 cm, the viewing distance for the youngest infants. As the animals grew, viewing distance was increased to 100 cm. Stimuli were presented within circular windows that subtended 11.3 deg of visual angle at 50 cm and 5.6 deg at 100 cm. Stimuli were either single gratings or 2D plaid patterns made from a combination of two gratings (Fig. 1). The 2D plaid patterns were created by superimposing two orthogonally oriented sinusoidal gratings that matched in speed and spatial frequency. The perceived velocity of the plaid pattern was 1.4 deg/s for the main experiment. To test the importance of perceived velocity to the developmental time course, we also tested two monkeys (QI and QJ) with a faster pattern speed, 9.8 deg/s. The overall contrast of the plaid patterns remained constant at 50% for monkeys younger than 20 weeks and at 25% for older monkeys.

Procedure

All subjects were tested binocularly in a darkened room using a spatial two-alternative forced choice procedure. Monkeys were either sitting in a primate chair or freely moving in a testing cage. Trials started when the monkey puts its face into a facemask mounted on the cage or chair, signaling the computer to present the stimuli. For animals younger than 20 weeks, we used a combination of preferential looking and standard operant conditioning techniques that we refer to as "reinforced looking" (Kiorpes & Kiper, 1996; Kiorpes & Movshon, 1998; Stavros & Kiorpes, 2008). When using reinforced looking, infants were trained to make an eye movement toward the side of the screen that displayed the target stimulus. A human observer, blind to the experimental display, judged the monkey's choice based on the animal's looking behavior (Kiorpes & Kiper, 1996). Older animals indicated their choice by pulling the appropriate one of two available grab bars. Stimuli were presented for up to 3 s for monkeys younger than 20 weeks and for 1 s for older monkeys. Animals were rewarded with infant formula or apple juice, according to age, for correct responses, while errors were signaled by an audible tone (1000 Hz).

Animals were tested on three tasks, two to compare the development of sensitivity to pattern motion with basic spatial vision and one to determine the time course over which pattern motion perception develops. A diagram of the stimuli used in these tasks is presented in Fig. 1. The first task was simple grating detection in which the monkey detected the presence of a drifting grating on either the left or the right side of the display as a function of contrast; the background in all cases was a homogeneous gray that matched the stimulus in space-average luminance. This task is comparable to conventional methods for assessing spatial contrast sensitivity, but in this case, the grating was drifting at a rate of 1 deg/s. The second task was to discriminate horizontal versus vertical grating motion as a function of contrast by signaling which side of the screen contained the stimulus drifting horizontally; each side contained the identical grating, both drifting at 1 deg/s, except for the direction of drift. This task was similar in cognitive demand to the primary plaid motion discrimination (the direction discrimination was the same in each case) and served as a 1D control task. The third, and primary, task was the pattern motion direction discrimination. For this task, two identical drifting plaid patterns were presented on either side of the screen simultaneously. The perceived direction of motion, to adult humans, of one plaid was horizontal, while the other was vertical. Both plaid patterns were matched in overall contrast,



Fig. 1. Stimuli for testing pattern motion perception. Diagram of stimuli used in behavioral tasks. (**A**) Simple detection of a drifting grating as a function of contrast. (**B**) Grating direction discrimination (H vs. V) as a function of contrast. (**C**) Plaid motion direction discrimination (H vs. V) as a function of the contrast ratio of the component gratings. Arrows indicate direction of motion.

perceived speed, and spatial frequency of their components. The subject's task was to indicate which side of the screen contained the stimulus drifting horizontally.

We tested plaid motion sensitivity with component gratings of 0.5, 1.0, 2.0, or 4.0 c/deg. To quantify plaid motion perception, we measured the ability to discriminate plaid motion direction under conditions of decreasing signal strength. The strength of the coherent motion percept was weakened by introducing a difference in the contrast of the component gratings comprising each plaid. In human observers, this manipulation yields a percept of transparency rather than coherence when the difference in contrast is large (Adelson & Movshon, 1982); we confirmed similar psychophysical performance in human observers and adult monkeys using this manipulation (Hall, 2008). The ratio of the contrast of the two component gratings determined the strength of the plaid signal (e.g., 1:1, 2:1, 4:1, 8:1, 16:1, 32:1), which we varied across trials using the method of constant stimuli. As noted above, the overall contrast of the pattern was the same regardless of contrast ratio.

Data analysis

We measured spatial contrast sensitivity using both the detection and 1D direction discrimination tasks for a range of spatial frequencies (0.5 and 1 c/deg for younger monkeys; 0.5, 1, 2, and 4 c/deg for older monkeys) prior to plaid motion testing. Threshold contrast values, the contrast level required for 75% correct performance, and standard errors of estimate were calculated using probit analysis (Finney, 1971) of the log-transformed data sets, based on three to five contrast levels and a minimum of 75 trials per level. For plaid motion discrimination, threshold *contrast ratio* was taken to be the ratio of the component gratings supporting 75% correct performance (Fig. 2). Plaid motion thresholds were also based on three to five strength levels and a minimum of 75 trials per level, for each of a range of spatial frequencies of the component gratings. For monkeys younger than 20 weeks, we tested pattern motion perception only with plaids made with low–spatial frequency components, 0.5 or 1 c/deg; for older monkeys, we tested the full frequency range.

Results

We measured the development of sensitivity to pattern motion in infant, juvenile, and adult monkeys. We found that young infants do not show evidence of perception of coherent motion in plaids in the early postnatal weeks, while at the same time, they show excellent performance on discrimination of 1D motion. However, between 10 and 16 weeks of age, monkeys begin to show evidence of coherent plaid motion perception with further development of sensitivity to pattern motion during the subsequent 9 postnatal months.

Plaid sensitivity, defined as the contrast ratio of the component gratings at threshold (see Materials and Methods), as a function of grating spatial frequency is shown in Fig. 3A for two adult monkeys. All adult monkeys tested were able to perform the task, although there was a fair degree of variation in sensitivity between



Fig. 2. Determination of plaid sensitivity. Representative psychometric functions for plaid discrimination are plotted for one infant and one adult monkey. Proportion correct is plotted as a function of the contrast ratio of the component gratings comprising the plaid. Threshold (75% correct, horizontal dashed line) is indicated for each function (vertical lines pointing to the abscissa). The data for the infant function (open circles) were collected with 1 c/deg component gratings; the data for the adult function (filled circles) were collected with 2 c/deg component gratings.

individuals (compare top and bottom plots). These examples represent the range of highest and lowest sensitivities of the adults tested. Fig. 3A shows that performance varies systematically with the spatial frequency of the component gratings. Over the range of spatial frequencies tested (0.5–4 c/deg), most adult monkeys show the highest sensitivity at 2 c/deg and the lowest at 0.5 c/deg. Typically, sensitivity declined when the component gratings were 4 c/deg, but this was not always the case.

Two monkeys were tested longitudinally beginning at 7 weeks postnatal. These monkeys failed to indicate perception of plaid motion at that age, while they had no difficulty with detection of single moving gratings (1D detection) or direction discrimination for pairs of single gratings (1D discrimination). Both monkeys were tested weekly until they were able to discriminate pattern motion. We required a criterion performance level of 80% correct or better, over three consecutive runs, to conclude that plaid perception had been achieved. Longitudinal data from both monkeys are shown in Fig. 3B. Plaid sensitivity is plotted as a function of spatial frequency of the grating components at three ages for LU (upper panel) and LW (lower panel); the youngest age plotted in each case reflects the earliest data obtained (LU: 18 weeks, LW: 14 weeks). Initially, both infants could discriminate pattern motion based on low-spatial frequency stimuli (open triangles); higher frequency stimuli were not tested at this age. Their sensitivity increased from the age at emergence to the next test age (around 35 weeks, filled triangles) for both spatial frequencies. There was a greater improvement in sensitivity at 1 c/deg than at 0.5 c/deg, especially for LW. In addition, at this age, both animals were able to discriminate pattern motion based on higher spatial frequency stimuli (2 and 4 c/deg) as well. After 35 weeks of age (open circles), sensitivity improved only for patterns composed of gratings with a spatial frequency of 4 c/deg, suggesting that plaid sensitivity develops at different rates depending on the underlying spatial scale of the patterns.

It is possible that the pattern of improvement in sensitivity shown by LU and LW was due to practice effects, since longitudinal testing involves repeated exposure to the same task. We think that this is unlikely since LU and LW were tested to the same degree prior to the emergence of the ability to discriminate pattern motion, yet they first demonstrated plaid discrimination at different ages. However, to explore this possibility further, two additional monkeys were tested at two ages beginning after the age when contrast sensitivity has reached adult levels (Boothe et al., 1988). Both were older than 1 year at the first pattern motion test, but both were experienced psychophysical subjects that had been tested longitudinally on a different task (Stavros & Kiorpes, 2008). Fig. 3C shows plaid sensitivity as a function of spatial frequency of the grating components for the two test ages for KG (upper panel) and KF (lower panel). Compared to LU and LW, sensitivity was high for both monkeys at the first test age, 63–68 weeks, respectively (filled symbols), and they performed within the range shown by the adults (Fig. 3A). However, neither subject was able to perform the task above criterion when the spatial frequency of the grating components was 4 c/deg at this age, consistent with the idea that plaid perception based on higher spatial frequency gratings develops relatively late. They were able to discriminate all the patterns regardless of the spatial frequency of the components at the older age (91-92 weeks, open symbols). The data from these monkeys, showing essentially adult-like sensitivity at the first test age, argue against the possibility that the developmental changes exhibited by the infants are due to practice effects.



Fig. 3. Plaid motion sensitivity as a function of spatial scale of the plaid. Plaid sensitivity is plotted as a function of the spatial frequency of the component gratings for individual monkeys tested at the ages indicated in each panel. (A) Plaid sensitivity is plotted for two monkeys tested as adults. The range of performance, best and worst sensitivities, is represented by the top and bottom panels, respectively. (B) Plaid sensitivity is plotted for two infants tested longitudinally. The earliest data set plotted in each case represents that age at which the task was first acquired. Both infants showed substantial subsequent improvement in sensitivity at older test ages. (C) Plaid sensitivity is plotted at two test ages for each of the two monkeys first tested on the pattern motion discrimination at 16 months. These monkeys had no prior practice on the task yet performed similarly to the longitudinally tested animals (shown in B) at a comparable age. Plaid speed was 1.4 deg/s in all cases. Error bars represent ± 1 s.E.M. plaid sensitivity.

Our longitudinal data show that perception of pattern motion emerges later than perception of global motion in RDKs. Kiorpes and Movshon (2004b) showed that sensitivity to coherent global motion is evident within the first 6 weeks after birth, while plaid perception was not demonstrated by the monkeys in the current study before 14 weeks. One feature of the developmental data of Kiorpes and Movshon (2004b) was that global motion perception develops earlier for fast speeds than for slow speeds. The standard speed for the plaid stimuli in the current study was in the low range, 1.4 deg/s. To test for the possibility that the young infants' inability to perceive pattern motion was limited by their poor sensitivity to slow speeds, we compared the emergence of sensitivity on the plaid motion task using a faster speed to that for the standard speed in two additional infant monkeys. For the fast speed, we chose 9.8 deg/s, which is close to the peak of the motion sensitivity function at young ages (Kiorpes & Movshon, 2004b). Developmental data from one monkey, QI, for the two speeds tested are shown in Fig. 4. Plaid sensitivity is plotted for the two spatial frequencies tested at each of the three ages: 10, 14, and 18 weeks. QI was able to discriminate pattern motion at 10 weeks with the faster speed (open squares), but she was not able to do the task with the slower speed until 18 weeks (open triangles). Sensitivity on the task improved between 10 and 14 weeks for the faster stimulus speed. Interestingly, this improvement did not impact performance with the slower speed; at 18 weeks, when she was first able to see the pattern motion at the slower speed,

her sensitivity was similar to that measured with the fast speed at 10 weeks. The same developmental pattern was shown by the second monkey tested with both speeds (QJ). He was successful on the task with the faster speed at 13 weeks, but not at younger ages (10 and 11.5 weeks), and could not perform the discrimination with the slower speed until 16 weeks, at which time his sensitivity to the slower speed was comparatively poor. These data show that the age of emergence and the degree of pattern motion sensitivity both depend on pattern speed as well as spatial frequency of the component gratings comprising the plaid. However, regardless of the underlying conditions, pattern motion sensitivity appears to develop substantially later than other metrics of global motion perception.

The developmental time course for sensitivity to plaid motion, based on data from all the animals, is shown in Fig. 5. For this comparison, we plot peak sensitivity, which we define as the highest sensitivity measured at any spatial frequency as an indicator of performance, at each age for every monkey tested with the 1.4 deg/s pattern speed. The filled rectangle along the abscissa indicates the range of ages over which animals failed to reach criterion. The saturating function fit to the data is a Naka– Rushton function typically used to describe contrast response data; we have used this function in the past to quantitatively compare developmental time courses (Stavros & Kiorpes, 2008). The data show that macaque monkeys were not able to perform the plaid discrimination task before about 14 weeks for the slow speed



Fig. 4. The effect of pattern speed on the development of plaid sensitivity. Plaid sensitivity is plotted as a function of the spatial frequency of the component gratings for one infant monkey tested with two plaid motion speeds: fast, 9.8 deg/s; slow, 1.4 deg/s. This monkey acquired the task at a younger age with the faster pattern speed.

(10 weeks for the fast speed). In addition, the population data indicate that plaid sensitivity developed from initial levels in the range of 3–6 up to 10–30 rapidly. By 35 weeks, sensitivity was already reaching asymptotic levels (15.6), but some individuals showed further improvement beyond this age in terms of overall sensitivity and in performance with high–spatial frequency patterns. Given the range of variation among adults, it is difficult to quantify precisely when sensitivity becomes adult-like; the semi-saturation point for the function is 19 weeks, which is somewhat later than temporal contrast sensitivity but earlier than spatial contrast sensitivity (Stavros & Kiorpes, 2008).

Since we varied the strength of the plaid signal by introducing a difference in the contrast of the component gratings, it is possible that the development of performance on this task was limited by the visibility of the low-contrast component. To evaluate this possibility, we measured contrast threshold for a single drifting grating in a simple detection task and also in a direction discrimination task (see Materials and Methods). In order to compare the amount of contrast needed to perform these 1D tasks at threshold with the pattern motion task, we calculated the value, in percent contrast, of the low-contrast component of the plaid at discrimination threshold. An example of this comparison for a representative adult monkey (FT) is shown in Fig. 6. Psychometric functions are plotted in Fig. 6A for each of the three tasks measured with single and component gratings of 2 c/deg; the threshold in each case is indicated by the vertical line through the function. While the functions for the single grating detection and



Fig. 5. The developmental time course for plaid motion sensitivity. Developmental progression of sensitivity to plaid motion for all monkeys tested at the pattern speed of 1.4 deg/s. Peak sensitivity is defined as the best plaid sensitivity achieved at any spatial frequency and is plotted as a function of age. The smooth curve fit to the data is a Naka–Rushton function: the semi-saturation point is 19 weeks; the asymptotic level is 15.6. The thick black bar along the abscissa indicates the range of test ages at which infant monkeys failed to reach criterion on the plaid discrimination task.

discrimination tasks are similar, they span a lower range of contrasts—and reflect a lower threshold—than the function for the pattern motion discrimination. The contrast required at threshold for each task is plotted as a function of spatial frequency for all frequencies tested in Fig. 6B. The data show that the contrast necessary to perform the simple detection and discrimination tasks at the same level of accuracy is essentially equivalent, as expected. However, it is evident that the contrast of the low-contrast grating component at plaid discrimination threshold (×s in Fig. 6B) was always higher than the single grating threshold. This comparison, made for all adults, showed that the low-contrast component in the pattern motion task was two to five times higher than the 1D threshold level for all spatial frequencies, suggesting that contrast sensitivity was not limiting performance.

For the monkeys that were tested longitudinally, we also found that the low-contrast component in the pattern motion task was well above the 1D threshold level for all spatial frequencies at all tested ages, indicating that contrast sensitivity was also not limiting the infants' ability to discriminate the direction of motion in the plaid task. Fig. 7 shows the comparison of thresholds across tasks for one of the longitudinally tested monkeys (LU). Each panel follows the same format as Fig. 6B and presents data from a specific test age. This figure shows several important findings. First, as stated above, at 9 weeks of age, LU was not able to perform the pattern motion task above criterion. Nevertheless, she was able to perform the single grating direction discrimination task at the same low-contrast level as the single grating detection (upper left panel); the 1D direction discrimination poses similar cognitive demands to the pattern motion discrimination. In both cases, her performance on these 1D motion tasks was excellent,



Fig. 6. Comparison of contrast threshold and plaid sensitivity. Comparison between the contrast sensitivity for pattern motion and that for simple discrimination/detection for a representative adult monkey (FT). (**A**) Psychometric functions for detection of a 2 c/deg drifting grating (filled circles) and direction discrimination of a pair of identical drifting gratings (open circles) are plotted as a function of contrast. Threshold (75% correct) is indicated by the vertical line through each function. The third function (\times s) illustrates the determination of the contrast of the low-contrast component of the plaid pattern at threshold. The component gratings were 2 c/deg. The \times s indicate the contrast for that component at each contrast ratio level tested; the vertical line indicates the contrast of the low-contrast component at each contrast ratio level tested; the vertical line indicates the contrast of the low-contrast sensitivity for the plaid pattern at threshold, plotted as a function of and discrimination tasks and contrast sensitivity for the plaid pattern at threshold, plotted as a function of spatial frequency. The symbols are the same as in **A**. The error bars represent \pm 1 s.E.M. percent contrast. Note that there are no error bars for the plaid discrimination (\times s) since the contrast represented is a derived measure.

yet she was unable to perform the pattern motion discrimination until 18 weeks. Interestingly, the contrast of the low-contrast component needed to perform the pattern motion discrimination at the earliest successful age (18 weeks, upper right panel) was substantially higher than her 1D contrast threshold. As she got older, the contrast of the low-contrast component at threshold improved relative to the 1D contrast threshold but in no case did it approach the 1D level. This result suggests that there is a different mechanism behind the ability to integrate the motion signal in the plaid than that required to discriminate 1D direction signals and confirms that contrast threshold is not limiting the development of performance on the plaid motion task.

In summary, the data show that young infant monkeys do not show evidence of pattern motion perception in plaids. However, the ability to perceive coherent motion is present as early as 10 weeks, at least for the fast pattern speed, and develops rapidly thereafter to adults levels.

Discussion

In the present study, we show that very young infant monkeys do not provide evidence for pattern motion perception as measured using plaids. Infants younger than 10 weeks could not perform a discrimination task based on plaid direction of motion, while they could perform well on an equivalent task using single gratings. However, longitudinal testing showed that performance on this task improves rapidly with age, once acquired, indicating that the ability to perceive pattern motion depends on developmental mechanisms. Furthermore, the time course for development depended to some degree on the speed and spatial scale of the patterns but was not limited by contrast sensitivity.

Several pieces of evidence indicate that the improvement in performance shown by the infants is the result of an emerging ability that was developing and not simply due to practice. First, adult monkeys show high plaid sensitivity with no practice needed, and monkeys of intermediate ages (KG/KF) show higher plaid sensitivity than infants (compare Fig. 3A–3C) at the first testing age with little further improvement with additional testing. Second, sensitivity improved at different rates for different spatial frequencies of the component gratings. Finally, one infant, QI, was able to discriminate pattern motion when the pattern was drifting at 9.8 deg/s at the first test age, while she required 8 weeks of additional development to perform the same task at 1.4 deg/s.

It is noteworthy that during the first 7 to 14 postnatal weeks, all monkeys failed to reach criterion in the plaid direction discrimination task (at the slow speed), whereas their performance in the single grating direction of motion discrimination task was good. Because both tasks pose very similar cognitive demands, these results suggest that the infants' failure in the plaid discrimination task was due to their inability to perceive pattern motion well enough to differentiate horizontal versus vertical motion. The results also show that their poor performance was not



Fig. 7. Comparison of contrast threshold and plaid sensitivity across ages. Comparison between the contrast sensitivity for pattern motion and that for simple discrimination/detection for one infant monkey tested longitudinally (LU). The symbols are the same as in Fig. 6B. The comparison is illustrated at four test ages. At 9 weeks, LU did not reach criterion in the pattern motion task but showed age-appropriate contrast thresholds for single grating detection and discrimination.

limited by the visibility of the low-contrast component in the stimuli. A direct comparison between the contrast of the low-contrast component of the plaid and the contrast threshold obtained on the single grating discrimination task showed that the low-contrast component was always well above the contrast threshold. Thus, performance on the pattern motion task in young infants was not limited by contrast sensitivity, a conclusion supported by data from human infants (Dobkins et al., 2004). All monkeys tested in this study showed a decline in performance on plaid motion discrimination as the contrast of the components was made less similar. This result mimics what has been previously reported in human psychophysical studies (Adelson & Movshon, 1982). In human studies, subjects typically report whether the pattern appears to be coherent or not; the variation in performance with contrast disparity in humans reflects a change from coherent pattern perception to transparency. The similarity of our monkeys' behavior to that of humans' subjective experience supports our supposition that this task indeed tested the ability of monkeys to perceive coherent motion in plaids.

We explored the developmental time course of pattern motion perception using macaque monkeys as a model for human visual development. Previous research has shown that monkeys and humans show nearly equivalent basic visual functions (e.g., acuity and contrast sensitivity) at birth but that further development occurs about four times faster in monkeys (4-to-1 rule) (Boothe et al., 1985; Teller, 1997). Global visual functions and some cognitive functions may have a slightly different metric: 3-to-1 (see Hall-Haro et al., 2008, for discussion), although it is difficult to be sure since full developmental time courses have in most cases not been described for humans. Since we found no evidence for pattern motion perception prior to about 10 weeks of age under any conditions in infant monkeys, and if the 4-to-1 rule is used as a metric, we would predict that human infants would begin to show this ability only near the end of the first postnatal year (10-18 months). However, this delayed development of pattern motion perception contrasts with what has previously been reported for human infants (Manny & Fern, 1990; Dobkins et al., 2004). These studies used an eye movement measure to investigate perception of coherent plaid motion. Manny and Fern (1990) showed, with an eight-alternative voting paradigm, OKN in directions consistent with coherent motion in plaids as early as 1 month of age. Also, Dobkins et al. (2004) showed ocular motor behavior consistent with pattern motion integration in 2-, 3-, 4-, and 5-month-old human infants. These two studies used very different speeds of pattern motion (3 and 20 deg/s), so pattern speed is unlikely to explain the discrepancy in results between human and nonhuman primates. These findings are all the more puzzling since, as reviewed in the Introduction, directional motion discrimination is not evident in human infants before about 8 weeks of age (Banton et al., 2001; Dobkins et al., 2004; see also Atkinson, 2000; Braddick et al., 2003, for reviews).

There is good evidence to suggest that the difference may lie in the use of an ocular motor paradigm, particularly OKN, versus psychophysics. Mason et al. (2003) documented earlier abilities and lower thresholds on a global motion discrimination task based on OKN measurements than when preferential looking was used. OKN is relatively robust in infants and is likely to reflect the function of subcortical structures like the nucleus of the optic tract (NOT), which gets strong direct retinal input in infants. The retinal input is dominant in newborn macaques and kittens; cortical input to the NOT appears only after a few weeks and gradually comes to balance the retinal influence over the directionality of NOT cells (Distler et al., 1999; Distler & Hoffmann, 2003). This gradual shift from retinally dominant to cortically driven activity in the NOT may explain the decrease in performance documented by Dobkins et al. (2004) over the early postnatal months in human infants. Whatever the case, it is possible that coherent motion signals in plaid stimuli are sufficient to drive OKN in a reflexive way but are not sufficient to control overt looking behavior. Furthermore, this suggests that psychophysical measurement of plaid motion sensitivity may more closely reflect the development of cortical motion mechanisms than OKN.

The ability to perceive motion has been directly related to neural activity in area MT. Newsome and colleagues have shown that psychophysical judgments in direction of motion tasks in macaque monkeys can be based on the physiological activity of a relatively small number of neurons in MT (Newsome et al., 1989; Britten et al., 1992). Moreover, neuronal discharges in MT are correlated with behavioral choices in direction discrimination (Britten et al., 1996), and electrical stimulation of neurons in MT appears to alter perceived direction in psychophysical tasks of motion discrimination (Salzman et al., 1990). In addition, acute physiological experiments in macaques have identified a class of MT neurons that are sensitive to pattern motion (Movshon et al., 1985; Rodman & Albright, 1989). Since these neurons selectively respond to the direction of motion signaled by a plaid pattern and not to the direction of motion signaled by the components of the plaid, it has been suggested that these PDS cells mediate coherent motion perception in plaids, specifically, and, more generally, the motion of complex objects (Movshon et al., 1985; Rodman & Albright, 1989). In further support of this idea, Stoner and Albright (1992) showed that PDS cells in MT changed their behavior when presented with perceptually incoherent plaids. Moreover, a functional magnetic resonance imaging study in humans revealed strong pattern motion selectivity in area MT+, a homologous area to macaque MT, when subjects viewed a sequence of moving plaids (Huk & Heeger, 2002). The strong pattern motion response in area MT+ was diminished when the subjects viewed plaids that rendered transparent rather than coherent pattern motion, directly linking the percept of coherent plaid motion and brain activity in MT+. These studies suggest that there may be a link between the emergence of PDS cells in MT and the ability to appreciate coherent motion in plaids.

Little is known about the development of area MT. Distler et al. (1996) used a metabolic assay, ¹⁴C-2-DG, to chart the functional maturation of the dorsal pathway in extrastriate cortex of macaque monkeys. They measured relative glucose utilization in different visual areas as a function of age and found that this metabolic measure was immature in newborns but improved to near adult levels relatively abruptly around 3 months of age for area MT. The increased function indicated by the maturation of metabolic activity around 3 months correlates well with our finding of emergence of plaid motion sensitivity between 3 and 4 months. At the level of single neurons, we documented the development of neuronal properties in area MT of macaque monkeys (unpublished data; Movshon et al., 2004; Kiorpes et al., 2007). While direction selectivity for gratings and RDKs was essentially adult-like in newborns, PDS cells were encountered infrequently. The proportion of PDS cells increased slowly with age such that at 16 weeks, PDS neurons were encountered about half as frequently as those in adult monkeys. The developmental course of pattern motion perception revealed in our behavioral study tracks reasonably well with the appearance of PDS cells in macaque MT: pattern motion perception was found in all tested infants by 18 weeks and only in one case before 13 weeks. Our finding that this ability develops rapidly after onset suggests that adult levels of PDS cells should be present by about 9 months postnatal although there are no neural data from that age. The results from our study are consistent with the finding, based on adult MT recordings, that PDS cells mediate the perception of coherent motion in plaids and suggest relatively late development of this cortical organization.

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