Pattern motion integration in infants

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To investigate the development of motion integration in infants, we used an eye movement technique to measure subjects' ability to track leftward versus rightward pattern motion in a stimulus consisting of a field of spatially segregated moving gratings. Each grating moved in one of two oblique directions, with the two directions interleaved across the display. When spatially integrated, pattern motion for these paired component motions was either rightward or leftward. To control for the possibility that horizontal eye movements elicited by this stimulus were due to the horizontal motion vector present in each obliquely moving grating, we also measured responses to a field where every grating moved in the *same* oblique direction. The difference in performance between the integration stimulus and this control stimulus was taken as a measure of integration. Data from 2-, 3-, 4-, and 5-month-old infants revealed significant motion integration, suggesting that higher order motion areas, such as the middle temporal area (MT) may develop at a relatively early age. In addition, the integration effect decreased consistently and significantly with age ($p < .005$), suggesting a reduction in the spatial extent of motion integration over the course of development.

Keywords: visual development, motion, integration, spatial summation

Introduction

Several previous studies in infants have demonstrated that the ability to discriminate direction of motion arises relatively early in visual development (for reviews, see Braddick, 1993; Banton & Bertenthal, 1997; Banton, Dobkins, & Bertenthal, 2001). Because mechanisms encoding direction are thought to emerge within early stages of processing in visual cortex (V1), these results indicate that, at least by the level of V1, infant directionally selective neurons function in a relatively mature fashion. However, there is a second-stage computation of motion processing that integrates local directionally selective signals into coherent global motion. This computation cannot be performed by V1 neurons because (1) individual V1 neurons view the world through a relatively small aperture (i.e., their receptive field) and (2) directionally selective V1 neurons are tuned for one-dimensional (1D) contours. Together, this results in only the velocity component *perpendicular* to the orientation of the contour being encoded within V1. Consequently, the direction of a moving 1D contour viewed through a circular aperture is ambiguous, being physically consistent with a family of real-world velocity "vectors," a phenomenon referred to as the "aperture problem." To overcome this ambiguity and calculate coherent global motion in a visual scene, the motion system must integrate signals across 1D-local motion detectors tuned for different directions.

How these local 1D-motion signals are combined into a coherent global signal has been extensively studied within the adult psychophysical and neurophysiological literature. The classically used stimulus is a moving 2D-"plaid" pattern (for a comprehensive review, see Stoner & Albright, 1994). Such plaid patterns consist of two superimposed 1D gratings, whose motion directions differ from one another (e.g., 90° apart). Unlike the motion of 1D stimuli, the direction of a 2D pattern is unambiguous because the multiple constraints provided by the 1D components allow only a single solution (i.e., there is a single unique resulting pattern direction [and speed] that is consistent with the "intersection of constraints" between the two components) (Adelson & Movshon, 1982, but see Mingolla, Todd, & Norman, 1992, for discussion of other integrative solutions, such as *vector averaging*). Thus, when two 1D gratings are combined, it is often (though not always, see Stoner & Albright, 1994) the case that a coherently moving plaid pattern is observed, which has a perceived direction and speed different from either of the underlying component gratings. This integration process appears to take place in area MT. In contrast to V1 neurons, which respond only to the 1D components of a moving plaid, a significant proportion of MT neurons respond to the integrated motion of 2D-plaid patterns (e.g.,

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Movshon, Adelson, Gizzi, & Newsome, 1985; Rodman & Albright, 1989).

It is not yet clear whether young infants integrate 1D-motion signals into coherent pattern motion, a result that would suggest maturity of higher order motion areas, such as MT. Employing moving plaid patterns, Manny and Fern (1990) found that 1-, 2-, and 3-month-old infants presented with moving plaids make directionally appropriate tracking eye movements in the pattern direction. Unfortunately, the investigators could not determine whether or not their results were really due to integration of component motion signals, because infants may have been tracking the "nodes" that made up the intersections of the plaid (see Movshon et al., 1985; Welch, 1989; Derrington & Badcock, 1992, for a discussion of this issue in the adult literature). One way to eliminate the potential for tracking nodes is to use component gratings that are spatially segregated, such that no intersections exist. Providing motion mechanisms pool across a sufficiently large area of visual space, spatially segregated components should be as potent at producing pattern motion responses as components that are superimposed.

In adults, spatially segregated 1D-motion components have, in fact, been shown to produce a coherent motion percept. This occurs when the apertures through which the moving contours are viewed are very small (Mingolla et al., 1992; Alais, van der Smagt, van den Berg, & van de Grind, 1998) or when the apertures are relatively large but viewed in the periphery, where motion mechanisms are thought to summate over a relatively large area (Adelson & Movshon, 1983, "Split Herring Bone Illusion"; and see Lorenceau & Shiffrar, 1992). These adult psychophysical results are supported by neural data from area MT, which show that a proportion of pattern-selective neurons maintain their selectivity when stimuli consist of spatially segregated 1D-motion components (Majaj, Carandini, Smith, & Movshon, 1999). In infants, the use of spatially segregated 1D-motion components may be a particularly suitable approach because there is reason to believe that infants summate over larger areas than do adults, even in central vision. For example, in experiments investigating the ability to detect variously sized luminance discs, it has been shown that 3-month-old infants exhibit spatial summation over an area four times larger than that of adults (Hamer & Schneck, 1984; and see Schneck, Hamer, Packer, & Teller 1984; Hansen, Hamer, & Fulton, 1992). In addition, within the infant motion literature it has been suggested that the breakdown in infants' ability to detect "relative motion" (i.e., patches of *oppositely* directed motion) under some conditions may result from summation (and thus cancellation) across visual space (Skoczenski & Aslin, 1992; Wattam-Bell, 1994; Roessler & Dannemiller, 1997; and see Banton, Bertenthal, & Seaks, 1999, for similar conclusions based on infants' sensitivity to statistical distributions of direction in moving dot stimuli). These psychophysical results in humans are consistent with the finding that receptive field sizes of neurons in young cats (Rusoff & Dubin, 1977; Norton, 1981) and monkeys (e.g., Blakemore & Vital-Durand, 1979) are significantly larger than those of adult animals.

In the current study, we presented infants with spatially segregated component motion gratings, with the assumption that infants' summation across space occurs over a relatively large area such that pattern motion integration occurs. The results of these studies demonstrate significant pattern motion integration in infants as young as two months, suggesting that higher order motion areas, such as MT, may develop at a relatively early age.

Methods

Subjects

Infant subjects were recruited from the San Diego area. All infants were born within 14 days of their due date and were reported to have uncomplicated births. A total of 54 infants participated in this study (2 months old, n = 18; 3 months old, n = 14; 4 months old, n = 13; and 5 months old, n = 9). Six infants failed to meet a minimum number of trials criterion (a total of at least 75 total trials). Another six failed to meet a minimum performance criterion (a score of greater than 85% correct on our eye movement reliability measure). Thus, data from a total of 42 infants (77%) were retained (2 months old, n = 9; 3 months old, n = 12; 4 months old, n = 12; and 5 months old, n = 9). On the first day of testing, the mean ages (and *SD*s) in days of our subjects were 2 months old: 64.6 ± 2.8; 3 months old: 91.4 ± 4.2; 4 months old: 119.1 ± 3.5; and 5 months old: 147.7 ± 4.2. For all infants, testing was completed within a week. For comparison to infant data, four adult subjects (aged 21-26 years) were tested under identical conditions.

Apparatus

Stimuli were generated on an Eizo Flexscan FX-E8 monitor (20 in., 1024 × 768 pixels, 75 Hz) driven by a G3 laptop computer. The voltage/luminance relationship of the monitor guns was linearized using a Minolta Chroma Meter II.

Stimuli

Stimuli consisted of moving sinusoidal gratings viewed through multiple stationary apertures. A total of 152 apertures was presented, each 2° by 4°, spaced evenly (with a 0.7° separation gap) across a grey field (total field size = 42.5° by 51.6°)[1]. The speed of the gratings was 6 deg/s, and the spatial frequency was 0.8 cpd (temporal frequency = 4.8 Hz). These spatiotemporal values were chosen to optimize detectability for ages two to five months (e.g., Atkinson, Braddick, & Moar, 1977; Banks & Salapatek, 1978; Hartmann & Banks, 1992; Rasengane, Allen, & Manny, 1997; Dobkins, Anderson, & Lia, 1999). The mean luminance of the grey background was 43 cd/m^2 (chromaticity coordi-

nates: $x = 0.346$, $y = 0.344$) and the gratings were presented at 80% contrast. The phase of each of the 152 gratings was determined randomly on each trial. Stimuli were viewed from a distance of 43 cm.

Using a directional eye movement technique (see Psychophysical paradigm below), leftward versus rightward directional discrimination performance on three different stimulus conditions was measured.

Integration stimulus

This stimulus consisted of a field of moving grating apertures, each containing one of two "component" directions, interleaved in a checkerboard pattern across the screen (see Figure 1A). As explained in the Introduction, the purpose of employing spatially segregated component gratings was to preclude the tracking of intersections, which exist in conventional plaid patterns made up of spatially overlapping component gratings. On half the trials, the two directions were 72° and -72° at 6 deg/s (Figure 1A, red arrows; 0° denotes rightward motion, 90° denotes upward motion, etc.). Based on the intersection of constraints, integrated pattern motion for this pair of component motions was 0° (i.e., rightward) at 20 deg/s (Figure 1A, blue arrow). On the other half of trials, the two directions were 108° and 252°, resulting in pattern motion at 180° (i.e., leftward).

Note that for integration to occur, the summation area of integrative motion mechanisms must be relatively large compared to the distribution of the grating apertures. That is, production of pattern motion responses requires that two or more apertures (containing different directions) fall within a motion summation area. Before accepting this premise, however, it is important to rule out the possibility that pattern motion responses could instead be due to refractive errors within the eye, specifically in our youngest infants. If the blur from refractive errors were great enough, it could potentially create spatial overlap of gratings in the retinal image. This explanation is extremely unlikely, however. First, for nearby stimuli (like those in the present experiment, 43 cm) infant accommodative abilities are quite good (Braddick, Atkinson, French, & Howland, 1979; Thorn, Gwiazda, & Held, 1996). Even for our youngest infants, 2 months old, whose spatial acuity should be about 2 cpd (e.g., Banks & Salapatek, 1978), accommodation is accurate enough to keep the retinal blur circle smaller than 0.2° (Green, Powers, & Banks, 1980). Because our grating patches were separated by 0.7°, the blur from each would be safely separated from one another. Second, and more importantly, the amount of blur required to produce overlap of apertures would serve to reduce the contrast of the gratings within the apertures to a point where they are no longer resolvable (see Figure 1B). In other words, no amount of blur could produce spurious "nodes" in the retinal image.

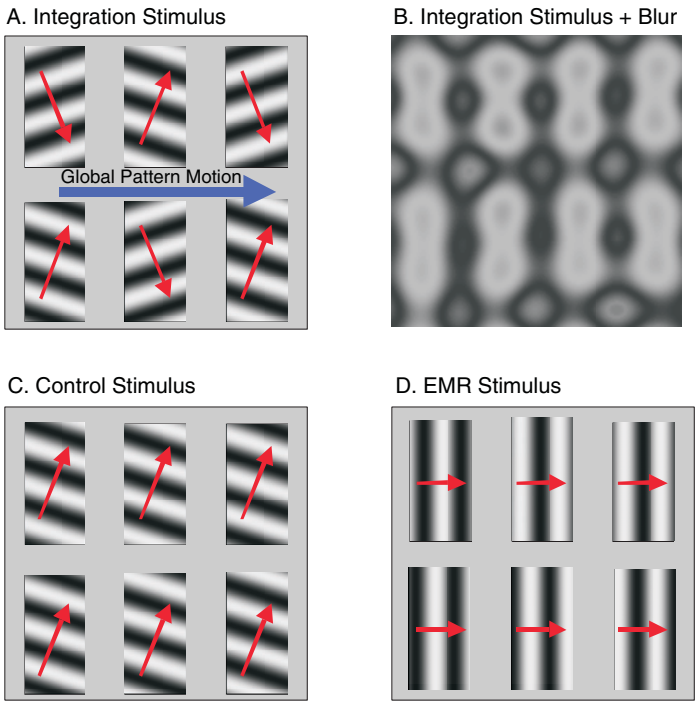

Figure 1. Stimuli. Stimuli consisted of a field of moving gratings (0.8 cpd, 80% contrast, 6 deg/s) viewed through multiple stationary apertures (2° by 4°) evenly spaced (with a 0.7° separation gap) across the display. For clarity, only 6 apertures are shown here, although 152 were presented in the actual experiment. A. Integration stimulus. Gratings moved in one of two directions, and were interleaved across the display in a checkerboard pattern. Motion directions were either 72° and -72° (as in this example), which produced integrated pattern motion rightward (i.e., 0°) at 20 deg/s, or 108° and 252°. (0° denotes rightward motion, 90° denotes upward motion, etc. Red arrows = component motions; blue arrow = global pattern motion.) B. Integration stimulus + blur. Simulated effects of optical blur that is 10× larger (2° blur circle) than the retinal blur thought to occur in 2-month-old infants (0.2° blur circle). The image in 1A was passed through a low pass filter removing spatial frequencies greater than 0.5 cpd. When the blur is great enough to produce overlap of apertures, the gratings within the apertures are no longer resolvable. C. Control stimulus. All grating apertures moved in the same direction, at 72° (as in this example), -72°, 108°, or 252°. D. Eye movement reliability (EMR) stimulus. All grating apertures moved either rightward (0°, as in this example) or leftward (180°).

Control stimulus

To control for the possibility that horizontal eye movements elicited by the *integration* stimulus were due to the horizontal motion vector present in each obliquely moving grating (which moved at 1.9 deg/s = Cos(±72°) × 6 deg/s), we measured horizontal eye movements elicited by a stimulus in which every grating aperture moved in the *same* direction on a given trial (at 72°, -72°, 108°, or 252°; see Figure 1C). Each grating moved at 6 deg/s, and therefore

contained the same horizontal motion vector (moving at 1.9 deg/s) as in the *integration* stimulus.

Left/right direction discrimination performance for the *integration* stimulus that was significantly greater than that on the *control* stimulus was taken as evidence for "true" motion integration. The logic behind this is as follows. For both conditions, the experimenter judged whether eye movements elicited by the *integration* and *control* stimuli were predominantly leftward versus rightward. The experimenter had only these two choices, leftward or rightward, so that non-horizontal directions were not encoded. Integration across grating directions yields much faster horizontal motion (20 deg/s, based on the intersection of constraints) than the horizontal motion vector present in each individual grating (1.9 deg/s). Because faster speeds produce more reliable eye movements than slow speeds (e.g., Watanabe, Ohashi, Ohmura, Itoh, & Mizukoshi, 1986), we expected discrimination of horizontal eye movements to be better for the *integration* stimulus than for the *control* stimulus if the component gratings were in fact being integrated. We verified that faster speeds produce more reliable eye movements by presenting an adult subject with horizontally moving gratings at 1.9 deg/s and 20 deg/s. We did indeed find leftward versus rightward eye movement discrimination to be far superior for the 20 deg/s condition.

Eye movement reliability (EMR) stimulus

To ensure that subjects' eye movements could reliably discriminate leftward versus rightward motion, we used a stimulus consisting of a field of grating apertures containing only horizontal motion. On each trial, all gratings moved either leftward or rightward, at 20 deg/s (see Figure 1D). Only data from subjects who performed at > 85% correct on the EMR stimulus were retained for further analysis. Mean percentage correct values were 94.6, 89.0, 93.4, 96.0, and 94.5% for 2-, 3-, 4-, and 5-month olds and adults, respectively. The results of a linear regression analysis (subject age by EMR performance) revealed no effect of age on performance (adults included: $r = 0.045$, $p = .77$, adults excluded, 0.147, $p = .35$).

Adults

Adults were tested on the same stimuli as infants. In addition, adults were tested at two lower contrasts: 20% and 5%, the purpose of which was to determine whether differences observed between infants and adults could be attributed to changes in contrast sensitivity with age. Adults were also tested under a condition in which the aperture size was halved (to 1° by 2°) and the spacing between each aperture was halved (to 0.35°). This resulted in 690 grating apertures in the display, and increased the density of gratings by approximately four-fold. The purpose of this condition was to increase the chance that multiple apertures would fall within an adult's motion summation field, and thereby enhance the integration effect. Although we tried to test apertures smaller than 1° by 2°, the direction of motion for these smaller apertures was difficult to discern even for the EMR stimulus, and thus we could not obtain data under these conditions.

Psychophysical paradigm

A directional eye movement technique was used to measure subjects' ability to discern direction of motion (for details, see Dobkins & Teller, 1996). This technique relies on the fact that infants (and adults) make directionally appropriate eye movements in response to moving stimuli (e.g., Kremenitzer, Vaugham, Kutzberg, & Dowling, 1979; Hainline, Lemerise, Abramov, & Turkel, 1984). Note that we choose to use the term "directionally appropriate eye movements," rather than a more narrow classification term, such as optokinetic nystagmus (OKN), to refer to the constellation of eye movement patterns (e.g., OKN, smooth pursuit and/or saccades) that can be elicited by a medium-sized (42.5° by 51.6°) moving display. Previous studies in adults have shown that eye movements can be used as a reliable indicator of perceived motion direction (e.g., Kowler & McKee, 1987), specifically in response to moving plaid patterns (Manny & Fern, 1990; Yo & Demer, 1992), and thus we assume this is likely to be true in infants as well. Although we cannot rule out the possibility that subcortical areas known to be involved in eye movement generation contribute to subjects' responses, results from previous studies (Newsome, Wurtz, Dursteler, & Mikami, 1985; Braddick, Atkinson, Hood, Harkness, Jackson, & Vargha-Khadem, 1992, but cf. Morrone, Atkinson, Cioni, Braddick, & Fiorentini, 1999) suggest that our eye movement measure is likely to be driven significantly by cortical areas (see Discussion).

On each trial, one of the three stimulus types (the integration, control, or EMR stimulus) was presented (in pseudo-random order). An adult experimenter who was blind to the stimulus used the infant's right eye movements (viewed through a zoom lens camera) to judge whether stimulus motion was predominantly leftward versus rightward. In addition, the experimenter rated the strength of the leftward versus rightward eye movement on a scale from 1 (weakest) to 5 (strongest), using factors such as the frequency of the eye movement and the horizontal distance traversed. Stimuli remained present until a decision was made. Our goal was to obtain approximately 90 trials from each infant, approximately 30 trials for each of the three stimulus conditions (the integration, control, and movement reliability stimuli). The mean number of trials (and SD) obtained was 91.4 ± 4.6, 89.5 ± 6.3, 95.9 ± 12.4, and 90.1 ± 2.2 for 2-, 3-, 4-, and 5 month-old infants, respectively.

Adults

In addition to obtaining eye movement data from adults, we also had each adult provide perceptual reports on a separate block of trials. After each trial, subjects reported both the perceived direction of motion (leftward vs. rightward) and the strength of the (leftward vs. rightward)

motion percept (on a scale from 1 to 5). For adult subjects, 60 trials were obtained separately per stimulus condition, for both the eye movement measure and the perceptual reports.

Data analysis

For each subject, we calculated the size of the "integration effect" as the difference in performance between the integration and control conditions, for both percentage correct and strength measures. Note that for the strength measure, we included *all* trials, not just those for which the decision was correct. Statistical analyses were applied to these difference scores to determine whether subjects showed significant integration effects. Unless stated otherwise, all p values based on t tests are one-tailed because we had specific predictions about the direction of effects.

Results

Example data

Example data from one 2-month-old infant are shown in Figure 2. Presented are percentage correct (left panel) and strength measures (right panel) for the EMR, integration stimulus (IS), and control stimulus (CS). This subject exhibited highly reliable eye movements, as evidenced by 93.1% correct performance on the EMR stimulus, with a corresponding strength measure of 4.7 (out of a scale of 5). For percentage correct data, her performance on the IS was close to perfect (96.6%), whereas her performance on the CS was near chance (54.5%). The difference in performance between the IS and CS conditions, 42.1%, was taken as a metric of the integration effect, thus providing clear evidence for pattern motion integration. Results for the strength measure were similar to percentage correct data; horizontal eye movements were stronger for the IS (4.21) than for the CS (3.87), with a resulting difference of 0.34. The size of the effect is smaller for the strength measure, which is likely to be due to a compression of the rating scale by the experimenter due to the more subjective nature of this judgment. In addition, the strength measure is likely to be less reliable than percentage correct, because non-smooth eye movements, such as saccades, might lead to relatively high strength ratings, yet be only loosely tied to stimulus direction, leading to a poor percentage correct performance.

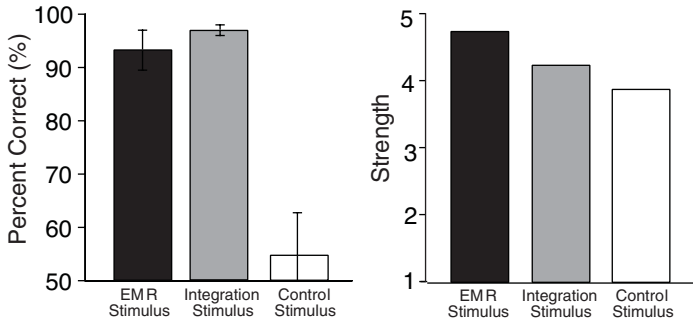

Figure 2. Example data from one 2-month-old subject. Shown are percentage correct (left panel) and strength measures (right panel) for the three different stimulus conditions: EMR stimulus (black bars), integration stimulus (gray bars), and control stimulus (white bars). Error Bars for percentage correct data denote binomial error. This subject exhibited highly reliable eye movements (EMR: percentage correct = 93.1%, strength = 4.7 out of 5). The difference in performance between the integration and control conditions (percentage correct difference: 42.1%, strength difference: 0.34) was taken as a metric of the "integration effect" for this individual

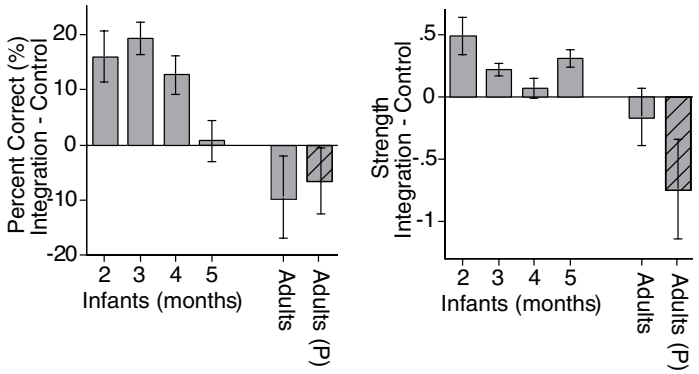

Figure 3. Mean integration effect versus age. Mean integration effects (i.e., difference in performance between the integration stimulus and control stimulus) are shown for percentage correct data (left panel) and strength measures (right panel). Adult data are shown for both the eye movement measure (solid bars) and perceptual reports (P, hatched bars). Error bars denote SEMs. Double and single asterisks presented above data points denote values with $p < .005$ and $p < .05$ statistical significance, respectively (see text for further details).

Group integration effects

Group mean integration effects and SEs are shown as a function of age in Figure 3, for both percentage correct (left panel) and strength measures (right panel). For adults, data obtained from both eye movements (solid bars) and perceptual reports (hatched bars) are presented. These data reveal two important findings. First, by two months of age, infants integrate local motion signals into coherent pattern motion, as evidenced by integration values significantly larger than zero at this age ($p < .005$). Second, the integration effect decreases with age. For percentage correct data, integration values went from 17% in 2-month-old infants to 2% in 5-month-old infants. By five months of age and into adulthood, there was no longer a significant integration effect ($p > .05$). Similarly, for strength measures, integration values decreased with age (though we observed an unusual

reversal in the data between 4 and 5 months). The results of a linear regression analysis revealed a significant correlation between percentage correct and eye movement strength measures ($r = 0.363$, $p = .018$).

For adults, similar results were observed for eye movements and perceptual reports, suggesting that eye movements provide a reasonable indicator of perception. Also, note that in all cases of adult data (both percentage correct and strength measures, and both eye movement and perceptual reports), there was a trend for worse performance on the IS than the CS (i.e., integration values below zero). This may have resulted from the integration stimulus containing two different directions of motion while the control stimulus contained only one direction. The two very different directions of motion in the integration stimulus may have made it harder to simultaneously track/perceive the joint horizontal motion shared between the two components.

To investigate the statistical significance of the age-related decrease in integration effect, we conducted a linear regression analysis, using each subject's age in days and their integration effect score. We found a significant decrease in integration effect with age, whether or not adult data were included ($r = 0.417$, $p < .005$) or excluded ($r = 0.424$, $p = .005$). Similar results were observed for integration effects based on strength measures; there was a significant decrease in integration effect with age when adults were included in the analysis ($r = 0.311$, $p = .045$). When adult data were not included, however, the effect was not significant ($r = 0.267$, $p = .11$), which is most likely due to the noisier nature of the strength judgment.

Absolute performance data

Mean absolute performance data and SEs for the IS (grey bars) and CS (white bars) conditions are presented in Figure 4. With the data in this format, we can determine whether the decrease in integration effect with age is driven by an age-related decrease in performance on the IS, an increase in performance on the CS, or a combination of the two. For percentage correct data (left panel), IS performance was significantly above chance at all ages ($p < .001$ for all infant ages; $p < .05$ for adults), and the results of a linear regression revealed a significant decrease in IS performance with age (adults excluded: $r = 0.513$, $p = .0005$; adults included: $r = 0.351$, $p = .017$). Specifically, IS performance varied from 84.8% in 2-month-old infants to 61.1% in adults. In contrast, CS performance did not vary significantly with age (adults excluded: $r = 0.013$, $p = .93$; adults included: $r = 0.167$, $p = .27$). Similar results were obtained for strength measures (right panel); IS performance decreased significantly with age (adults excluded: $r = 0.429$, $p = .007$; adults included: $r = 0.427$, $p = .005$), whereas CS performance did not vary with age (adults excluded: $r = 0.270$, $p = .10$; adults included: $r = 0.251$, $p = .11$).

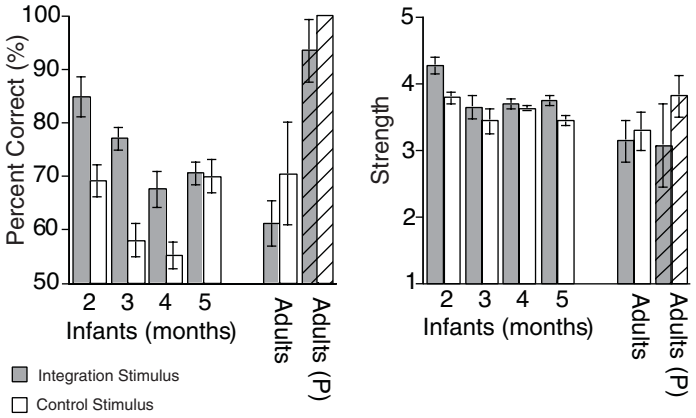

Figure 4. Absolute performance versus age. Mean performance is shown separately for percentage correct data (left panel) and strength measures (right panel) for the integration stimulus (gray bars) and control stimulus (white bars). Adult data are shown for both the eye movement measure (solid bars) and perceptual reports (P, hatched bars). Error bars denote SEMS. Double and single asterisks presented above data points (for percentage correct data) denote values significantly greater than chance (50%), with $p < .005$ and $p < .05$ statistical significance, respectively (see text for further details).

Based on the above analyses, the decrease in integration effect with age can be attributed to a decrease in performance on the IS, rather than an increase in performance on the CS. It should be pointed out, however, that although percentage correct performance on the CS condition did not increase significantly with age (as revealed by our linear regression analysis), it appeared to vary with age in a U-shaped fashion. To test the significance of this effect, we applied a *quadratic* regression analysis to the CS percentage correct data. When data for the four infant ages were analyzed alone, a significant U-shaped function was observed for the CS data ($r = 0.588$, $p = .0003$). In fact, percentage correct data for the IS condition were also well fit by a U-shaped function ($r = 0.595$, $p = .0002$). These results imply that for both conditions, performance first declines and then improves with age. In any case, the age-related decrease in integration effect is not simply attributable to an age-related increase in performance on the CS. These U-shaped functions might suggest the interaction of multiple processes during development, an issue we return to in the Discussion.

The data in Figure 4 also allow for a comparison between eye movement data (solid bars) and perceptual reports (hatched bars) in adults. For strength measures, similar results were obtained for eye movement and perceptual reports. For percentage correct data, however, perceptual performance was much higher (near 100%) than eye movement-based performance (for both the IS and the CS). We believe this is a result of the forced-choice nature of the perceptual task, whereby adult subjects can almost always

get the answer correct even if they do not perceive strong horizontal motion.

Effects of aperture size and contrast on adult performance

In our paradigm, integration of component motions requires integration across space, and therefore motion summation fields must be large enough to include at least two motion apertures. Given this, the decrease in integration effect with age can be explained by proposing that motion summation fields decrease in size with age. Previous studies have shown that *luminance* summation fields decrease in size with age (Hamer & Schneck, 1984; Schneck et al. 1984; Hansen et al. 1992). Our study suggests that motion summation fields might do the same. If this hypothesis is correct, it should be possible to compensate for the decrease in the size of the motion summation field by using smaller and more densely packed apertures. To investigate this, we tested adults with smaller (1° by 2°) grating apertures for which the density of the array increased by approximately four-fold. However, this manipulation produced results nearly identical to those obtained with the larger grating apertures (see Figures 3 and 4); the integration effect was insignificant for both percentage correct data (mean = -10.1%, p = .27) and strength measures (mean = -0.5, p = .17). We suspect that the 1° by 2° grating size was still too large relative to adults' motion summation field sizes. Unfortunately, for grating apertures smaller than 1° by 2°, direction of motion was difficult to determine even in the EMR condition (see Methods), and so we could not test for motion integration with apertures reduced further in size. We did, however, informally ask adult subjects to view the integration stimulus in their periphery, where motion summation fields are presumably larger. Consistent with previous studies (e.g., Adelson & Movshon, 1983), adults reported stronger horizontal motion (consistent with greater motion coherence) under peripheral viewing conditions.

An alternative explanation for the age-related decrease in integration might be that the effective contrast of our stimuli increased with age, because it is known that contrast sensitivity increases significantly between two months and adulthood (e.g., Banks & Salapatek, 1976; Atkinson et al., 1977; Dobkins et al., 1999). If motion integration occurs over wider regions of space for stimuli of lower effective contrast (e.g., Lorenceau & Shiffrar, 1992), this could account for our results. To investigate this possibility, we tested adults with gratings of two lower contrasts: 20% and 5% contrast. In total, integration effects were computed for 8 conditions: 2 contrasts (20% and 5%) × 2 data collection types (eye movements and perceptual reports) × 2 response types (percentage correct and strength measures). In no case was the integration effect significantly above zero (p > .05). Given that the 80% contrast stimulus presented to our infant subjects was at least as effective (i.e., detectable) as a 5% contrast stimulus presented to adults (Dobkins, Anderson, & Kelly, 2001), such findings suggest that the difference in motion integration effect between infants and adults is not due to differences in effective contrast.

Discussion

The results of these experiments demonstrate that very young infants integrate component motions into coherent pattern motion, and that this integration occurs over relatively large regions of space. Our findings are consistent with previous studies demonstrating infants' sensitivity to dots moving with a Gaussian distribution of directions (Banton et al., 1999) and infants' discrimination of shapes defined by kinetic cues (Yonas, Arterberry, & Granrud, 1987; Spitz, Stiles, & Siegel, 1993; Arterberry & Yonas, 2000), abilities that also require the existence of integrative motion mechanisms. In addition, our experiments show that the motion integration effect decreases significantly with age. This effect surely cannot reflect an age-related decrease in motion integration abilities per se, because numerous studies have demonstrated the existence of integrative motion mechanisms in adults (see Stoner & Albright, 1994). Instead, the decrease might be attributed to:

1. age-related differences in the stimulus conditions yielding optimal motion integration (regardless of the issue of integration across space),

2. age-related differences in the spatial extent of motion integration, and/or

3. age-related differences in the relative contributions of subcortical versus cortical mechanisms.

We address these possibilities below.

Stimulus conditions yielding optimal motion integration

In a previous adult study, Alais et al. (1998) demonstrated that the strength of pattern motion integration (as measured via perceptual reports) is affected by both local factors (e.g., grating direction, spatial frequency, speed, and contrast) and global factors (degree of similarity and common fate between the gratings, and symmetry in the configuration of the grating pattern). Changes in the influence of these factors with age could potentially account for our results. For example, subjects in the Alais et al. study reported poor motion integration when the direction difference between the two component gratings was *greater than or equal to* ±68°, consistent with the absence of motion integration observed in our adult subjects tested with gratings of ±72°. If the direction difference over which motion mechanisms integrate *narrows* with age, this could account for the age-related decrease in motion integration observed in the current study. Analogous arguments can be made for spatial frequency and speed (i.e., these aspects of our

stimuli may have been optimized for infant but not adult motion integration).

Spatial extent of motion integration

The age-related decrease in motion integration might be due to a decrease in the spatial extent of motion integration with age. This could arise from receptive fields of motion detectors shrinking in size with age. As described in the Introduction, there exists neurophysiological evidence from animal studies that receptive fields of neurons at early stages of visual processing decrease in size with age (Rusoff & Dubin, 1977; Blakemore & Vital-Durand, 1979; Norton, 1981, but see Rodman, Scalaidhe, & Gross, 1993, for evidence of constant receptive field sizes with age in higher level visual areas, such as inferior temporal cortex). Consistent with these neural data, psychophysical studies have demonstrated decreasing summation areas (for nonmotion tasks) with age (Hamer & Schneck, 1984; Schneck, et al., 1984; Hansen et al., 1992). Support for the possibility that motion summation areas (and thus motion receptive fields) also decrease in size with age has been provided by Wattam-Bell (1994), who measured relative motion sensitivity in 3-month-old infants and adults using interleaving stripes of opposite directions. He found that the effect of stripe width asymptoted at larger widths for infants, compared to adults, suggesting a greater spatial extent of motion summation in infancy. This conclusion should be reviewed with some caution, however, because the motion stimuli in the Wattam-Bell study were of a much lower "effective" contrast for infants as compared to adults (see below).

Although the results of the current and previous (Wattam-Bell, 1994) study may be consistent with the notion of shrinking motion summation fields, there is an alternative explanation based on the concept that summation fields are not fixed in size, but rather, are adaptable in nature, varying with stimulus parameters and task demands (see Braddick, 1993, and Anderson & Burr, 1987). With this in mind, it is possible to explain the age-related decrease in motion integration effect by assuming that this adaptability increases over the course of development, with young infants possessing relatively fixed (and large) summation areas, while adult summation fields adapt to a smaller size under certain task conditions.

Related to this possibility, the stimulus parameters used in our study might have encouraged the use of small summation fields in adults, but not in infants. Contrast is a particularly important stimulus parameter to consider because given the known increase in contrast sensitivity with age (e.g., Banks & Salapatek, 1976; Atkinson et al., 1977; Dobkins et al., 1999), a stimulus of fixed contrast can be thought of as increasing in "effective" contrast with age. If motion summation areas decrease with increasing contrast, this could potentially account for the decrease in motion integration with age observed in the current study. Such effects of contrast are supported by the results of Lorenceau and Shiffrar (1992), who measured motion integration across space in adults by testing the ability to discern the rotational direction of a diamond viewed through four apertures. They found that motion integration across space was stronger for stimuli of lower versus higher contrast (also see Lombrozo & MacLeod, 2000, for contrast effects on spatial integration in a nonmotion task, and Sceniak, Ringach, Hawken, & Shapley, 1999, for neural evidence of contrast dependent receptive field sizes in area V1). In other words, the observed decrease in integration effect with age might be attributable to age-related increases in effective contrast decreasing the spatial extent of motion integration. This explanation seems unlikely, however, because our adult subjects tested at a contrast 16-fold lower than that employed for infants still did not exhibit a motion integration effect (see Results). As discussed above, the absence of a motion integration effect in adults is likely to be due either to the use of stimulus parameters (such as direction, speed, and spatial frequency) that were not optimal for producing integration in adults or to adults having smaller or more adaptable summation fields.

Subcortical versus cortical contributions to eye movements

The current study employed an eye movement technique that relies on subjects making directionally appropriate eye movements in response to moving stimuli. The first issue regarding the use of this technique is whether eye movements can be considered a reliable indicant of motion perception. In adults, it has been shown that the direction of eye movements and perceived direction are highly correlated with each other, specifically in response to moving plaid patterns (Manny & Fern, 1990; Yo & Demer, 1992, and see Beutter & Stone, 1997), suggesting that one response type can be used to predict the other. Because it is essentially impossible to ascertain what an infant perceives, we must, to a certain extent, take it on faith that the same relationship between eye movements and perception holds in infants.

A second and related issue is whether infant eye movements are directly mediated by subcortical mechanisms (which are presumably imperceptive) or by cortical mechanisms (which are presumably perceptive) that exert control over subcortical mechanisms. The relative role of cortical versus subcortical mechanisms hinges, in part, on the type of eye movements elicited. Optokinetic nystagmus (OKN) is thought to have a strong subcortical (reflexive) component, whereas smooth pursuit (and saccades to a lesser extent) is thought to be dominated by cortically based (volitional) mechanisms (for a review, see Hainline, 1993). As described in the Methods, we use the broad term "directionally appropriate eye movements" to refer to the constellation of eye movement patterns (OKN, smooth pursuit and/or saccades) that are elicited by a medium-sized moving display of the sort used in our study. After each trial, we did not record the type of eye movement produced by our stimuli, but it was our impression that approximately half

of the eye movements were clearly OKN-like in nature (the rest had a saccade- or pursuit-like quality), and that this percentage did not vary in any obvious way with age.

Although not all of the eye movements elicited in our subjects were clearly OKN, a discussion of this type of eye movement is nonetheless relevant because one frequently discussed possibility is that OKN in very young (2 to 3 months old) infants is heavily dominated by direct subcortical projections, whereas for older infants and adults, OKN is thought to involve cortical control over subcortical mechanisms (Atkinson & Braddick, 1981; Hoffman, 1981; Braddick, 1996; Morrone et al., 1999). Particularly relevant to this point, Mason, Braddick, and Wattam-Bell (2003) reported differences in motion sensitivity and age trends for OKN responses versus forced-choice preferential looking (FPL) responses between 6 and 27 weeks of age. Such findings suggest that in early infancy, OKN and FPL responses reflect the performance of *separate* directionally selective mechanisms, presumably subcortical and cortical in nature, respectively.

Could this switch over from reliance on subcortical to cortical mechanisms contribute to the effects observed in our study? To account for the robust motion integration effect observed in very young infants, we would have to suppose that subcortical mechanisms mediating eye movements (such as the nucleus of the optic tract) integrate oriented component motions into global pattern motion. To further account for the *decrease* in motion integration effect with age, we would have to assume that these subcortical mechanisms mediating performance in infants integrate component motions over larger regions of space than do the cortical mechanisms that mediate performance in adults. (See Johnson, Gilmore, Tucker, & Minister, 1996, for discussion of this possibility with regard to the development of saccadic eye movements). However, there is reason to believe that subcortical mechanisms do not integrate oriented component motions into coherent pattern motion (based on behavioral evidence from adult humans: Harris, Lewis, & Maurer, 1993, and adult cats: Smith & Harris, 1991). This latter notion, together with the fact that only about half the eye movements in our subjects were of the OKN type, lead us to believe that the pattern motion responses we observed in infants were probably mediated by cortical mechanisms. This does not, of course, contradict the possibility of a decreasing reliance on subcortical mechanisms with age, but rather, simply suggests that infants and adults employ the same cortical mechanisms for pattern motion integration.

U-Shaped function relating percentage correct performance versus age

In our analyses, we found that age-related changes in leftward versus rightward percentage correct eye movement performance for both the control and the integration stimulus could be described by a U-shaped function, first decreasing between 2 and 4 months, and then increasing between 4 and 5 months (see Results and Figure 4A). A remarkably similar finding was previously reported by Banton et al. (1999). They used a directional eye movement technique (as in the current study) to measure the ability to discriminate direction of random dot fields moving with a Gaussian distribution of directions defined by a mean of 0° (rightward) or 180° (leftward) and a SD of 0°, 34°, or 68°. For the two highest SDs, performance declined between 6 and 18 weeks of age, and then improved by adulthood. They concluded that the decline in infant performance between 6 and 18 weeks was consistent with a narrowing of neural direction tuning with age, as well as shrinking of receptive field sizes with age.

In addition to the explanations provided by Banton et al., we suggest that the decline in performance (observed in both the Banton et al. and the current study) could reflect an age-related decrease in reliance on subcortical mechanisms. Data from animal studies have demonstrated that neurons in the nucleus of the optic tract, which mediate OKN, have a strong preference for horizontal motion, being entirely unresponsive to vertical motion (Hoffmann & Fischer, 2001), and that the direction tuning of their responses is very broad (i.e., the range of directions that yield half maximum response is ± 63°, Hoffmann & Distler, 1989). Thus, the fact that the youngest infants yield the most reliable horizontal eye movements in response to obliquely-moving gratings in the current study and to moving dot fields containing a large distribution of dot directions in the Banton et al. study could reflect a greater reliance on horizontally-biased, broadly-tuned subcortical mechanisms early in infancy.

An alternative explanation for why the youngest infants in our study yielded the best leftward versus rightward performance on the *control* stimulus is that they were less influenced by the "barber pole" illusion. The use of vertical apertures in this stimulus should have biased the motion of each grating vertically, thereby reducing horizontal eye movements. If sensitivity to the barber pole illusion increases with age, resulting horizontal eye movements would presumably decrease with age. It is also possible that the barber pole illusion is *perceived* at all ages, but that the youngest subjects produce strong horizontal eye movements to this stimulus because (1) their eye movements are dominated by subcortical mechanisms and (2) these subcortical mechanisms are insensitive to barber pole effects. Future experiments in our laboratory addressing these possibilities are currently underway.

What, then, might account for the apparent *increase* in eye movement performance seen between 4 months and adulthood in both our study and the Banton et al. study? This effect could simply reflect a nonspecific improvement with age in the ability to correctly judge eye movement direction, for example, because older subjects are more attentive or have bigger eyes than younger subjects. (Note that there was, in fact, a trend toward this in our EMR data; see Methods). Thus, the U-shaped function may reflect the combination of two processes; a specific age-related *decrease*

in horizontal eye movements elicited by obliquely moving stimulus (possibly as a result of decreasing reliance on subcortical mechanisms) and a nonspecific age-related *increase* in the ability to judge eye movement direction (but see Banton et al., 1999, for alternative hypotheses).

In summary, the results of the current study demonstrate the existence of integrative motion mechanisms in very young infants, suggesting that extrastriate visual areas known to underlie pattern motion integration (such as area MT) develop rather quickly. The motion integration effect also decreases with age, which may be due to age-related differences in the stimulus conditions yielding optimal motion integration, the spatial extent of motion integration, or the relative contributions of subcortical versus cortical mechanisms.

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Footnotes

[1]We used rectangular apertures because we were interested in obtaining data on whether infants show the "barber pole effect" (Wallach, 1935; Shimojo, Silverman, & Nakayama, 1989), a phenomenon in which the direction of a moving grating viewed through an aperture is biased along the long axis of the aperture. To this end, in some stimulus conditions, we obtained data for gratings presented within both vertical and horizontal apertures. Preliminary results suggest that infants as young as two months may exhibit the barber pole effect. These data are not presented here.

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