

Integration of one- and two-dimensional motion signals in infants: Evidence from the barber-pole illusion

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Abstract

Several previous studies in adults have investigated how one- and two-dimensional moving features are integrated into a coherent global motion percept by studying the “barber-pole illusion”; when a one-dimensional moving grating is presented within a rectangular aperture, the two-dimensional line terminators at the edges of the aperture bias the perceived direction of motion toward the longer axis of the aperture. In the current study, we used barber-pole stimuli to investigate the development of motion mechanisms that integrate one- and two-dimensional motion signals. Using a directional eye movement technique, we measured responses to obliquely moving gratings presented within horizontally vs. vertically oriented apertures, in infants (ages 2–5 months) and adults. For all ages, we found that horizontal eye movements were significantly stronger when gratings were presented within horizontal than within vertical apertures, as predicted by the barber-pole illusion. Additionally, we devised a way to infer the “effective shift” in eye movement direction produced by the barber-pole illusion. Using a simple motion integration model, effective shift values were then used to calculate the relative weightings of one- and two-dimensional motion signals to direction coding. The results show that by 2 months of age, infants integrate one- and two-dimensional motion signals, and that the relative weighting of one- and two-dimensional signals remains roughly constant from 2 months of age into adulthood.

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1. Introduction

Several previous studies in adults have investigated how one-dimensional (1D) and two-dimensional (2D) moving features are integrated into a coherent global motion percept (see Stoner & Albright, 1994 for review). The velocity of 1D motion features, such as gratings or lines, is inherently ambiguous since the motion system can only recover the velocity component perpendicular to the orientation of a 1D contour, even though that velocity signal is physically consistent with a wide range of possible vectors. In contrast, 2D features, such as endpoints, corners and intersec-

tions (jointly referred to as “terminators”) allow for unambiguous velocity estimates. Moving objects typically contain both 1D and 2D features, and the motion system must integrate the two signal types in an appropriate fashion to find a direction of motion for the entire object that is consistent with both signals. One of the best-known examples of this integration process is the “barber-pole illusion.” When a 1D moving contour is presented within a rectangular aperture, the perceived direction of motion is biased toward the orientation of the longer axis of the aperture (Wallach, 1935). It is thought that the presence of more 2D terminators along the longer, than along the shorter, axis produces a mean 2D motion signal that is biased in direction toward the longer axis. When this biased 2D motion signal is integrated with the 1D motion

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signal arising from the interior of the grating, the consequence is that the stimulus is perceived to move in a direction biased toward the longer axis.

Evidence for the existence of separate mechanisms underlying the detection of 1D vs. 2D motion signals has come from studies demonstrating that the relative contribution of 1D and 2D motion signals to perceived direction varies across different stimulus conditions. For example, studies employing classic barber-pole stimuli (Mussap & Te Grotenhuis, 1997), lines moving obliquely to their orientation (Castet, Lorenceau, Shiffrar, & Bonnet, 1993; Lorenceau, Shiffrar, Wells, & Castet, 1993), and 1D stimuli viewed through multiple apertures (Alais, van der Smagt, van den Berg, & van de Grind, 1998; Lorenceau & Shiffrar, 1992; Shiffrar & Lorenceau, 1996) have all shown that the contribution of 2D motion signals to perceived direction is weaker at low contrasts. These effects suggest separate 1D and 2D motion mechanisms, with lower contrast sensitivity for the latter (but see Majaj, Carandini, Smith, & Movshon, 1999 for an alternative explanation). In addition, it has been suggested that 1D and 2D motion mechanisms differ in their spatial frequency and speed selectivities (Alais et al., 1998) as well as in their response latencies (Lorenceau et al., 1993; Masson & Castet, 2002; Masson, Rybarczyk, Castet, & Mestre, 2000; Pack & Born, 2001), although these apparent latency differences between 1D and 2D motion mechanisms could be secondary to contrast sensitivity differences between the two. It has also been shown that the contribution of 2D motion signals depends on whether 2D terminators appear to belong to the moving object itself (“intrinsic” terminators), or are perceived as being due to an accident of occlusion (“extrinsic” terminators). For example, Shimojo, Silverman, and Nakayama (1989) showed that the barber-pole illusion is significantly reduced when 2D terminators at the edges of the aperture are made to appear extrinsic to the moving 1D grating by using retinal disparity cues to make the moving grating appear to lie behind the surface of the aperture. This manipulation serves to gate the integration process, with the result that the contribution of 2D motion signals to perceived direction is substantially reduced (see Duncan, Albright, & Stoner, 2000; Hegde, Albright, & Stoner, 2003; Liden & Mingolla, 1998; Lorenceau & Shiffrar, 1992; Pack, Gartland, & Born, 2004 for similar results). In sum, these previous studies suggest that the relative contribution of 1D vs. 2D motion mechanisms to direction coding depends on the relative sensitivities of 1D and 2D mechanisms to the stimulus, as well as on contextual cues that gate the integration process.

Two recent studies (Pack & Born, 2001; Pack et al., 2004) have investigated the neural basis of the integration of 1D and 2D motion signals by recording from the middle temporal area (MT) of macaque monkeys, an area that contains a very large proportion of directionally selective neurons, and is believed to play a key role in motion perception (see Britten, 2004 for review). Both

studies demonstrated that MT neurons integrate 1D and 2D motion signals. In particular, the more recent study (Pack et al., 2004) used barber-pole stimuli, and obtained MT direction tuning for moving 1D gratings presented in square vs. rectangular apertures. This study revealed significant shifts in direction tuning between the two aperture conditions, with the magnitude of the shift suggesting that MT responses were largely dominated by the direction of the 2D motion signal. Similar findings were obtained in directionally selective V1 neurons, but only when the edge of the aperture fell inside the receptive field. In addition, it has been suggested that responses of end-stopped neurons in V1 are likely to provide the 2D motion signal (Pack, Livingstone, Duffy, & Born, 2003).

In infants, several previous studies have demonstrated an ability to discriminate the motion direction of 1D contours such as gratings and 2D features such as dot fields (see Banton & Bertenthal, 1997; Braddick, 1993 for reviews). Recently, we have further shown that infants are able to integrate spatially segregated 1D local motion signals (moving in two different directions) into a coherent 2D global motion percept (Dobkins, Fine, Hsueh, & Vitten, 2004). In the current study, we used classic barber-pole stimuli to investigate infants’ ability to integrate 1D and 2D motion signals. In Experiment 1, we employed a directional eye movement technique to determine whether horizontal eye movements elicited by obliquely moving gratings were significantly stronger when gratings were presented within horizontal vs. vertical apertures, as would be predicted if infants experience the barber-pole illusion. In Experiment 2, we repeated this paradigm, and in addition, calculated the effective shift in eye movement direction produced by the barber-pole illusion, which we used to determine the relative contribution of 1D vs. 2D motion signals to direction encoding. The results from these experiments suggest that by 2 months of age, infants can integrate 1D and 2D motion signals, and that the relative weighting of the 1D vs. 2D signals is roughly constant from 2 months of age into adulthood.

2. Methods

2.1. Subjects

2.1.1. Infants

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. In Experiment 1, a total of 54 infants participated (2-month-olds, $n = 18$; 3-month-olds, $n = 14$; 4-month-olds, $n = 13$; 5-month-olds, $n = 9$). Six infants failed to meet a minimum number of trials criterion (at least 75 total trials). Another six failed to meet a minimum eye movement performance criterion (see Section 2.4.2 below). Data from a total of 42 infants (78%) were retained (2-month-olds: $n = 9$; 3-month-olds: $n = 12$; 4-month-olds: $n = 12$; 5-month-olds: $n = 9$). On the first day of testing, the mean ages in days (and standard deviations) of our subjects were: 2-month-olds: 64.6 ± 2.8 ; 3-month-olds: 91.4 ± 4.2 ; 4-month-olds: 119.1 ± 3.5 ; and 5-month-olds: 147.7 ± 4.2 . For all infants, testing was completed within a week.

In Experiment 2, a total of 95 infants participated (2-month-olds, $n = 30$; 3-month-olds, $n = 33$; 4-month-olds, $n = 18$; 5-month-olds, $n = 14$). Thirty-four infants failed to meet a minimum number of trials criterion (at least 175 total trials), 17 failed to meet a minimum eye movement performance criterion (see Section 2.4.2, below) and six yielded data that were too noisy to be used in our analysis of “effective shift” (see Section 2.5, below). Thus, data from a total of 38 infants (40%) were retained for analysis (2-month-olds: $n = 11$; 3-month-olds: $n = 9$; 4-month-olds: $n = 10$; 5-month-olds: $n = 8$). On the first day of testing, the mean ages in days (and standard deviations) of our subjects were: 2-month-olds: 62.3 ± 4.5 ; 3-month-olds: 91.1 ± 3.8 ; 4-month-olds: 122.1 ± 5.5 ; and 5-month-olds: 152.1 ± 3.7 .

2.1.2. Adults

In Experiment 1, six adults (ages 20–26) were tested under identical stimulus and test conditions as were presented to infants. In Experiment 2, nine adult subjects were tested under identical conditions as infants, as well as tested at additional stimulus contrasts. In three of these subjects, the data yielded were too noisy to be used in our analysis of “effective shift” (see Section 2.5, below). Thus, data from six adults (ages 20–31) were retained for analysis.

2.2. Apparatus

Stimuli were generated on an Eizo Flexscan FX-E8 monitor (20", 1024×768 pixels, 75 Hz) driven by a Macintosh G3 laptop computer using code written using Matlab and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). The voltage/luminance relationship of the monitor guns was linearized using a Minolta Chroma Meter II.

2.3. Stimuli

Stimuli consisted of moving sinusoidal gratings presented within a grid (rows and columns) of stationary apertures. A total of 152 or 154 apertures was presented (see below), each 2° by 4° , spaced evenly (with a 0.7° separation gap) across a grey field (mean luminance: 43 cd/m^2 , chromaticity coordinates: $x = 0.346$, $y = 0.344$). The total field size of the multi-aperture display was 42.5° by 51.6° . Note that the use of multiple apertures within a large field was needed to drive eye movements. Also note that the gap between apertures (0.7°) was large enough to ensure that poor refraction (which can occur in infants) would not result in overlap of apertures in the retinal image (see Dobkins et al., 2004 for details). The spatial frequency of the gratings was 0.8 cpd, which was chosen to

optimize detectability for ages 2–5 months (e.g., Atkinson, Braddick, & Moar, 1977; Banks & Salapatek, 1978). Grating phase was randomized across apertures. Both infants and adults were tested with gratings at 80% contrast. In addition, adults were tested with gratings at lower contrasts: 20% and 5%, to determine whether differences observed between infants and adults could be attributed to changes in contrast sensitivity with age.

As shown in Fig. 1, moving gratings were presented within horizontal or vertical apertures. In the horizontal aperture display, there were 154 apertures, made up of 11 apertures along each row and 14 apertures along each column. In the vertical aperture display, there were 152 apertures, made up of 19 apertures along each row and eight apertures along each column. Both the horizontal and vertical aperture displays, in their entirety, were rectangular (aspect ratio ~ 1.21). The direction of motion inside the apertures was perpendicular to grating orientation, and we denote direction using a coordinate system in which 0° is upward, $+90^\circ$ is rightward and -90° is leftward motion. In this coordinate system, direction pairs can be described as + and – values around 0° . The display was viewed from a distance of 43 cm.

In Experiment 1, two different direction pairs were employed, $\pm 18^\circ$ (up to the right vs. up to the left), and $\pm 162^\circ$ (down to the right vs. down to the left). Note that the two direction pairs had the same horizontal motion component (the only difference being that $\pm 18^\circ$ had an upward vertical component while $\pm 162^\circ$ had a downward vertical component). In Experiment 2, we employed a single direction pair for gratings presented within vertical apertures: $\pm 45^\circ$, and five direction pairs for gratings presented within horizontal apertures, which varied in their horizontal motion component: $\pm 10^\circ$, $\pm 22.5^\circ$, $\pm 45^\circ$, $\pm 67.5^\circ$ and $\pm 90^\circ$. In both Experiments 1 and 2, on a given trial, all gratings moved in the same direction. Grating direction and aperture orientation were varied pseudorandomly across trials, with an equal number of trials for each condition. The exception was that in Experiment 2, in the second half of subjects tested, we doubled the number of trials for the vertical aperture condition, to increase the accuracy of this data point. The speed of the 1D grating was kept constant across the different grating directions (speed parameters are described below). This results in the speed of the motion signals provided by the 2D terminators varying with grating direction, however, it should be noted that the temporal frequency of these terminators remains constant (and equal to the temporal frequency of the 1D grating). We chose this design (but cf. Fisher & Zanker, 2001) because goodness of eye movements has been shown to be more closely tied to temporal frequency than to speed (Holm-Jensen, 1981; Holm-Jensen & Peitersen, 1979 and see Burr & Ross, 1982; Kelly, 1979 for similar conclusions based on contrast sensitivity data). We return to this point later in the model section of Section 3.

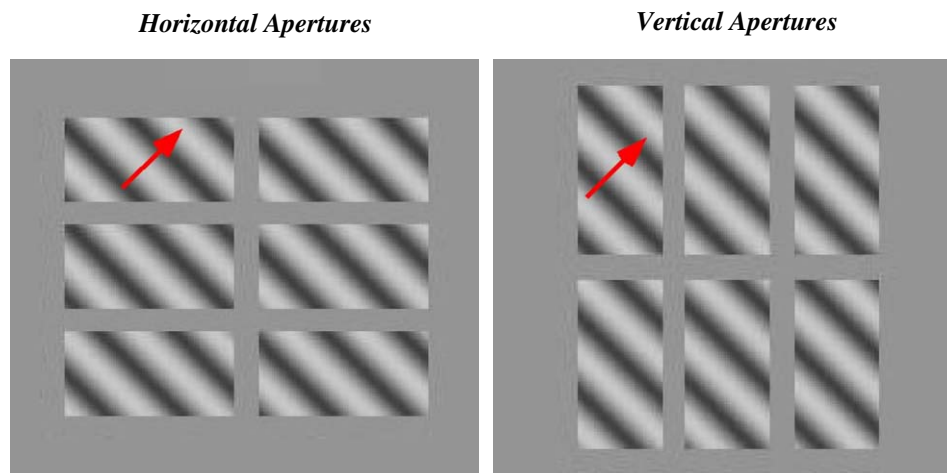


Fig. 1. Stimuli consisted of a field of moving gratings presented within multiple, evenly spaced stationary apertures. For clarity, only six apertures are shown here, although 152 or 154 apertures were presented in the actual experiment (see text for details). On a given trial, all gratings moved in the same direction (in this example, the gratings are moving at 45° , red arrows). Gratings were presented within horizontal apertures (left panel) or vertical apertures (right panel).

There were a few differences in the grating stimuli used in Experiment 1 vs. Experiment 2¹: (1) The speed of the gratings was 6 deg/s (temporal frequency = 4.8 Hz) in Experiment 1 vs. 20 deg/s (temporal frequency = 16 Hz) in Experiment 2. The one exception to this was that for 2-month-olds in Experiment 2, we used a slower speed (10 deg/s) because for this younger age group, the slower speed appeared to elicit more reliable eye movements. (2) The different grating directions employed in Experiment 1 had either an upward ($\pm 18^\circ$) or a downward ($\pm 162^\circ$) vertical component, while all non-horizontal grating directions in Experiment 2 had only an upward vertical component (i.e., all were less than $\pm 90^\circ$). (3) The direction of the obliquely moving gratings used for quantifying a “difference score” (i.e., the difference in performance between the horizontal and vertical aperture conditions, see below), was $\pm 18^\circ$ in Experiment 1 and $\pm 45^\circ$ in Experiment 2.

2.4. Paradigm

2.4.1. Measuring directional eye movements

An adult experimenter (author LBL or a laboratory assistant) held the infant up to the video monitor (either in her arms or inside a Baby Bjorn) facing forward. Although head position was not explicitly stabilized, head movement was minimized by having the infant’s head lean back on the experimenter’s body. The experimenter, who was blind to the stimulus, used the movements of the infants’ right eye (viewed through a zoom lens camera) to judge whether the stimulus-elicited eye movements were predominantly leftward vs. rightward. Adult subjects were instructed to simply watch the motion, and to do nothing special other than that, and eye movement data were obtained in an identical fashion as for infants. Infants and adults are known to make directionally appropriate eye movements in response to moving stimuli (e.g., Dobkins & Teller, 1996b; Hainline, Lemerise, Abramov, & Turkel, 1984; Kremenitzer, Vaughan, Kutzberg, & Dowling, 1979). These eye movements can include optokinetic nystagmus (OKN), smooth pursuit and/or saccades when using a medium-sized moving display as used in the current study (42.5° by 51.6°). In adults, these eye movements are a reliable indicator of perceived motion direction (Beutter & Stone, 2000; Stone & Krauzlis, 2003), specifically in response to moving barber-pole patterns (Beutter & Stone, 1998; Masson et al., 2000) and we assume this is likely to be true in infants as well (see Section 4). Stimuli remained present until a decision was made, and thus, the experimenter used the entire stimulus duration to form a judgment (mean duration for adults = 2.6 s, mean duration for infants = 14.8 s). Accordingly, we could not determine whether eye movement responses varied between the early and later portion of the trial, as might be expected from previous adult eye movement studies investigating responses to 1D vs. 2D motion within the first half second of stimulus onset (Masson et al., 2000; Pack & Born, 2001). Given our relatively long response latencies we expect that our experimenter responses were probably dominated by the later components of the eye movement response, in both infants and adults.

Note that the experimenter had only two choices (leftward or rightward), even though the direction of 1D grating motion was non-horizontal for the majority of stimuli. In these non-horizontal cases, responses were considered correct when they matched the leftward vs. rightward bias of the grating (i.e., responding “rightward” for directions between 0° and $+180^\circ$, and “leftward” for grating directions between 0° and -180°). Our assumption is that the more horizontal the perceived direction is to the subject, the more horizontal his/her eye movement direction will be, and the better the experimenter’s judgment should be regarding the leftwardness vs. rightwardness of the subject’s eye movement. This assumption is based on the fact that it is generally harder for experimental observers to discern eye movements in non-horizontal directions (e.g., Hainline et al., 1984, and personal observations), which is due to a combination of factors: (1) As eye movement direction veers away from horizontal, even if the overall speed of that eye movement is

constant, the horizontal speed component of the eye movement will necessarily be smaller and thus harder to detect, and (2) The oval shape of the eye means that the less horizontal the eye movement direction, the harder it is to see any eye movement at all.

2.4.2. Eye movement reliability

Subject data were included in our analyses only if that subject’s eye movements for horizontal motion were deemed to be a reliable indicator of leftward vs. rightward stimulus motion. In Experiment 1, we tested eye movement reliability using a field of horizontal apertures containing vertical gratings moving either rightward ($+90^\circ$) or leftward (-90°). Only data from subjects who performed at $>85\%$ correct on this stimulus were retained for further analysis. For Experiment 1, mean percent correct values on this stimulus were 92.1%, 93.0%, 91.8%, 97.8% and 96.3% for 2-, 3-, 4-, 5-month olds and adults, respectively. In Experiment 2, we retained data from a subject if they performed at $>85\%$ correct for any one of the five direction pairs presented within horizontal apertures. In Experiment 2, mean percent correct values for the $\pm 90^\circ$ stimulus were 90.0%, 93.3%, 91.0%, 94.4% and 91.7% for 2-, 3-, 4-, 5-month olds and adults, respectively. ANOVAs conducted for each experiment revealed no effect of age on performance for these stimuli (Experiment 1: $F(4, 43) = 1.56$, $p = 0.20$; Experiment 2: $F(4, 39) = 0.60$, $p = 0.67$), indicating that the reliability of our eye movement measure did not vary across the different age groups in our study.

2.4.3. Data collection

For all subjects, we obtained at least 25 trials for each stimulus condition. In Experiment 1, there were three stimulus conditions: horizontal apertures, vertical apertures (with data collapsed across the two direction pairs, $\pm 18^\circ$ and $\pm 162^\circ$) and the eye movement reliability stimulus. For infants, the mean number (and standard deviation) of total trials collected 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-olds, respectively. For adults, we obtained 60 trials for each stimulus condition (180 total trials). In Experiment 2, there were six stimulus conditions: five direction pairs within horizontal apertures ($\pm 10^\circ$, $\pm 22.5^\circ$, $\pm 45^\circ$, $\pm 67.5^\circ$ and $\pm 90^\circ$) and one direction pair within vertical apertures ($\pm 45^\circ$, with twice as many trials for the vertical apertures), and data were again collapsed across directions pairs. For infants, the mean number (and standard deviation) of total trials was 197.8 ± 14.9 , 211.3 ± 18.3 , 202.5 ± 18.0 and 202.9 ± 17.6 for 2-, 3-, 4- and 5-month-olds, respectively. For adults, we obtained 30 trials for each of the five directions for the horizontal apertures and 60 trials for the single direction presented within vertical apertures (210 total trials).

2.5. Quantifying the barber-pole effect

In adults, barber-pole effects can easily be measured by having subjects report the perceived direction of gratings presented within vertical vs. horizontal apertures, and assessing differences in perceived direction between aperture types (Fisher & Zanker, 2001). Ideally, in infants, one could measure barber-pole effects by determining the eye movement direction elicited by gratings presented within vertical vs. horizontal apertures, and assessing the difference in eye movement direction. However, as stated above, it is difficult for experimental observers to judge subjects’ eye movement directions elicited by non-horizontally moving stimuli, and this is especially true for infant subjects (e.g., Hainline et al., 1984). We therefore had to infer the apparent shift in direction caused by the barber-pole illusion indirectly. We did this in two ways.

(1) In both Experiments 1 and 2, a “difference score” was computed for each subject as the difference in percent correct left/right eye movement discrimination performance between the horizontal and vertical aperture conditions, for a fixed direction of grating motion. In Experiment 1, percent correct data were obtained by collapsing data across the two direction pairs ($\pm 18^\circ$ and $\pm 162^\circ$, which contained the same horizontal motion component), separately for the horizontal and vertical aperture conditions. In Experiment 2, percent correct data were obtained for a single direction pair ($\pm 45^\circ$), separately for the horizontal and vertical aperture conditions.

¹ The data in Experiment 1 were collected during the course of another experiment (Dobkins et al., 2004) in which stimuli were optimized to study pattern motion integration, rather than the barber-pole effect.

The logic behind this difference score is represented in Fig. 2A. In this example, the gratings move at 45° , as in Experiment 2 (solid arrow). When these 45° gratings are presented within vertical apertures, the perceived (and eye movement) direction will be biased vertically, for example 10° counterclockwise, resulting in an eye movement direction of 35° (dashed arrow). Conversely, when these 45° gratings are presented within horizontal apertures, the perceived (and eye movement) direction will be shifted clockwise, for example, by 10° , resulting in an eye movement direction of 55° (dotted-dashed arrow). In other words, changing the aperture orientation from vertical to horizontal creates a 20° clockwise shift in eye movement direction. Thus, if subjects experience the barber-pole illusion, perceived (and eye movement) direction should be more horizontal for gratings presented in horizontal than in vertical apertures, yielding better left/right eye movement discrimination performance for the former. Group mean difference scores greater than 0 were accordingly taken as evidence for a barber-pole effect. Because we had specific predictions about the direction of effects, unless stated otherwise, all p values based on statistical t -tests were 1-tailed.

(2) In Experiment 2 only, we employed a method that allowed us to infer the “effective shift” in the perceived (and eye movement) direction produced by changing the aperture orientation. We refer to this method as the “equivalent direction” (EqDIR) paradigm. EqDIR is defined as the direction of gratings presented in horizontal apertures that yields the same left/right eye movement discrimination performance as gratings moving at $\pm 45^\circ$ in vertical apertures. Here, the assumption is that when left/right eye movement discrimination performance is equated between two conditions, eye movement direction (and presumably perceived direction) is the same for those two conditions. The logic behind the EqDIR paradigm is represented in Fig. 2B. In this example, gratings moving at 25° in horizontal apertures (solid arrow) elicit the same eye movement direction, and presumably the same left/right eye movement discrimination performance, as gratings moving at 45° in vertical apertures (solid arrow). The common direction of eye movement elicited by these two different sets of conditions is presumed to be some angle ϕ that lies between

45° and 25° (dashed arrow). Overall, the effect of changing the aperture orientation from vertical to horizontal is 20° (i.e., $45^\circ - 25^\circ$). We refer to this value as the “effective shift” in eye movement direction due to aperture orientation. In Section 3, we present a simple model that uses the observed effective shift to determine the value of ϕ , as well as the relative weightings of 1D vs. 2D motion signals to direction coding. In this model, we also show that the *speed* of the eye movement (and motion percept) is expected to be roughly constant across the different aperture orientations/grating directions.

To find the direction of motion in horizontal apertures that produced equivalent performance as in vertical apertures, we fit a Weibull function to the data describing percent correct performance as a function of grating direction in horizontal apertures for each subject (see Fig. 3). To constrain the fit, we added a hypothetical data point, setting performance to be 50% correct for 0° (purely vertical motion). From this Weibull fit, an “equivalent direction” (EqDIR) was computed as the direction in the horizontal aperture condition that yielded the same percent correct discrimination performance as $\pm 45^\circ$ motion in the vertical aperture condition. Effective shift was computed as the difference between 45° and the EqDIR value (i.e., $45^\circ - \text{EqDIR}$). In some cases, percent correct for the vertical barber pole condition fell above the Weibull function for the horizontal barber pole condition. This produced an EqDIR *greater* than 45° , and thus a *negative* effective shift. Of the 18 effective shifts in adults included in our analyses (6 adults \times 3 contrasts), this occurred in 4 (22%) cases. Of 38 infants included in our analyses, this occurred in 4 out of 38 (10%). Also, as noted earlier, data from some subjects needed to be excluded from our analyses. This occurred when the data describing percent correct performance as a function of grating direction in horizontal apertures was either too noisy to be fit with a Weibull function (2 adults, 5 infants) or was near ceiling for most grating directions such that there was no EqDIR solution (1 adult, 1 infant). Group mean effective shifts that were significantly greater than 0 were taken as evidence for a significant barber-pole effect. Because we had specific predictions about the direction of effects, unless stated otherwise, all p values based on statistical t -tests were 1-tailed.

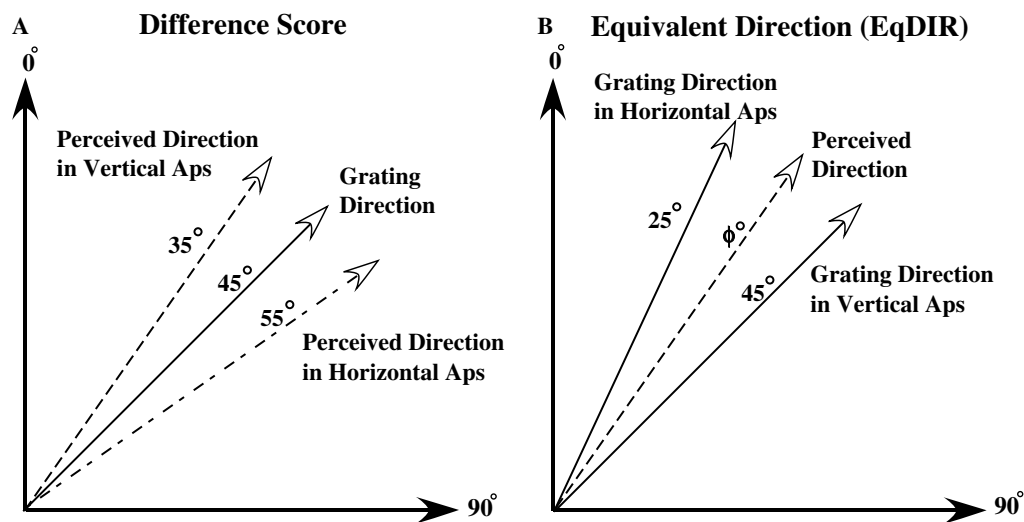


Fig. 2. Two methods for measuring shift in eye movement direction due to changes in aperture orientation. (A) A *difference score* was calculated as the difference in percent correct left/right eye movement discrimination performance between horizontal and vertical aperture conditions for a fixed direction of grating motion (in this example, 45° , solid arrow). For vertical and horizontal apertures, perceived (and eye movement) direction should be biased vertically (dashed arrow) and horizontally (dotted-dashed arrow), respectively (in this example, the shift in direction between the two is 20°). Thus, left/right eye movement discrimination performance should be better for horizontal apertures, yielding a difference score greater than 0. (B) Equivalent direction (EqDIR) was calculated by determining the direction of grating motion presented in horizontal apertures (for example, 25° , solid arrow) that yields the same left/right eye movement discrimination performance as gratings moving at 45° presented in vertical apertures (solid arrow). The assumption is that equal left/right discrimination performance on these two stimuli implies that the two elicit the same perceived (and eye movement) direction (represented as ϕ , dashed arrow). “Effective shift” was defined as the difference between the two physical directions (in this example, 20° clockwise). Note that we use a coordinate system in which 0° denotes upward, $+90^\circ$ denotes rightward, and -90° denotes leftward. In both (Fig. A and B, all vectors are depicted as having equal lengths, indicating that perceived (and eye movement) speed is constant across the different sets of aperture orientations/grating directions. This assumption is confirmed in the model section of Section 3.

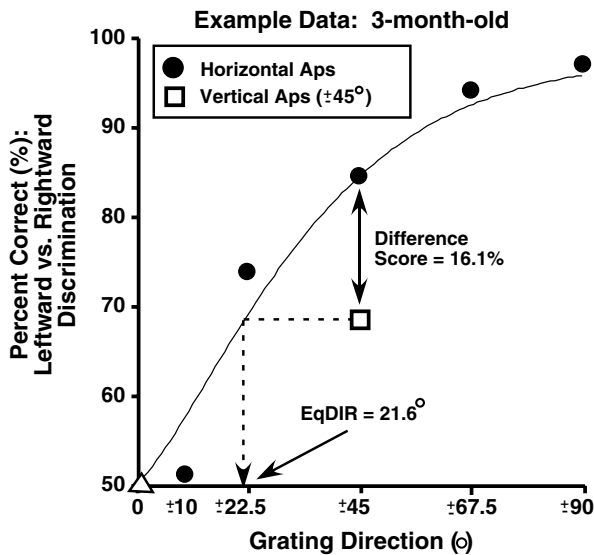


Fig. 3. Example data from a 3-month-old subject in Experiment 2. Percent correct left/right eye movement discrimination performance plotted as a function of grating direction for the horizontal aperture condition (filled circles) and for the single direction pair tested ($\pm 45^\circ$) in the vertical aperture condition (open square). Data for the horizontal aperture condition were fit with a Weibull function (solid line). Note that a performance point of 50% correct was added at 0° to help constrain the fit (open triangle). For this infant, the difference score (performance horizontal apertures – performance vertical apertures, for the $\pm 45^\circ$ gratings) was 16.1%, consistent with the presence of a barber-pole effect. EqDIR, defined as the direction of grating motion in horizontal apertures that yields the same left/right eye movement discrimination performance as in the $\pm 45^\circ$ vertical apertures condition, was 21.6° . The effective shift was then calculated as the difference between 45° and EqDIR (21.6°), which was 23.4° for this infant.

3. Results

3.1. Example data

Example data from one 3-month-old infant tested in Experiment 2 are shown in Fig. 3. Plotted is percent correct left/right eye movement discrimination performance as a function of direction for gratings presented within horizontal apertures (filled circles). The data were fit with a Weibull function (solid line). Also plotted is percent correct performance for gratings presented within vertical apertures, where only a single direction pair was tested ($\pm 45^\circ$, open square). From these data, we derived two measures, the “difference score” and the “effective shift.” For this infant, the difference score was 16.1%, indicating that left/right eye movement discrimination was better in the horizontal than in the vertical aperture condition, as predicted by the barber-pole effect. The direction of grating motion in the horizontal aperture condition that yielded the same eye movement direction discrimination performance as $\pm 45^\circ$ gratings in the vertical aperture condition, the EqDIR, was 21.6° for this infant. This results in an effective shift of 23.4° , which is the difference between 45° and the EqDIR of 21.6° . That is, a change in aperture orientation from

vertical to horizontal seems to shift the perceived (and eye movement) direction by approximately 23.4° .

3.2. Group mean difference scores

Group mean difference scores and standard errors are plotted as a function of age in Fig. 4, separately for Experiment 1 (grating direction = $\pm 18^\circ$, left panel) and Experiment 2 (grating direction = $\pm 45^\circ$, right panel). In Experiment 2, adults were tested at the contrast employed for infants (80%: Fig. 4, black squares) as well as two additional contrasts (20%: Fig. 4, grey square, and 5%: Fig. 4, white square). We return to a discussion of the effects of contrast later in Section 3. In both Experiments 1 and 2, difference scores were significantly above 0 for all age groups, consistent with the existence of a barber-pole effect (Experiment 1: $p < 0.05$ for all age groups, Experiment 2: $p < 0.002$ for all age groups, t -tests). In Experiment 1, mean difference score values were 16.0%, 7.8%, 9.2%, 6.8% and 11.2% for 2-, 3-, 4- and 5-month-olds, and adults, respectively. In Experiment 2, mean difference score values were 7.9%, 11.8%, 11.7%, 9.4% and 20.6%, for 2-, 3-, 4- and 5-month-olds and adults (tested at the same contrast as infants, 80%), respectively. For adults, difference scores for the 80% contrast condition were slightly higher in Experiment 2 than in Experiment 1, although this difference was not significant ($F(1, 10) = 1.68$, $p = 0.22$, ANOVA). Likewise, for infants, difference scores were larger in Experiment 2, although not significantly so ($F(1, 78) = 0.04$, $p = 0.85$, ANOVA), possibly because the difference scores of 2-month-olds in Experiment 1 were surprisingly high. The somewhat larger difference scores in Experiment 2 are not surprising since the $\pm 45^\circ$ gratings, employed in Experiment 2, should produce bigger shifts in perceived direction than the $\pm 18^\circ$ gratings, employed in Experiment 1 (Beutter, Mulligan, & Stone, 1996; Musap & Crassini, 1993, and see our model, below).

In both Experiments 1 and 2, difference scores did not vary across the different infant age groups (Experiment 1: $F(3, 38) = 1.06$, $p = 0.38$, Experiment 2: $F(3, 34) = 0.86$, $p = 0.47$, ANOVA). However, in Experiment 2, difference scores were significantly larger in adults as compared to infants (all infant ages combined), when adults were tested at the same contrast (80%) as infants ($F(1, 42) = 9.96$, $p < 0.01$, ANOVA). In Experiment 1, there was a slight trend for larger difference scores in adults as compared to infants, but this effect was not significant ($F(1, 46) = 0.07$, $p = 0.79$, ANOVA), probably because the difference scores of 2-month-olds in Experiment 1 were surprisingly high.

3.3. Absolute performance data

The absolute performance data that were used to calculate the differences scores in Fig. 4 are presented in Fig. 5. Plotted are group mean percent correct performance on the left/right eye movement discrimination task (and standard errors) as a function of age, for Experiment 1 (grating

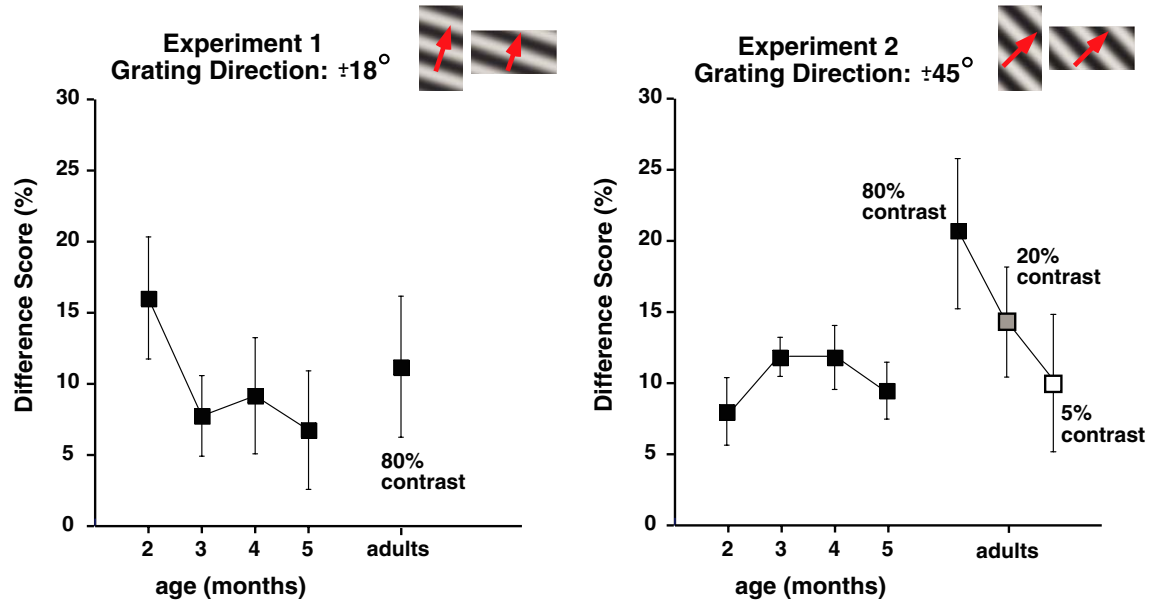


Fig. 4. Difference scores as a function of age. Group mean difference scores plotted as a function of age, for Experiment 1 (left panel) and Experiment 2 (right panel). For Experiment 2, adult data are shown for three different contrasts: 80%, which was the same contrast used in infants (black square), 20% (grey square) and 5% (white square). Error bars denote standard errors of the means. For both experiments, and for all ages, difference scores for the 80% contrast condition were significantly greater than 0, consistent with the barber-pole effect (Experiment 1, $p < 0.05$ for all age groups, Experiment 2: $p < 0.002$ for all age groups). For adults in Experiment 2, the difference scores decreased with decreasing contrast (see text for details).

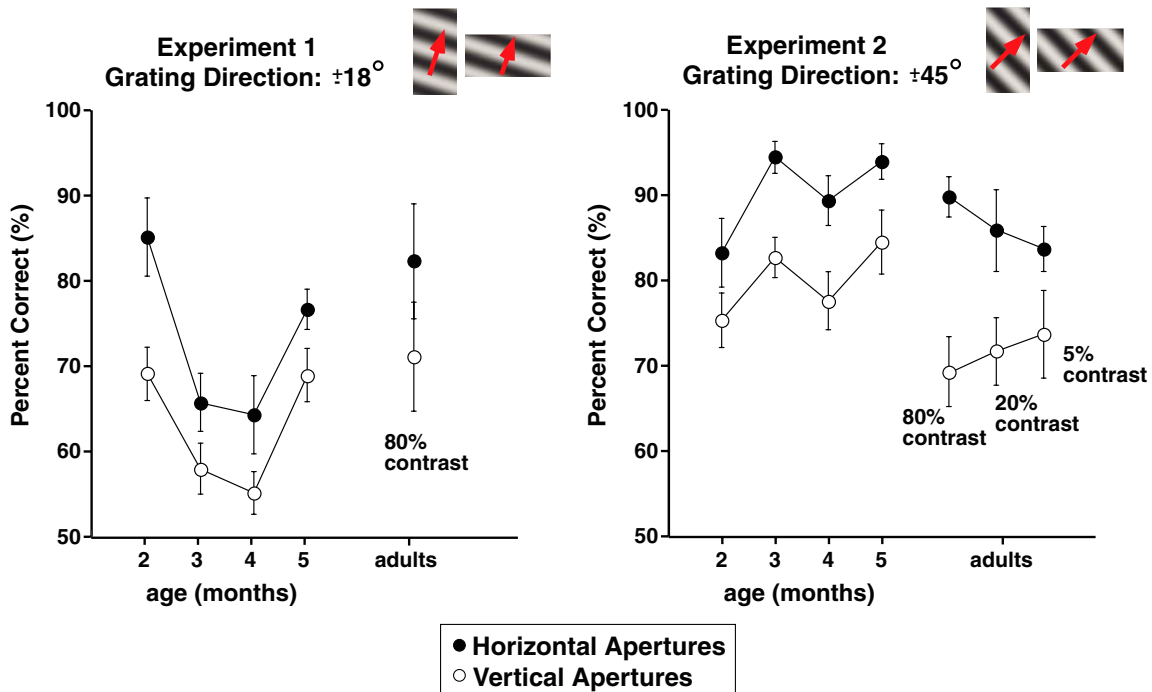


Fig. 5. Absolute performance as a function of age. Group mean absolute percent correct performance on the left/right eye movement discrimination task plotted as a function of age, for Experiment 1 (left panel) and Experiment 2 (right panel). Data are shown separately for the horizontal (filled circles) and vertical (open circles) aperture conditions. For Experiment 2, adult data are shown for three different contrasts: 80%, which was the same contrast used in infants, 20% and 5%. Error bars denote standard errors of the means.

direction = $\pm 18^\circ$, left panel) and Experiment 2 (grating direction = $\pm 45^\circ$, right panel). Data are shown separately for the horizontal (filled circles) and vertical (open circles) aperture conditions. These data show that across all infant

ages, percent correct performance for horizontal apertures was higher than performance for vertical apertures by a roughly constant amount, leading to relatively constant difference scores across infant ages (see Fig. 4). For both

Experiments 1 and 2, in all conditions performance was significantly above 50% ($p < 0.05$ in all cases, t -tests) and significantly below 100% ($p < 0.02$ in all cases, t -tests), suggesting that floor/ceiling effects did not limit the magnitude of difference scores. Also note that left/right discrimination performance was better in Experiment 2, which is most likely because: (1) the grating direction in Experiment 2 ($\pm 45^\circ$) was more horizontal than that in Experiment 1 ($\pm 18^\circ$) and (2) the grating speed in Experiment 2 (20 deg/s, 16 Hz) was faster than that in Experiment 1 (6 deg/s, 4.8 Hz).

These data also allow us to investigate changes in overall performance with age. For this analysis, we did not include adult data because superior performance in adults could be due to the fact that adults are usually more attentive subjects than are infants (as opposed to adults exhibiting superior directional eye movements). For Experiment 1, the results of ANOVAs revealed significant effects of age on absolute performance in both the horizontal ($F(3, 38) = 5.98$, $p < 0.002$) and vertical ($F(3, 38) = 6.63$, $p < 0.001$) aperture conditions. Remarkably, for both conditions, performance declined with age (between 2 and 4 months), and then improved with age (between 4 and 5 months). The significance of this U-shaped function was confirmed statistically by the results of a quadratic regression analysis (age in days by percent correct) applied to the data (horizontal apertures: $r = 0.55$, $p < 0.001$, vertical apertures: $r = 0.59$, $p < 0.001$). For Experiment 2, ANOVAs yielded a significant effect of age, although only for the horizontal aperture condition ($F(3, 34) = 2.96$, $p < 0.05$). This effect was likely driven by the poorer performance of 2-month-olds, which could be related, in part, to the fact that the 2-month-olds in Experiment 2 were tested at a somewhat slower speed (see Section 2). Unlike the data in Experiment 1, no U-shaped pattern was observed in Experiment 2. We believe that the difference in performance vs. age functions between Experiments 1 and 2 may be due to the different grating directions used in the two experiments (Experiment 1 = $\pm 18^\circ$, Experiment 2 = $\pm 45^\circ$), see Section 4.

3.4. Group mean effective shifts

Group mean effective shifts and standard errors from Experiment 2 are plotted as a function of age in Fig. 6. These results reveal mean effective shifts of 15.8° , 12.2° , 16.6° , 19.7° and 23.0° for 2-, 3-, 4- and 5-month-olds, and adults (tested at the same contrast as infants, 80%), respectively, which were significantly greater than 0 for all age groups ($p < 0.005$, t -tests). Similar to our difference score metric, the size of the effective shift did not vary across the different infant age groups ($F(3, 34) = 0.37$, $p = 0.77$, ANOVA). And, as might be expected, there was a significant correlation between effective shifts and difference scores (adults included in analysis: $r = 0.59$, $p < 0.0001$, adults excluded from analysis: $r = 0.49$, $p < 0.01$). Effective shifts were slightly larger in adults at

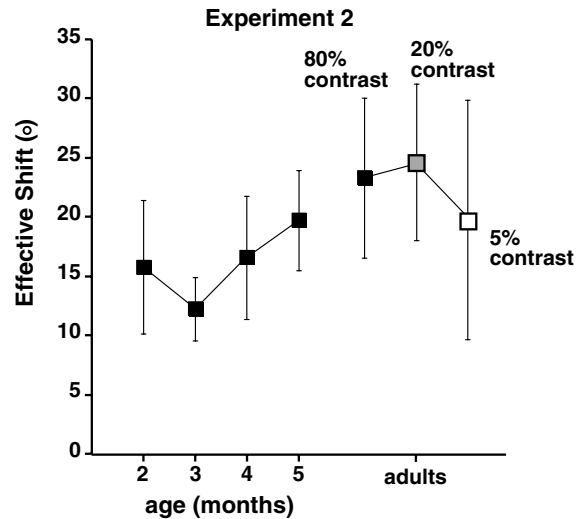


Fig. 6. Effective shift as a function of age. Group mean effective shifts from Experiment 2 plotted as a function of age. Adult data are shown for three different contrasts: 80% (black square), 20% (grey square) and 5% (white square). Error bars denote standard errors of the means. For all ages, effective shifts for the 80% contrast condition were significantly greater than 0, consistent with a barber-pole effect ($p < 0.005$ for all age groups). For adults, the effective shift was roughly constant across contrasts (see text for details).

80% contrast (23.0° , Fig. 6, black square) as compared to infants (all infant ages combined = 16.0°), although this difference did not reach significance ($F(1, 42) = 1.19$, $p = 0.28$). Mean effective shift values for adults tested at the two lower contrasts, 20% (grey square) and 5% (white square), are also presented in Fig. 6. These effects of contrast are discussed below.

3.5. Effects of contrast

Adults tended to show stronger barber-pole effects than infants for 80% contrast gratings (although this result only reached significance in the difference scores of Experiment 2). This age-related difference could be driven by the fact that the effective contrast of our stimuli (or any stimuli) is higher for adults, since contrast sensitivity increases significantly between infancy and adulthood (e.g., Atkinson et al., 1977; Banks & Salapatek, 1976; Dobkins, Anderson, & Lia, 1999). If the barber-pole effect decreases with decreasing contrast, as suggested by previous data obtained from adults (Mussap & Te Grotenhuis, 1997), this might explain why the barber-pole effect was somewhat weaker in infants. In Experiment 2, we therefore measured barber-pole effects in adults for 20% and 5% contrast gratings. In particular, the 5% contrast condition for adults should be roughly the same effective contrast as 80% contrast for infants, given the spatiotemporal frequencies we used (Dobkins et al., 1999; Dobkins & Teller, 1996a).

Mean difference scores in adults tested at different contrasts are presented in Fig. 4 (right panel). For 80%, 20% and 5% contrast gratings, mean difference scores were

20.6%, 14.2% and 10.0%, respectively, which were all significantly greater than 0 ($p < 0.03$, t -tests). Although there was a decrease in difference score with decreasing contrast, this effect was not significant ($F(2, 10) = 1.94$, $p = 0.19$, ANOVA). Mean *effective shifts* in adults tested at different contrasts are presented in Fig. 6. For 80%, 20% and 5% contrast gratings, mean effective shifts were 23.0°, 25.2° and 19.9°, respectively, which were all significantly greater than 0 ($p < 0.03$, t -tests). The effect of contrast on effective shift was essentially constant ($F(2, 10) = 0.14$, $p = 0.87$, ANOVA). Most importantly, there was no significant difference between infant data at 80% contrast and adult data at 5% contrast for either *difference scores* ($F(1, 42) = 0.00$, $p = 0.96$, ANOVA) or *effective shifts* ($F(1, 42) = 0.31$, $p = 0.58$, ANOVA). We should note, however, that our failure to find significant differences between infants and adults (or between different infant age groups) could be due to the fact that the variability across subjects is somewhat high. Nonetheless, these results demonstrate that when adults and infants are tested at the same “effective contrast,” i.e., adults at 5% contrast and infants at 80% contrast, the relative contribution of 2D signals to motion processing is roughly the same between infants and adults.

3.6. Modeling the relative contribution of 1D and 2D motion signals to motion processing

The perceived direction (and resulting eye movement direction) elicited by a moving stimulus presumably reflects an integration of the 1D and 2D motion signals within that stimulus (see Section 1). Here, we present a simple model that assumes that the integration process involves a simple weighted average of the 1D and 2D vectors. Two different versions of the model were compared. (1) The “*speed model*,” in which vector length reflects the speeds (deg/s) of the 1D and 2D signals, and (2) the “*temporal frequency model*,” in which vector length reflects the temporal frequencies (Hz) of the 1D and 2D signals. As mentioned earlier (see Section 2), while the speed of the 2D terminators varied across grating direction, the temporal frequency remained constant (and equal to the temporal frequency of the 1D motion signal).

For both models, the direction (ϕ) of the weighted vector average of the 1D and 2D signals is computed as follows:

$$\phi = \arctan\left[\frac{(w \times S_{1D\text{vert}}) + ((1-w) \times S_{2D\text{vert}})}{(w \times S_{1D\text{hor}}) + ((1-w) \times S_{2D\text{hor}})}\right], \quad (1)$$

$S_{1D\text{vert}}$ and $S_{2D\text{vert}}$ are the speeds (or temporal frequencies) of the vertical components of the 1D and 2D vectors, respectively. $S_{1D\text{hor}}$ and $S_{2D\text{hor}}$ are the speeds (or temporal frequencies) of the horizontal components of the 1D and 2D vectors, respectively. And, w and $1-w$ are the relative weightings assigned to the 1D and 2D vectors, respectively. The length (L) of this weighted vector average is computed as:

$$L = \left[\left((w \times S_{1D\text{vert}}) + ((1-w) \times S_{2D\text{vert}}) \right)^2 + \left((w \times S_{1D\text{hor}}) + ((1-w) \times S_{2D\text{hor}}) \right)^2 \right]^{-1/2}. \quad (2)$$

In the *speed model*, the horizontal and vertical components of the 1D motion vector are:

$$S_{1D\text{hor}} = S \cos(\alpha)$$

$$S_{1D\text{vert}} = S \sin(\alpha),$$

where S is the speed of the 1D grating, and α is the direction of the 1D motion signal in the standard coordinate system, where 0° is rightward, 90° is upward, etc. (Note that this standard co-ordinate system differs from the co-ordinate system used elsewhere in this paper, where leftward/rightward pairs of motion directions were symmetrical around 0°).

To compute the horizontal and vertical components of the 2D motion vector, 2D terminators are considered analogous to dots traveling either vertically or horizontally along the edges of the aperture. The average 2D vector of all the terminators is then dependent on both the relative number of vertical and horizontal terminators, and on the speed at which the terminators travel along the edge of the aperture. The number of horizontal terminators (N_{hor}) and vertical terminators (N_{vert}) is computed as:

$$N_{\text{hor}} = 2 \times \lambda \times \text{VL} \times \sin(\alpha)$$

$$N_{\text{vert}} = 2 \times \lambda \times \text{HL} \times \cos(\alpha),$$

where λ is the spatial frequency of the 1D grating, and VL and HL are the vertical and horizontal lengths of the aperture in degrees, respectively. The speeds of the horizontal and vertical terminators are $S/\cos(\alpha)$ and $S/\sin(\alpha)$, respectively. Then,

$$S_{2D\text{hor}} = (S/\cos(\alpha)) \times (N_{\text{hor}}/(N_{\text{hor}} + N_{\text{vert}}))$$

$$S_{2D\text{vert}} = (S/\sin(\alpha)) \times (N_{\text{vert}}/(N_{\text{hor}} + N_{\text{vert}})).$$

In the *temporal frequency model*, the horizontal and vertical components of the 1D motion vector are:

$$S_{1D\text{hor}} = \text{TF} \cos(\alpha),$$

$$S_{2D\text{vert}} = \text{TF} \sin(\alpha), \text{ where TF is the temporal frequency of the 1D grating.}$$

The 2D terminators are still considered analogous to dots traveling either vertically or horizontally along the edges of the aperture, however, their temporal frequency is equal to that of the 1D grating, which is independent of grating direction.

$$S_{2D\text{hor}} = (\text{TF} \times (N_{\text{hor}})/(N_{\text{hor}} + N_{\text{vert}})),$$

$$S_{2D\text{vert}} = (\text{TF} \times (N_{\text{vert}})/(N_{\text{hor}} + N_{\text{vert}})).$$

In our study, EqDIR is defined as the direction of motion in horizontal apertures that yields the same ϕ as gratings of a fixed direction (45°) in vertical apertures. Eq. (1) can be used to solve analytically for w (the weight of the 1D motion signal) given a known EqDIR value, which of course also provides us with the ϕ value. The mean effective shift in infants in our study (averaged across

2-, 3-, 4- and 5-month-olds) was 16.0° , which reflects a mean EqDIR of 61.0° in standard coordinates. In adults, mean effective shifts were 23.0° , 25.2° and 19.9° , for 80%, 20% and 5% contrast gratings, resulting in mean EqDIRs of 68.0° , 70.2° and 64.9° , respectively. In the *speed model*, for infants, w was calculated to be 0.72 ($\phi = 50.3^\circ$). For adults, w was 0.66, 0.65 and 0.69 for 80%, 20% and 5% contrast gratings, respectively. In the *temporal frequency model*, for infants, w was 0.49 ($\phi = 53.0^\circ$). For adults, w was 0.28, 0.21 and 0.38 for 80%, 20% and 5% contrast gratings, respectively.

Note that even though the model is designed to equate the ϕ of the weighted vector averages between the two stimulus conditions (i.e., horizontal apertures with gratings moving in direction = EqDIR and vertical apertures with gratings moving at 45°), without regard for equating the lengths of the vector averages, by obtaining L from Eq. (2) we were able to show that the lengths of the vector averages (L) were also nearly identical between the two sets of aperture orientations/grating directions. As examples, we present results for the lowest (61.0°) and highest (70.2°) EqDIR determined in our study (see above). When EqDIR is 61.0° , which produces a w of 0.72 in the *speed model*, the L values are 20.09 and 20.37 deg/s for the vertical and horizontal aperture conditions, respectively. For the same EqDIR in the *temporal frequency model*, which produces a w of 0.49, the L values are 13.75 and 13.45 Hz for the vertical and horizontal aperture conditions, respectively. When EqDIR is 70.2° , which produces a w of 0.65 in the *speed model*, the L values are 20.14 and 21.08 deg/s for the vertical and horizontal aperture conditions, respectively. For the same EqDIR in the *temporal frequency model*, which produces a w of 0.21, the L values are 12.65 and 12.32 Hz for the vertical and horizontal aperture conditions, respectively.

There are two reasons why we believe the *temporal frequency model* is more feasible than the *speed model*. First, in previous adult studies where barber pole effects are measured by presenting gratings of a fixed direction in differently oriented apertures, the largest shifts in perceived direction are observed when grating direction and aperture orientation differ by 45° (Beutter et al., 1996; Mussap & Crassini, 1993). Likewise, in the current study, difference scores were somewhat larger in Experiment 2, which used 45° gratings, than in Experiment 1, which used 18° gratings, thus suggesting larger shifts in perceived direction for 45° gratings (see Fig. 4). This greater effect for 45° gratings is predicted by the *temporal frequency*, but not the *speed*, model (for all values of w and all aspect ratios). That is, only for the *temporal frequency model* is it the case that ϕ computed for vertical apertures minus ϕ computed for horizontal apertures (determined from Eq. (1)) is greatest when the grating direction is 45° .

Second, the *temporal frequency model* produces results that are roughly consistent with neurophysiological data from motion area MT (Pack et al., 2004). In these MT

studies, high contrast (100%) barber-pole stimuli were used, which is similar to the 80% contrast condition of the current study (and the spatial frequency of the Pack et al. stimuli, 0.5 cpd, was also similar to that used in the current study, i.e., 0.8 cpd). Pack et al. reported that the observed shift in MT direction tuning could be accounted for by a vector sum of the 2D motion signals along the long and short axes of the aperture, without any contribution from the 1D motion signal. That is, under their testing conditions, MT data suggest a w value close to 0. Although this neural value is lower than that computed by our *temporal frequency model* ($w = 0.28$), it is much closer to the *temporal frequency model* results than to the *speed model* results ($w = 0.66$). Still, w appears to be lower in MT as compared to that determined from our *temporal frequency model* of behavioral data. The discrepancy could be due to stimulus differences between the two studies; 100% contrast (Pack et al.) vs. 80% contrast (current study), a single aperture (Pack et al.) vs. multiple apertures (current study). Alternatively, the discrepancy could suggest that our eye movement measure does not rely entirely on activity in cortical motion areas like MT, an issue we return to in Section 4. In any event, assuming the *temporal frequency model* is correct, the results of both the current study and the Pack et al. study suggest that for high contrast stimuli, direction encoding is determined predominantly by 2D motion signals.

In sum, our *temporal frequency model* of 2D and 1D motion signal integration is consistent with the results of the current and previous studies, suggesting that temporal frequency, rather than speed, may be more influential in the production of eye movements, at least for these types of stimuli. Previous studies in adults have similarly found that eye movements are more tied to temporal frequency than speed (Holm-Jensen, 1981; Holm-Jensen & Peitersen, 1979). It will be interesting to see how this model generalizes across grating directions and aperture aspect ratios. Our prediction is that the relative weighting of 1D and 2D motion signals should not vary across grating direction or aspect ratios. Conversely, their relative weighting should vary with changes in stimulus conditions that change the relative sensitivities of the 1D and 2D motion mechanisms (e.g., contrast, spatiotemporal frequency), as well as vary with changes in contextual cues that affect the extent to which the 2D motion signals appear extrinsic rather than intrinsic. It is also possible that the weightings are influenced by the relative number of units (neurons) devoted to processing the 1D vs. 2D motion signals. If this were the case, we might expect the weight of the 1D signal to increase with increasing aperture size (keeping aspect ratio constant), since, as size is increased, the interior area of the grating (which contains the 1D motion signal) grows faster than does the perimeter of the aperture (which contains the 2D motion signal). That is, increasing aperture size should lead to relatively greater recruitment of 1D vs. 2D motion units. Finally, it would be interesting to determine whether a nonlinear combination of 1D and 2D signals could

account for psychophysical data, as previously suggested in studies that employ Bayesian models to account for motion integration data (e.g., Weiss, Simoncelli, & Adelson, 2002).

4. Discussion

The results of the current study reveal that by two months of age, direction encoding in infants is significantly influenced by 2D motion signals, as evidenced by inferred shifts in eye movement direction produced by barber-pole stimuli. The magnitude of the direction shift is found to be roughly constant between two and five months of age, and between infancy and adulthood, suggesting that the weight of 2D motion signals is constant over the course of development, at least for the stimulus conditions tested in the current study. In this section, we first address issues related to the use of our eye movement measure. We then address possible explanations for why the function relating eye movement direction discrimination performance vs. age was found to differ between Experiment 1 and Experiment 2.

4.1. Issues related to the use of an eye movement measure

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 reliable indicators of motion perception. In adults, it has been shown that the direction of eye movements and perceived direction are highly correlated with each other (e.g., Beutter & Stone, 2000; Stone & Krauzlis, 2003), specifically in response to moving barber-pole patterns (Beutter & Stone, 1998; Masson et al., 2000), 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 assumption is that variations in perceived speed were not a confound in our EqDIR measure. As illustrated in Fig. 2B, EqDIR is based on the assumption that two stimuli yielding the same left/right eye movement discrimination performance elicit the same perceived (and eye movement) *direction*, regardless of whether the perceived (and eye movement) speed for the two stimuli are the same. But what if two stimuli yield the same left/right eye movement discrimination performance because they are matched with respect to their horizontal speed components? For example, imagine in the illustration of Fig. 2B that 45° gratings in vertical apertures are perceived to move at some angle less than 45°, but relatively *slowly*, and that 25° gratings in horizontal apertures are perceived to move at some angle greater than 25°, but relatively *quickly*. In this case, the perceived directions elicited by these two stimuli would be different, yet the two stimuli nonetheless yield the same horizontal speed component. If this were the case,

our measure of EqDIR, based on apparent direction, would be confounded with apparent speed. We strongly believe that this is not the case, however, since the results from our model show that the predicted speeds (and temporal frequencies) for horizontal apertures with gratings moving in a direction equal to EqDIR and vertical apertures with gratings moving at 45° are essentially identical.

A third issue is whether infant eye movements are mediated by subcortical motion mechanisms or by cortical motion mechanisms that exert control over subcortical mechanisms. It has been suggested that one particular type of eye movement, *optokinetic nystagmus* (OKN), is mediated predominately by subcortical motion mechanisms in very young infants (~2- to 3-month-olds), and then switches over to cortical motion mechanism control over these subcortical mechanisms later in development (Atkinson & Braddick, 1981; Braddick, 1996; Hoffman, 1981; Mason, Braddick, & Wattam-Bell, 2003; Morrone, Atkinson, Cioni, Braddick, & Fiorentini, 1999). In our study, our impression was that in both infants and adults, approximately half of the eye movements we observed were OKN-like in nature, with the rest resembling pursuit eye movements. Motion driven saccadic eye movements seemed to be quite rare. For adults, we can assume that these OKN-like eye movements were driven by cortical motion mechanisms (such as area MT), which have previously been shown to be influenced by 2D motion signals (Pack & Born, 2001; Pack et al., 2004). It is therefore not surprising that we, and others, have found that adult eye movements are influenced by 2D motion signals (Beutter & Stone, 1998; Masson et al., 2000). However, in our youngest infants, the observed OKN-like eye movements may have been mediated predominantly by subcortical motion mechanisms. Because our infant subjects exhibited significant barber-pole effects which were of the same magnitude as those of adults, this opens the intriguing possibility that subcortical motion mechanisms may be influenced by 2D motion signals, and to the same degree as cortical mechanisms.

4.2. U-Shaped function relating percent correct performance vs. age

In Experiment 1, which employed gratings moving at $\pm 18^\circ$, we found that age-related changes in left/right eye movement discrimination performance for both the horizontal and vertical apertures conditions could be described by a U-shaped function, first decreasing between two and four months, and then increasing between four and five months and into adulthood (see Fig. 5, left panel). The similarity in this U-shaped function between vertical and horizontal aperture conditions suggests that these effects were not related to the influence of 2D motion signals. We have previously discussed this U-shaped pattern in Dobkins et al. (2004) (since the data from Experiment 1 of the current study were part of that larger study), and remarked that this trend was similar to the results from a previous study that investigated infants' ability to discriminate

direction of random dot fields moving with a Gaussian distribution of directions (Banton, Bertenthal, & Seaks, 1999). In that paper, we suggested that the decline in performance with age could reflect an age-related decrease in reliance on subcortical motion mechanisms that drive eye movements, which exhibit a strong bias for horizontal stimulus motion and fairly broad direction tuning (Hoffmann & Distler, 1989; Hoffmann & Fischer, 2001). However, if this scenario were correct, we would have expected a similar U-shaped function in Experiment 2. This was not the case; in Experiment 2, eye movement direction discrimination performance was roughly constant as a function of age (see Fig. 5, right panel).

To account for the different shapes of performance vs. age functions between Experiments 1 and 2, we suggest that it is the broadness of tuning of the horizontally biased subcortical motion mechanisms that decreases with age. In this scenario, the $\pm 18^\circ$ gratings of Experiment 1, which were mostly vertical in their direction, would produce strong horizontal eye movements in 2-month-olds because, at this age, subcortical motion mechanisms are broadly tuned. As the tuning of these mechanisms narrows with age, the ability of 18° motion to drive horizontal eye movements is expected to decrease. However, we can also expect an overall 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). Thus, we suggest that the U-shaped function in Experiment 1 may reflect the combination of two processes: a specific age-related narrowing in the tuning bandwidths of horizontally biased subcortical motion mechanisms (which will lessen the ability of obliquely moving stimuli to elicit horizontal eye movements), and a non-specific age-related increase in the ability to judge eye movement direction. In Experiment 2, the fact that we did not find a decrease in the strength of horizontal eye movements between two and four months of age would be explained by supposing that the age-related narrowing of direction tuning in subcortical motion mechanisms has less effect on responses elicited by less obliquely moving stimuli, such as those employed in Experiment 2 (i.e., $\pm 45^\circ$).

In summary, the results of the current study demonstrate the existence of motion mechanisms that integrate 1D and 2D motion signals in very young infants, as evidenced by the finding of significant barber-pole effects. The fact that the relative weightings of 1D vs. 2D motion signals to direction coding (modeled from the magnitude of effective shift in direction) are roughly constant between two months of age and adulthood suggests that this integrative motion process (and the neural areas involved) develop remarkably quickly. Our finding of rapid development of relatively complex motion mechanisms is consistent with recent data examining the effects of visual deprivation early in development suggesting that other relatively complex forms of motion processing develop quickly (Ellemberg, Lewis, Maurer, Brar, & Brent, 2002; Fine

et al., 2003; Lewis et al., 2002). In future studies, it will be interesting to study the development of more complex forms of motion processing, including tests of whether infant integrative motion mechanisms are sensitive to contextual cues that affect the intrinsic vs. extrinsic nature of the 2D motion signal information (e.g., Shimojo et al., 1989).

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