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Sensitivity to first- and second-order drifting gratings in 3-month-old infants

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Abstract. In two experiments, we investigated 3-month-old infants' sensitivity to first- and second-order drifting gratings. In Experiment 1 we used forced-choice preferential looking with drifting versus stationary gratings to estimate depth modulation thresholds for 3-month-old infants and a similar task for a comparison group of adults. Thresholds for infants were more adult-like for second-order than first-order gratings. In Experiment 2, 3-month-olds dishabituated to a change in first-order orientation, but not to a change in direction of first- or second-order motion. Hence, results from Experiment 1 were likely driven by the perception of flicker rather than motion. Thus, infants' sensitivity to uniform motion is slow to develop and appears to be driven initially by flicker-sensitive mechanisms. The underlying mechanisms have more mature tuning for second-order than for first-order information.

Keywords: Development, first-order, second-order, motion, flicker, infants.

1 Introduction

Cues to form and motion are provided by first- and second-order characteristics of an image. First-order cues to form and motion are provided by spatiotemporal variations that give rise to luminance boundaries. Second-order cues to form and motion are provided by spatiotemporal variations that give rise to contrast or texture boundaries without a change in mean luminance.

The results of psychophysical (Chubb and Sperling 1988; Ellemberg, Lewis et al 2003; Ledgeway and Smith 1994), electrophysiological (Ellemberg, Lavoie et al 2003; Zhou and Baker 1993), human imaging (Ashida et al 2007; Dumoulin et al 2003; Smith et al 1998), and neuropsychological (Greenlee and Smith 1997; Vaina and Cowey 1996; Vaina et al 1998) experiments suggest that first- and second-order motion are processed, at least in part, by separate mechanisms (but see Ashida et al 2007 for a review of conflicting evidence). For example, adults do not integrate alternating frames containing first- and second-order local motion cues into an unambiguous percept of motion (Ledgeway and Smith 1994), and both the latency of the visual evoked potential (VEP) and the reaction time for a psychophysical response are longer for the onset of second-order motion than for the onset of first-order motion (Ellemberg, Lavoie et al 2003). As well, functional magnetic resonance imaging demonstrates segregation between the areas involved in processing first- versus second-order motion (Ashida et al 2007; Dumoulin et al 2003). Specifically, Dumoulin and colleagues found that first-order motion most strongly activates the early visual areas (V1) whereas

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second-order motion most strongly activates the higher visual areas (near V5). Similarly, Ashida and colleagues (2007) found direction selective-adaptation in fMRI activity in the human MT complex. However, when the adaptation and test stimulus were of the opposite type, no direction-selective adaptation occurred.

The purpose of the current study was to evaluate sensitivity to first- and second-order cues to motion in infants. To do so, we used both forced-choice preferential looking and habituation methods. Forced-choice preferential looking relies on a tester's judgment of infants' visual behaviour (eg, direction of first eye movement, direction of most frequent fixations, or direction of the longest fixations) to provide evidence that infants can discriminate between two simultaneously presented stimuli. One limitation of forced-choice preferential looking is that infants' visual behaviour may be based on any parameter that differs between a test and control stimulus, provided that the difference is salient to the infants. Therefore, it is important to ensure that the test and control stimulus vary only on the parameter of interest, rather than over a number of parameters. Another limitation of preferential looking is that it relies on intrinsic preferences. Thus, this method cannot be used to determine whether infants can, for example, discriminate leftward from rightward motion because infants may not have a robust preference for one direction over the other. The habituation method is useful in this case. Rather than rely on intrinsic preferences, habituation relies on the fact that once infants tire of looking at (or habituate to) one stimulus, they will look longer at another stimulus, provided they perceive it as a new stimulus. More formally, recovery of looking time indicates that infants can tell the difference between a habituated and a novel stimulus (Bornstein 1985).

Although habituation allows one to test infants' ability to discriminate stimuli that do not result in robust looking preferences, the habituation phase can be time consuming, and the method is limited to one or two test trials that must follow the habituation phase immediately. Therefore, it is impractical to use this method for threshold measures. In the current study, we used both forced-choice preferential looking and habituation to characterise 3-month-olds' sensitivity to first- and second-order moving stimuli. Forced-choice preferential looking allowed us to measure infants' sensitivity to moving versus stationary stimuli, while the habituation paradigm allowed us to determine whether infants could discriminate the direction of the moving stimuli, and hence whether their preferential looking was mediated by direction of motion or by sensitivity to flicker, which is not directionally selective.

Previous work shows that infants' sensitivity to motion emerges early in life. However, the age at which this is demonstrated varies with stimulus parameters. In a number of experiments, Wattam-Bell (1996a; 1996b;1996c) used forced-choice preferential looking and habituation to investigate infants' sensitivity to first-order motion with a shearing stimulus that contained three horizontal regions of dots. The centre region of dots moved left or right, while the upper and lower flanking regions of dots, depending upon condition, either moved coherently in the direction opposite to the centre strip, moved incoherently, or were static. If the direction of the dots' motion is perceived, the stimulus appears to have three horizontal stripes (form-from-motion) and looks different from a stimulus in which the dots all move in a uniform direction, all move incoherently, or all are static.

Wattam-Bell (1996a; 1996b;1996c) found that infants, 3 to 6 weeks of age, discriminated the shearing motion pattern from a patch of dots moving incoherently (for comparable evidence at an older age group, see Atkinson et al 1993; Braddick et al 1996), but at the same age, showed no evidence of being able to discriminate a shearing motion pattern from uniform motion or one direction of uniform motion from the opposite direction of motion (Wattam-Bell 1996a; 1996b;1996c). By 6 to 8 weeks of age, infants discriminated the shearing motion stimulus from uniform motion (Wattam-Bell 1996b), but still did not show evidence of being able to discriminate uniform motion moving in one direction from uniform motion moving in the opposite direction, a test they failed even at 9 to 12 weeks of age (Wattam-Bell 1996b; 1996c). There are no published studies of infants older than 9 to 12 weeks using behavioural methods that have established the age at which infants demonstrate sensitivity to the direction of uniform motion.

Only two studies have tested infants with second-order dynamic stimuli. In the first, Atkinson and colleagues (Atkinson et al 1993; Braddick et al 1996) found that infants as young as 8 to 12 weeks of age can discriminate a second-order shearing motion stimulus from a dynamic pattern containing no motion, as they could do with a similar first-order stimulus. Although the tester's mean percent correct responses were higher for first-order than for second-order stimuli at both ages tested, the authors drew no conclusions about the relative rate of development of sensitivity to first- versus second-order stimuli because they did not measure thresholds.

In the second study, Thibault et al (2007) compared contrast thresholds for first-order (luminance-modulated) and second-order (contrast-modulated) drifting gratings in older infants, children, and adults. They used forced-choice preferential looking to determine if infants and children can discriminate a drifting first-order or second-order grating from static grey-scale noise. The magnitudes of the luminance- and contrast-modulations varied according to the method of constant stimuli. Using results from the tester's judgments of looking preferences, they extrapolated first- and second-order motion thresholds for each infant and child, defined as the stimulus value corresponding to the experimenter's 75% correct response. Thibault et al found that infants as young as approximately 11 to 12 months, the youngest tested, can detect both first- and second-order moving gratings. Based on trend analyses of results from a clinical control group and a similar pattern in a nonclinical control group, they concluded that thresholds improved with age at an equal rate for first- and second-order stimuli.

Thibault and colleagues' (2007) results must be interpreted with caution. The task was designed to test infants' visual response to a drifting grating versus a field of static noise. Thus, infants may have responded to form (grating versus noise field), flicker (induced by the drifting grating but not the static control stimulus), or motion in the drifting grating—the static noise field differed from the drifting grating on all three of these parameters. Furthermore, because the nonclinical control group included only 20 children ranging from less than 1 year to almost 7 years of age, thresholds at each age were based on data from only one or two children.(1)

When stimuli are stationary, one study found evidence that infants can detect a change in a second-order pattern defined by texture at 12 weeks of age (Freedland and Dannemiller 1990). However, other studies using different methods found that sensitivity to second-order pattern does not emerge until 14 to 18 weeks of age (Atkinson and Braddick 1992; Rieth and Sireteanu 1994b) or even as late as 9 to 12 months of age (Rieth and Sireteanu 1994a; Sireteanu and Rieth 1992). Despite the great variability in the estimate of onset of sensitivity to second-order pattern, one reliable finding has been obtained in every study that measured sensitivity to both first- and second-order stationary patterns: infants' sensitivity to first-order pattern emerges earlier than sensitivity to second-order pattern (Atkinson and Braddick 1992; Rieth and Sireteanu 1994b; Sireteanu and Rieth 1992).

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(1) Trend analyses for first- and second-order conditions were done using a larger group of clinical controls ($n = 72$) who attended the vision clinic because of risk for visual disorder. Although they performed normally on visual screening tests, there is no assurance that this group is visually normal or representative of the general population. This concern does not arise for the nonclinical control group, which consisted of only 20 individuals ranging in age from infancy to 7 years.

In the current study, we measured sensitivity to first- and second-order drifting gratings using a design similar to the one used by Thibault et al (2007). However, to rule out the possibility that infants' visual behaviour was based on the perception of form rather than motion, we used gratings that had identical form for both the test and the control stimulus. The test stimulus was a drifting grating, while the control stimulus was an identical stationary grating. To quantify sensitivity to first- and second-order stimuli, the visibility of the stimulus was varied over trials to determine the smallest difference in luminance (first-order) or contrast (second-order) between adjacent stripes sufficient to allow infants to indicate that they could discriminate the two gratings. We tested infants at 3 months of age because results from other motion tests are mixed at this age (Wattam-Bell 1996a; 1996b; 1996c).

The forced-choice preferential looking method of Experiment 1 allowed us to quantify sensitivity to drifting first- and second-order stimuli compared with a static control stimulus. To determine whether 3-month-olds are sensitive to direction of first-order and second-order local motion, or only to differences in flicker between static and moving stimuli, in Experiment 2 we used a habituation design. After habituating 3-month-olds to one direction of motion, we compared their looking times to the familiar direction and a novel direction to see if the infants recovered attention to the novel direction of motion.

We measured infants' and adults' sensitivity to first- and second-order drifting gratings. Our purpose was to determine infants' relative immaturity for first- versus second-order stimuli.

2 Methods

2.1 Participants

The participants included in the analyses were twenty-four 3-month-olds (3.00–3.99 months; mean = 34 months), and 10 adults (mean age = 21.2 years, range 19.0–23.5 years). All infants were healthy and born full term with no history of eye problems. An additional two 3-month-olds were excluded from the data analysis because of fussiness. The adults had normal or corrected-to-normal vision. Infants were recruited using contact information provided by parents who expressed interest in participating in our studies at the time of the child's birth. Adults were recruited from a pool of undergraduate students registered in Introductory Psychology at McMaster University. They received class credit for participation.

2.2 Apparatus and stimuli

The stimuli were generated by a Macintosh G4 computer by means of VPixx software™ and were displayed on a 50.8 cm Clinton Monochrome monitor (model number DS2000HB). The monitor had a frame rate of 75 Hz and pixel resolution of 1024 × 768. The stimuli were two 0.5 cy/deg vertical sinusoidal gratings, each contained within a 15 × 15 deg square viewed from 50 cm. Each display consisted of two identical gratings whose inner edges were separated horizontally by a 3.4 cm (5 deg) gap. One grating drifted outward (leftward when it was on the left side of the screen and rightward when it was on the right side of the screen) at 6 deg/sec, while the other remained stationary. The gratings were surrounded by a grey background with a mean luminance of 72 cd/m^2. We used outward rather than inward drifting gratings in case infants' eye gaze followed the direction of motion. With outward motion, infants may look closer to the outer edge of the screen rather than toward the centre of the screen, thus improving accuracy of judgments of looking behaviour.

The gratings were either luminance modulated (first-order) or contrast modulated (second-order) and were like those described by Ellemberg and colleagues (Ellemberg, Lewis et al 2003; Ellemberg, Lavoie et al 2003). The carrier was static two-dimensional unmodulated noise like that described by Smith and Ledgeway (1997). Each noise element subtended 2 × 2 arc min and was assigned independently with a probably of 0.5 to be either 'light' or 'dark'. Prior to modulation, the Michelson contrast of the noise measured over adjacent noise elements with opposite polarity was 30%. For luminance-modulated stimuli, the noise carrier was added to a luminance-modulated sinusoidal grating. This created a series of regions that alternated between higher and lower luminance. The amplitude of the luminance modulation (Michelson contrast or modulation depth) varied within the range of 0 to 0.5 as defined by:

$$\text{Modulation depth} = (L_{\max} - L_{\min}) / L_{\max} + L_{\min}) \,,$$

where $L_{\max}$ and $L_{\min}$ are the maximum and minimum luminances, respectively, averaged over adjacent pairs of noise dots.

For contrast-modulated stimuli, the noise was multiplied by a sine wave to create a contrast-modulated stimulus. The stimulus consisted of a series of alternating regions of higher and lower contrast, with every region having the same mean luminance. The amplitude of the contrast modulation (modulation depth) varied within the range of 0 to 1 as defined by:

$$\text{Modulation depth} = (C_{\max} - C_{\min}) / (C_{\max} + C_{\min}) \,,$$

where $C_{\max}$ and $C_{\min}$ are the maximum and minimum mean local contrast (Michelson) of adjacent pairs of noise dots. The monitor was calibrated every few weeks to ensure that the luminance of higher and lower contrast regions of the contrast-modulated stimuli differed by less than 1 cd/m^2 and that the mean luminance of the luminance- and contrast-modulated stimuli also differed by no more than 1 cd/m^2 when the gratings were displayed at maximum contrast. The mean luminance of the stimuli as measured at maximum contrast was 72 cd/m^2 for both the luminance- and contrast-modulated stimuli.

2.3 Design

We compared estimates of infants' group thresholds for first- and second-order stimuli to the means of adults' individual thresholds. This allowed us to determine the relative difference in maturity for sensitivity to first- versus second-order stimuli. We estimated infants' group thresholds by measuring an experimenter's accuracy in using the infants' looking behaviour to judge the side of the drifting grating (see below). The thresholds were measured at four different modulations for each type of stimulus (see Table 1).

Table 1. Luminance- and contrast-modulated values (log units) that were tested in Experiment 1.

Luminance-Modulation	Contrast-Modulation
0.70	1.85
1.00	1.90
1.30	1.95
1.60	2.00

2.4 Procedure

The procedures were explained to and informed consent was obtained from adults and from parents of the infants. The experimental protocol was approved by the McMaster Research Ethics Board.

2.4.1 *Infants* .

Half of the infants were tested with first-order drifting gratings, and the other half with second-order drifting gratings. Each infant was positioned on his or her parent's lap so that the infant's eyes were 50 cm away from the computer monitor. Parents wore opaque glasses to prevent them from seeing the stimuli and possibly influencing the infant's responses. The experimenter was positioned behind the computer monitor, hidden from the infant's view by a screen. A Sony Digital 8 Handycam camcorder (model number TRV260) was placed behind a peephole directly above the computer monitor to allow the experimenter to view the infant's eye movements on a television monitor. Because the room was lit only by the glow of the computer monitor, we used the video camera's NightShot feature, which uses infrared to allow an image to be visible in very low light conditions and works especially well to show corneal reflections.

At the beginning of each trial, a central fixation target appeared on a grey background. The fixation target consisted of white looming dots on a 3 deg circular black disk. Once the experimenter (VA) judged the infant to be fixating the central target, she pushed a key causing the fixation target to be replaced with two gratings, one drifting outward and one stationary. The experimenter, unaware of the side with the drifting grating or of its contrast, used any reliable cue provided by the infant (eg, the direction of the first eye movement, or the direction of the longest fixation) to make a forced-choice decision as to whether the drifting grating was on the left or right side of the monitor. Each trial ended once the experimenter entered a judgement on the keyboard. At that time, the looming dots reappeared and a new trial began. Although the experimenter was given an unlimited time to make this judgement, it typically took less than 10 seconds. The experimenter did not receive feedback about the accuracy of her observations during testing.

Sensitivity to first- and second-order stimuli was measured separately, in each case with a test consisting of 16 trials. The depth modulation of the stimuli was varied according to the method of constant stimuli to include four different depth modulations per motion type (see Table 1 for modulations tested). We estimated group thresholds for infants based on the pattern of mean experimenter accuracy across infants for each modulation tested and for each type of motion.

A second experimenter made independent forced-choice decisions as to the side of the moving grating for half of the infants tested with each stimulus type, for a total of 12 infants across the two groups. The second experimenter agreed with the primary experimenter on at least 75% of the trials for each infant (range 75–100%). The mean reliability was 87.5% for first-order motion and 86.4% for second-order motion. Only the data from the first experimenter were used in the final analyses.

2.4.2 *Adults* . Adults were tested using the same displays. However, adults, unlike infants, provided an individual threshold for both first- and second-order stimuli based on a staircase procedure. The order of testing (first-order first versus second-order first) was counterbalanced across participants.

Adults were told that they would see two squares containing stripes and that the stripes in either the left or right square would move outward. They were asked to indicate verbally which square contained the moving stripes, the left or the right. At the start of each trial, adults were asked to fixate on the looming white dots that appeared in the centre of the screen. The looming dots were then replaced by the stimulus. The experimenter, who was blind to the display on each trial, entered responses on the keyboard and watched the participant's eyes to ensure that he or she was looking at the computer screen. The contrast of the grating was varied over trials using the VPIXX VPEST adaptive staircase that is similar to Harvey's (1986) ML-TEST. The staircase terminated when the 95% confidence interval of the estimated threshold was ±0.1 log units of the estimate. Thresholds were defined as the minimum luminance-modulation (first-order) or contrast-modulation (second-order) necessary to respond correctly 82% of the time.

Prior to each test block, adults completed demonstration, criterion, and practice phases for both first- and second-order stimuli. For the demonstration phase, participants were presented with two trials with the gratings at maximum luminance- or contrast-modulation, one trial for each of the two alternative choices (left/right). To verify that the adults understood the task, they were presented with a criterion phase consisting of four test trials, again at maximum depth modulation, with verbal feedback. To be included in the study, participants had to respond correctly on all four trials in a test block, and all participants met this criterion. After the criterion phase, participants completed a practice staircase. Feedback occurred after each trial and consisted of a high-pitched tone for a correct response and a low-pitched tone for an incorrect response. Practice was terminated after the depth-modulation was reduced to the point where two incorrect responses occurred consecutively. Participants then completed the test phase with feedback.

2.5 Data analysis

For each infant and each modulation tested, we determined the percent of trials for which the experimenter correctly guessed the side of the drifting grating based on the infant's responses. The percentages of correct responses were averaged across subjects to give a group psychometric function that related accuracy to the luminance- and contrast-modulations tested (see Figure 1). We estimated group thresholds by determining the lowest luminance- and contrast-modulations that resulted in the experimenter's accuracy being above chance, as indicated by one-sample t-tests with a Bonferroni correction. Estimated thresholds were compared with adults' mean thresholds to determine how many log units worse infants were than adults. This allowed us to compare immaturity for first- versus second-order stimuli.

Although others have used more stringent criteria to determine infants' thresholds for sensitivity to moving stimuli (eg, Aslin and Shea [1990] used a criterion of 75%) or have used the same threshold criterion for infants and adults (eg, Thibault et al 2007), we chose the current approach because any result significantly above chance is a clear indication that infants at that age can detect a stimulus, or discriminate a difference between two stimuli. This approach has also been used to assess other aspects of infants' visual perception, such as face processing (Macchi Cassia et al 2006), texture segmentation (eg, Rieth and Siretenau 1994b), and motion detection (Braddick et al 1996) and has been used to measure grating acuity in infants (Teller 1979) and animals (Wilkinson 1995). A stricter criterion would likely underestimate infants' capabilities. Moreover, using the same accuracy criterion for infants and adults would be to assume that infants and adults were performing the same task. This is clearly not the case. Infants' responses were based on implicit visual behaviours, while adults were responding based on explicit task requirements, with feedback. Any method with infants is likely to underestimate sensitivity to what is being measured. Although the absolute size of the difference between infants and adults is hard to interpret because of such differences, we used the adult values to compare conditions, that is, to ask whether infants are more or less mature for first-order versus second-order stimuli. Although we acknowledge that infants' sensitivity to first- and second-order information is likely underestimated, there is no reason to suspect that this underestimation would differ for first- and second-order stimuli.

3 Results

Mean experimenter accuracies for each group of infants are shown in Figure 1 for first-order (Panel A) and second-order (Panel B) stimuli. For first-order gratings, the experimenter's accuracy was above chance for the 3-month-olds when luminance-modulation was 1 log unit (10%) or higher ($ps < .005$), but did not differ from chance when luminance-modulation was 0.7 log units (5%) ($p = .048$, alpha = .0125). Based on these results, we estimate first-order thresholds to be between 0.7 and 1 log unit at 3 months of age.

For second-order gratings, the experimenter's accuracy was above chance only when the contrast-modulation was 2 log units (100%) ($p < .005$) and did not differ from chance when contrast-modulation was 1.95 log units (90%) or lower ($ps > .08$). Thus we estimate that 3-months-olds' threshold for second-order gratings is between 1.95 and 2 log units.

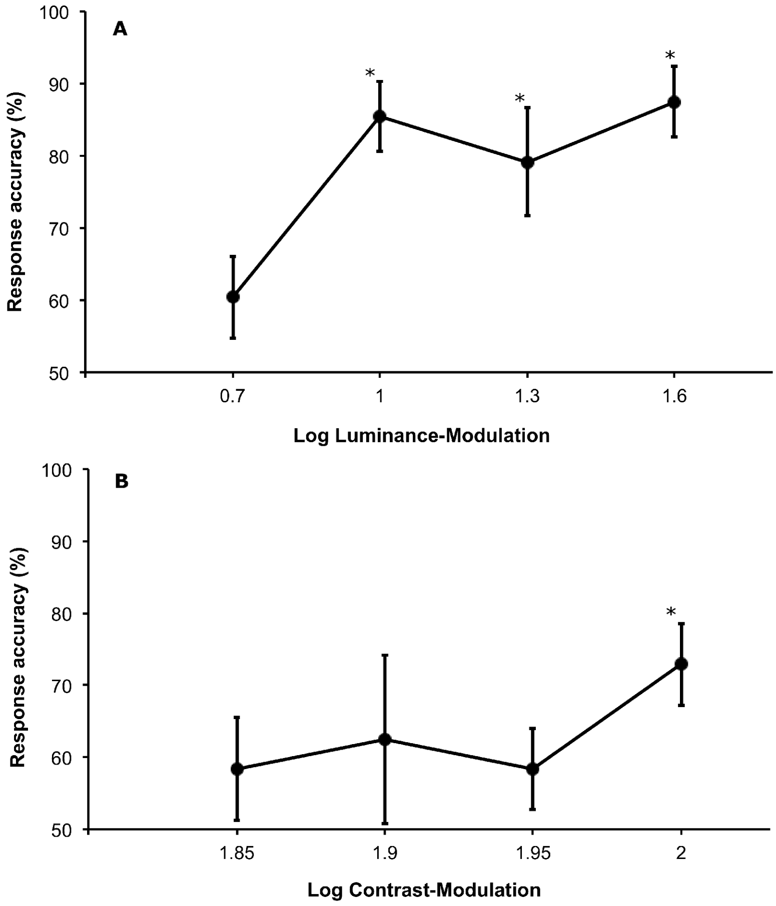

Figure 1. Experimeter's accuracy (mean percent of correct responses (±1 s.e) based on 3-month-olds' responses to moving versus stationary (a) first-order gratings and (b) second-order gratings. The 50% value on the y-axis represents performance expected by chance. Values marked with an asterisk indicate values that are significantly above chance ($p < .0.125$). Note that the values on the x-axes (log luminance- or contrast-modulation) cannot be compared directly because they are in units relevant to two different properties (change in luminance versus in contrast, respectively).

Adults had a mean threshold of −0.5 log units (0.3%) (range = −0.7 to −0.4 log units or 0.19 to 0.45%) for first-order stimuli and 1.5 log units (32%) (range = 1.3 to 1.6 log units or 20 to 43%) for second-order stimuli. Infants' estimated thresholds are plotted with adults' mean log thresholds in Figure 2. Note that data for first- and second-order conditions are plotted on the same scale for convenience of presentation. Absolute differences in first- and second-order thresholds are not meaningful because the thresholds are based on different image attributes (Bertone et al 2008). However, the difference between infants and adults—that is, the relative immaturity—can be compared. As shown in Figure 2, infants were more immature for first-order than second-order motion. Specifically, infants' sensitivity to drifting first-order gratings was about 1.2 to 1.5 log units worse than adults' mean threshold. Sensitivity to second-order drifting gratings was only 0.45 to 0.50 log units worse than adults' mean threshold.

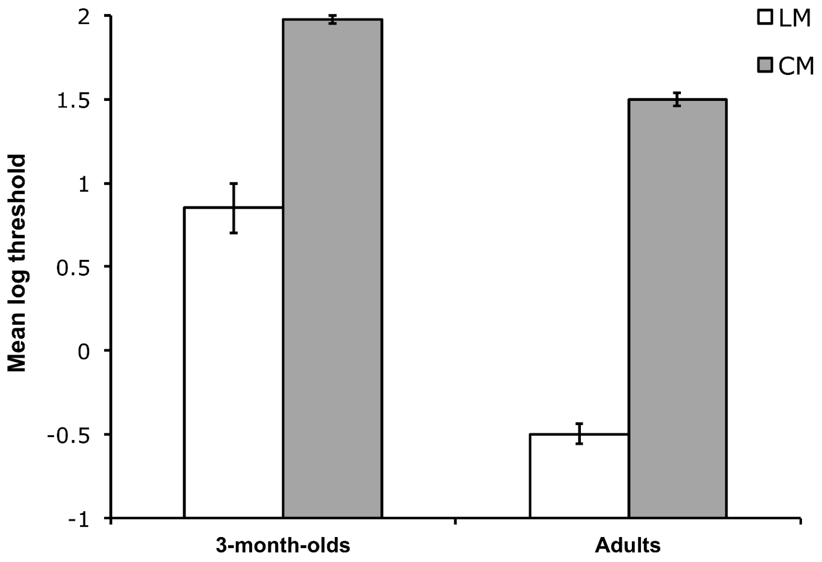

Figure 2. Infants' estimated log thresholds and adults' mean log thresholds for luminance-modulated (LM) and contrast-modulated (CM) stimuli. Error bars denote the estimated range of the threshold for infants and standard error of the mean for adults. On a log scale, negative values represent modulations lower than 1%.

4 Discussion

Like many previous studies (eg, Aslin and Shea 1990; Volkmann and Dobson 1976), we found that infants in Experiment 1 discriminated a moving grating from a stationary grating of the same spatial frequency and orientation. These preferences could not have been based on differences in form because, on each trial, both stimuli contained identical stripes, but only one stimulus was moving. Therefore, infants' discrimination must have been based on sensitivity to motion and/or flicker.

Experiment 1 also indicates that 3-month-olds can discriminate a moving from a stationary grating whether the grating is defined by first-order (luminance) or second-order (contrast) information. This is consistent with previous evidence that infants of that age can discriminate shearing motion based on either type of information (Atkinson et al 1993; Braddick et al 1996). Our design allowed us to also evaluate the relative immaturity of sensitivity to the two types of information. The results for adults tested with the same stimuli were similar to previous studies (Ledgeway and Hutchinson 2005). Specifically, adults' mean first-order thresholds were −0.5 log units (0.3%) while their mean second-order thresholds were 1.5 log units (32%). The comparison to the estimated thresholds for infants indicated that infants' sensitivity to second-order information was more adult-like than their sensitivity to first-order information. They were only about 3 times worse than adults for second-order cues but 20 to 30 times worse than adults for first-order cues.

Infant thresholds may be more similar to those of adults for second-order than for first-order drifting gratings, perhaps because those mechanisms are less efficient and hence easier to develop (Bertone et al 2008; see General Discussion). Our finding that 3-months-olds' sensitivity to second-order stimuli was more adult-like than their sensitivity to first-order stimuli is consistent with evidence indicating that the mechanisms underlying the perception of these two types of motion are, at least in part, separate (eg, Ellemberg, Lavoie et al 2003; Ledgeway and Smith 1994; Vaina and Cowey 1996). However, it is unclear whether these results reflect sensitivity to motion or flicker. Infants might have detected the direction of motion in the stimuli or they might have detected only that the moving stimulus induced flicker because as they fixated a given point, like the edge nearest to centre, the stimulus changed from dark to light (first-order condition) or low to high contrast (second-order condition).

5 Experiment 2: Habituation

The purpose of Experiment 2 was to determine whether the preferential looking results from Experiment 1 were mediated by sensitivity to flicker, which is not directionally selective, or by direction of motion. We tested 3-month-olds' sensitivity to the direction of first- and second-order motion by habituating them to stimuli like those of Experiment 1 with one direction of motion (left or right) and testing whether they recovered attention to the opposite direction of motion.

Similar to previous studies (Wattam-Bell 1996b;1996c), we used an infant-controlled habituation procedure to test infants' sensitivity to direction of motion. One group of 3-month-olds was tested with first-order vertical gratings, and another with second-order vertical gratings. We presented all gratings at maximum luminance- or contrast-modulation. Infants saw one direction of motion (left or right) until they met the predetermined habituation criterion. We then showed infants vertical gratings in both the novel (opposite to habituated) and the habituated directions of motion. Sensitivity to direction of motion would be indicated if infants looked longer at the novel than the habituated direction of motion. As a final test trial, we presented each infant with a horizontal grating moving downward that was novel in both orientation and direction of motion. This trial was included to verify that our method was sensitive enough to measure infants' detection of a change in a stimulus parameter (orientation) shown previously to be discriminable even by 1-month-olds who were tested with a similar habituation paradigm with first-order stimuli (Maurer and Martello 1980).

6 Methods

6.1 Participants

The participants were forty 3-month-olds (3.00–3.99 months; mean = 34 months) divided into two groups of twenty. Inclusion criteria were the same as for Experiment 1. An additional eight infants were excluded from the data analysis because of fussiness ($n = 7$) or because they did not stay awake long enough to complete the task ($n = 1$).

6.2 Apparatus and stimuli

The apparatus and stimuli were identical to those in Experiment 1, except that each display consisted of only one grating in the centre of the monitor. The grating was either vertical and drifted left or right (habituation and initial test phase) or horizontal and drifted downwards (final test trial). The stimuli were presented at the maximum luminance- or contrast-modulation.

6.3 Procedure

At the beginning of each trial, a central fixation target, consisting of white looming dots on a 3 deg circular black background, appeared on the screen. Once the infant was judged to be fixating the target, it was replaced by a vertical grating that drifted to the left or to the right. The experimenter pressed a key to record the duration of on and off looks based on the corneal reflection of the stimulus. As in Experiment 1, corneal reflections were viewed using the infrared feature of the video camera. Each trial ended once the experimenter judged the infant to have looked away from the stimulus for a cumulative duration of 2 seconds. Custom VPixx™ software tabulated total on and off looking times and used these tabulated times to control the stimulus display according to the predetermined criteria.

The procedure consisted of two phases: habituation and test. During the habituation phase, the same direction of motion was presented on every trial. The habituation phase continued until the mean looking times of three consecutive trials dropped to 50% (or less) of the mean looking time during the first three trials. The test phase began immediately after the habituation criterion was reached. The experimenter was unaware of when the task transitioned between the habituation and test phases and unaware of the direction of motion on each trial. In the test phase, infants were given one trial with the grating drifting in the familiar direction (leftward or rightward) and one trial with the grating drifting in the opposite direction. As in the habituation phase, each trial of the test phase lasted until the infant looked away for 2 seconds.

Because even 1-month-olds can discriminate a 90 deg difference in the orientation of sequentially presented luminance-modulated gratings (Maurer and Martello 1980), we presented a horizontal grating drifting downward at the end of each test phase. Thus, if infants dishabituated to the novel orientation, a lack of dishabituation to the novel direction of motion could not be attributed to fatigue.

Half the participants were tested with first-order motion and half with second-order motion. The direction of motion during habituation (left or right) was counterbalanced across infants so that half of the infants in each group were habituated to rightward motion and half were habituated to leftward motion. During the test phase, the order of presentation of leftward and rightward motion was counterbalanced so that half of the infants in each group saw the habituated direction of motion first and the other half saw the novel direction of motion first. All infants saw downward motion last.

Because total trial duration depends on an infant’s on and off looks as judged and keyed by one experimenter, the infant-controlled procedure does not allow for independent observations from multiple experimenters. If one experimenter judges the infant to be looking off for a sufficient amount of time, the trial will end, as will any further observation for Experimenter 2 on the same trial. Thus, only one Experimenter (VA, or SR, a student assistant) observed each infant included in the main habituation experiment.

To assess the reliability of the measure of infants' looking times, the experimenters conducted a pilot study comparing their observations to each other’s and to those of one other experimenter. Five additional infants who were not included in the main study viewed 10 different stimuli, presented sequentially ranging in interest from faces to stationary gratings. Each of the 10 stimuli remained on the screen for 20 seconds. The experimenters made independent judgements of the infants’ on and off looks. These looking times were significantly and positively correlated, $r \geq 0.95$, for each infant.

6.4 Data analysis

One-tailed paired t-tests were used to compare mean looking times for the familiar versus the novel direction of motion, as well as the familiar direction of motion versus the novel orientation (downward motion). Looking times that had a Z-score of 2.5 above or below the group and condition mean were identified as outliers. In total, four subjects had looking times that fit this criterion. The data from these four subjects (two for first-order and two for second-order) were excluded from the analysis. Alpha was set to .025 to correct for multiple comparisons. Recovery from habituation, and thus sensitivity to change in the stimulus, is indicated if looking times are significantly longer for the novel than the habituated stimulus.

7 Results

Infants required 6 to 70 trials to become habituated to the moving stimuli (overall mean = 21 trials; first-order stimuli: mean = 20 trials, range = 6–58 trials; second-order stimuli: mean = 21 trials, range = 6–70 trials). During the habituation phase, total mean looking times were

94.9 sec (range = 23.4–326.2 sec) for first-order stimuli and 62.7 sec (range = 14.3–184.7 sec) for second-order stimuli.

Mean looking times for familiar and novel directions of motion and for the novel orientation (moving down) are shown in Figure 3, for both first-order (Panel A) and second-order (Panel B) stimuli. For luminance-modulated stimuli, there was no difference in looking times for the familiar and the novel directions of motion, $t(17) = 0.14$, $p = .44$, Cohen's $d = 0.05$. However, there was a significant difference between the familiar direction of motion and the novel orientation (moving down), $t(17) = 2.5$, $p < .025$, Cohen's d = 0.78. On average, infants looked at the downward motion with the novel orientation 1.7 times longer than they looked at the familiar direction of motion. For second-order stimuli, there was no difference in looking time for the familiar and the novel directions of motion, $t(17) = 0.87$, $p = .20$, Cohen's d = 0.21, or the familiar direction of motion and the novel orientation, $t(17) = 1.6$, $p = .06$, Cohen's d = 0.45. These results indicate that infants recovered attention from habituation only for the novel orientation and only when tested with first-order stimuli.

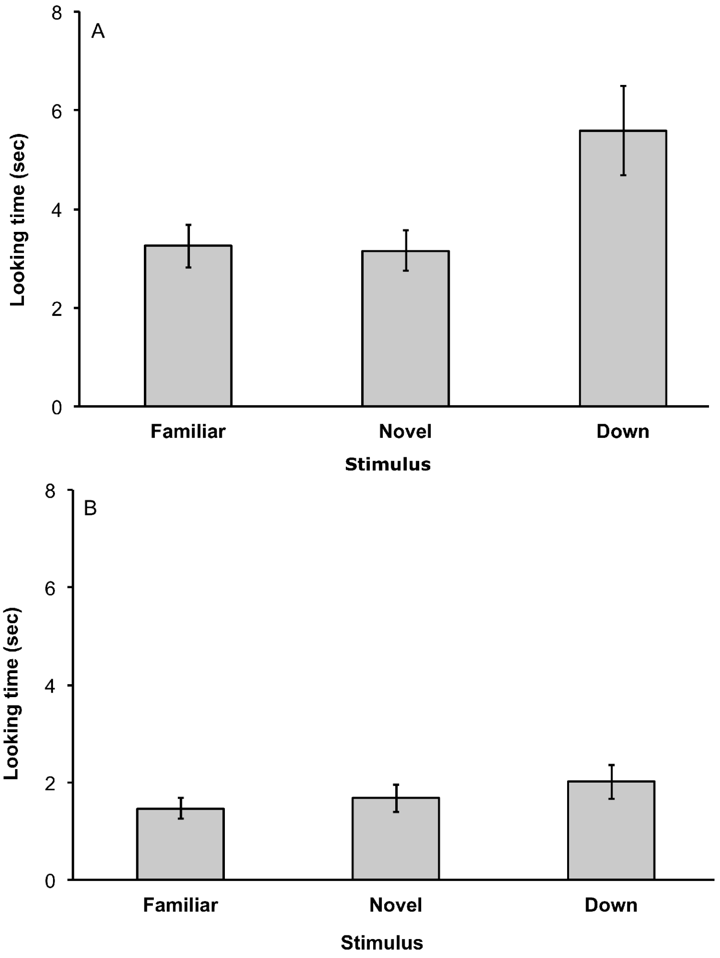

Figure 3. Three-month-olds' looking times (±1 s.e) during the test phase after habituation to vertical gratings moving leftward or rightward. Results are for vertical gratings moving in the habituated direction, vertical gratings moving in a novel opposite direction, and horizontal gratings moving downward (both a novel orientation and direction of motion) for (a) first-order and (b) second-order motion. Infants' looking times did not differ for the novel versus habituated direction of motion. However, infants did look significantly longer at the grating with novel orientation than the habituated orientation, but only when tested with first-order stimuli.

8 Discussion

After habituation to a moving first-order grating, 3-month-old infants' looking times increased when there was a change in both orientation and direction of motion, but not when there was a change in direction of motion alone. This comparison implies that 3-month-olds are sensitive to first-order cues to orientation but not first-order cues to direction of uniform motion. After habituation to a moving second-order grating, 3-month-old infants showed recovery to neither a change in orientation nor direction. These findings are consistent with earlier reports that sensitivity to first-order pattern emerges within the first 3 months of life (Atkinson and Braddick 1992; Rieth and Sireteanu 1994b; Sireteanu and Rieth 1992) while sensitivity to second-order pattern emerges at 14 to 18 weeks of age (Atkinson and Braddick 1992; Rieth and Sireteanu 1994b) or 9 to 12 months of age (Sireteanu and Rieth 1992), depending on test conditions. Regardless of the exact ages, infants in each of those studies demonstrated sensitivity to first-order pattern at a younger age than they demonstrated sensitivity to second-order pattern.

Infants did not dishabituate to a change in direction of motion for either first- or second-order stimuli. It is unlikely that the failure resulted from an insensitive method because the same method revealed recovery of attention for a change in first-order orientation. The results are consistent with evidence from other labs that young infants are sensitive to relative motion, but not the direction of uniform motion (see General Discussion).

These findings suggest that the 3-month-olds in Experiment 1 may have discriminated the static and moving stimuli on the basis of flicker rather than motion per se: when any point on the grating is fixated, its movement would create a flickering pattern of increases and decreases in luminance or contrast on the retina. For the first-order stimuli, infants may have detected a pattern of flickering vertical stripes paired with static vertical stripes. For the second-order stimuli, they may have detected the second-order flicker but not the second-order pattern in either the moving or static grating. If this is true, then results from Experiment 1 may be based on a perception of flicker versus a plain field for the second-order task and a perception of a flickering versus static grating for the first-order task. Another possibility is that infants may have detected a flickering pattern and a static pattern in Experiment 1, without being able to discriminate its orientation in Experiment 2. That interpretation is suggested because in Experiment 1 infants discriminated the second-order moving grating from the stationary grating, but in Experiment 2, failed to dishabituate to the change in orientation for second-order stimuli. Even adults perform better on tasks that require simple detection compared to tasks that require discrimination. For example, adults are more accurate at detecting a static grating than discriminating a vertical from an oblique grating (Orban et al 1997). The same pattern of results holds true for more complex visual tasks. Specifically, d prime measures for object detection are better than object discrimination in natural scenes (Rohaly et al 1997), while contrast thresholds are better for letter detection than letter identification (Pelli et al 2006).

9 General discussion

In Experiment 1, using forced-choice preferential looking, we found that 3-month-olds' sensitivity to drifting gratings was more adult-like for second-order than first-order stimuli. Because stimulus discrimination could have been based on motion or flicker, we tested 3-month-olds' sensitivity to direction of motion using a habituation design in Experiment 2. The results of the habituation study suggest that 3-month-olds are not sensitive to the direction of first- or second-order motion and hence suggest that 3-month-olds used cues to flicker rather than motion in Experiment 1. Previous reports show that infants are sensitive to flicker when there are no motion cues and that this sensitivity matures rapidly (eg, Regal

1981). Although evidence from VEP studies suggests that cortical sensitivity to the direction of motion emerges at about 2 to 3 months of age (Braddick et al 2005; Wattam-Bell 1991), infants in that age range fail behavioural tests (this study; Wattam-Bell 1996c). Older infants have not been tested with behavioural methods distinguishing flicker from uniform motion, likely because the habituation technique is no longer effective with simple stimuli.

9.1 First- versus second-order information

At first glance, it seems paradoxical that sensitivity to second-order information might be more mature given filter-rectify filter models in which second-order mechanisms include additional processing stages beyond what is required for first-order mechanisms (Wilson et al 1992). However, the same pattern has been reported in monkeys and in some studies of development during later childhood. Specifically, when tested with stationary stimuli, monkeys' sensitivity to texture modulation when discriminating horizontal from vertical texture (a second-order task) was adult-like by 20 weeks of age, while their contrast sensitivity for discriminating luminance-defined horizontal from vertical gratings (a first-order task) did not reach adult-like levels until the monkeys were 40 weeks of age (Kiorpes et al 2006).

Similarly, children's sensitivity to second-order motion is adult-like before sensitivity to first-order motion and is more adult-like from 3 years onward (Armstrong et al 2009; Bertone et al 2008), at least under some conditions (Ellemberg, Lewis et al 2003) and when log thresholds are compared appropriately (see Armstrong et al 2009 for details). Bertone et al (2008) explained the earlier maturity of sensitivity to second-order motion by noting that in adults second-order mechanisms are less efficient than first-order mechanisms (Allen et al 2004) and hence may require less development to reach mature sensitivity. Other evidence supports this hypothesis. Specifically, second-order motion mechanisms in adults are less directionally selective than first-order motion mechanisms (Ledgeway and Hess 2002), and human observers are less efficient at detecting contrast-modulations than luminance-modulations compared to an ideal observer (Manahilov et al 2005). If adults' second-order mechanisms are less efficient or less sensitive than their first-order mechanisms, less neural development may be required to reach adult-like levels of second-order processing than first-order processing (Bertone et al 2008). The lesser efficiency may also make second-order mechanisms more vulnerable to insult, as is in the case of amblyopia (Ellemberg et al 2005; Thibault et al 2007).

Some evidence appears to contradict these conclusions by suggesting that sensitivity to second-order information develops more slowly than sensitivity to first-order information. For example, Ellemberg Lewis et al (2003) reported that 5-year-olds' immaturity scores were smaller for first- than second-order motion (but see reanalysis in Armstrong et al 2009). Similarly, using C-Optotypes, Bertone et al (2010) found that, by 12 years of age (the oldest age tested), children's contrast thresholds were adult-like for luminance-defined, but not texture-defined, static form. Results from an eye-tracking study also suggest that, at 10-months of age, first-order motion mechanisms are more mature than second-order motion mechanism (Kato et al 2008). However, although Kato and colleagues argue that their results are not accounted for by stimulus visibility, it should be noted that their first- and second-order stimuli differed in both contrast and flicker content. Therefore, it is likely that target salience also varied across stimuli. Stimulus differences are an important consideration when comparing development or maturity of first- versus second-order mechanisms. For example, Bertone et al (2010) suggests that differences in spatial frequency content of stimuli across studies may account for differences in patterns of development of first- versus second-order motion mechanisms (Armstrong et al 2009; Bertone et al 2008 versus Bertone et al 2010).

It is also important to consider that reorganization of the extrastriate cortex that occurs between infancy and adulthood likely does not occur at uniform rates across different areas

(Wattam-Bell et al 2010). Using visual event related potentials (VERPs), Wattam-Bell et al (2010) demonstrated that, at 5 months of age, global form mechanisms are less mature than global motion mechanisms. Furthermore, based on topography of the high-density VERPs, 5-month-olds' global motion and form VERPs were based on different cortical sources than found for adults. Thus, significant functional reorganisation of both global motion and form mechanisms occurs between 5 months of age and adulthood. For example, based on topography, the global motion stimuli used in their study may be processed by area ~ V5 at 5 months, but around areas V3/V3A and V6 in adulthood (Wattam-Bell et al 2010). Similarly, comparisons of infants' and adults' responses to equiluminant moving stimuli suggest that initially there is ventral input into dorsal stream processing of motion that is retracted during infancy (Dobkins and Teller 1996).

The findings by Wattam-Bell and colleagues (2010) that global motion mechanisms are more mature than global form mechanisms at 5 months of age contrasts with VEP evidence that local form mechanisms emerge earlier than local motion mechanisms in an earlier period of infancy (eg, Braddick et al 2005). Wattam-Bell and colleagues suggest that this pattern of results indicates that development of global motion mechanisms occur rapidly after the emergence of local motion mechanisms, while global form mechanisms have a more protracted period of development after the emergence of local form mechanisms. Therefore, it is possible that our results from Experiment 1, indicating more mature second-order mechanisms, likely are based on flicker detection, and our results from Experiment 2, indicating emergence of first- but not second-order orientation sensitive mechanisms, reflect this pattern of variable development across different areas of the visual cortex.

9.2 Shearing versus uniform motion

As described in the Introduction, previous results do indicate that by 6 to 8 weeks of age infants can discriminate shearing motion that contains regions or segments that move in opposite directions to each other from uniform motion (Wattam-Bell 1996b). However, infants 9 to 12 weeks of age, as in the current study, show no evidence of being able to discriminate uniform motion moving in one direction from uniform motion in the opposite direction, when tested with a habituation design (Wattam-Bell 1996c). In the same study 9- to 12-week-olds, but not 6- to 8-week-olds, did show sensitivity to direction when the stimulus contained shearing motion in which stationary segments flanked a moving centre strip.

Taken together, these findings suggest that sensitivity to shearing motion with a moving reference strip develops prior to sensitivity to shearing motion with a stationary reference strip, which in turn, develops before sensitivity to uniform motion.(2) Thus, it may be that 3-month-olds are sensitive to the direction of motion when a moving or stationary reference point is available but lack robust directional sensitivity without such a reference, whether the motion is defined by first-order or second-order cues. It is also possible that shearing motion taps mechanism responsible for detecting edges defined by motion contrast, rather than motion mechanisms per se.

Wattam-Bell (1996d) suggested that this pattern of development makes sense because relative motion provides information about the environment while uniform motion is more important for control of eye movements. Furthermore, evidence from adults also suggests that uniform motion and shearing motion are processed by different mechanisms. Shioiri

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(2) This contradicts Banton and Berthenthal's (1997) conclusion that sensitivity to uniform motion emerges before sensitivity to shearing motion. Their conclusion was based on evidence from OKN, which is likely controlled by subcortical mechanisms during early infancy (Atkinson and Braddick 1981; Braddick et al 1996; van Hof-van Duin and Mohn 1983). In contrast, behavioural methods, like preferential looking, likely reflect cortical motion mechanisms (Atkinson and Braddick1981).

et al (2002) compared velocity thresholds for shearing motion (opposite directions) to uniform motion. In general, they found that adults' thresholds varied differently with changes in contrast and spatial frequency for the two types of motion. Relative motion thresholds improved with increases in contrast (up to 85%) and were best when spatial frequency was around 5 cyc/deg; thresholds decreased as spatial frequency was higher or lower than this point. On the other hand, uniform motion thresholds varied little with changes in contrast or spatial frequency. Therefore, it is important that conclusions about the development of sensitivity to one type of motion are not generalised to other types of motion, as the developmental progression may vary with stimulus attributes.

One possible reason that we and others have failed to find evidence of sensitivity to uniform motion in 3-month-old infants may be that the speeds were too slow (and/or temporal frequencies too low). For example, here we used a speed of only 6 deg/sec (temporal frequency = 3 Hz), and Wattam-Bell (1996a; 1996b; 1996c) used speeds of only 8–16 deg/sec for his uniform motion experiments. Using an indirect method that depended on a summation-near-threshold paradigm, Dobkins and Teller (1996) found that 3-month-olds used directionally selective mechanisms for relatively high speeds/temporal frequencies of motion (22.3 deg/sec and 5.6 Hz; speed and temporal frequency varied together), but non-directionally selective mechanisms at lower speeds/temporal frequencies. Thus, had we used higher speeds and/or higher temporal frequencies, we might have found positive evidence for discrimination of uniform motion even at 3 months.

9.3 Conclusion

In conclusion, our results suggest that 3-month-olds discriminate drifting from static gratings on the basis of flicker, at least for stimuli moving at a relatively slow speed. The underlying mechanisms appear to be more mature for second-order than for first-order stimuli. The finding of earlier maturity for second-order mechanisms is consistent with data from older children tested on a motion discrimination task (Armstrong et al 2009) and with evidence that different mechanisms mediate sensitivity to these two types of motion (eg, Ledgeway and Smith 1994).

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