

Sensitivity to second-order motion in 10-month-olds

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Abstract

Ten-month-old infants' sensitivity to first-order motion (FOM) defined by luminance and second-order motion (SOM) defined by flickering was measured in an eye-tracking paradigm. We used a small single disc or gratings moving horizontally. Although infants could track the SOM of a small disc, they failed to exhibit smooth pursuit eye movements. They also failed to track SOM gratings with smooth pursuit. However, the gain of tracking based on slow eye movement was influenced by the motion direction of SOM in cases when both FOM and SOM were presented simultaneously, suggesting some sensitivity to SOM.

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1. Introduction

Motion in everyday life is actually a mixture of two types of motion: First-order motion (FOM), which is defined by the spatiotemporal change in luminance, and second-order motion (SOM), which is defined by the spatiotemporal change of other visual properties such as contrast, flickering and texture. Fundamentally, linear filter models are able to capture the neural mechanism in FOM perception; however, these models are unable to extract SOM. In order to extract the direction of SOM, non-linear processes such as rectification are required (e.g., Chubb & Sperling, 1988). A mathematical model proposed by Wilson, Ferrera, and Yo (1992) describes the neural processes of FOM and SOM to be, at least partially, processed independently. This two-stream processing model of motion perception is supported by a number of studies, for example, by psychophysical findings on the motion aftereffect (Ledgeway, 1994; Nishida, Ledgeway,

& Edwards, 1997; Nishida & Sato, 1995). Nishida et al. (1997) demonstrated that adaptation to FOM or SOM reduces sensitivity to the same motion type but not to the other motion type. Further support for the two-stream model of motion perception comes from a functional magnetic resonance imaging (fMRI) study of two patients who had lesions in different locations, resulting in a clear double dissociation between processing FOM and SOM (Vaina, Cowey, & Kennedy, 1999). Finally, physiological studies revealed that neurons in the visual cortex of cats respond to SOM in a highly selective manner (Mareschal & Baker, 1999; Zhou & Baker, 1996). For example, responses to the SOM of cat neurons in A18 (comparable to human V2) exhibited a narrow band response to the orientation of the envelope (second-order information), and a weak response to the orientation of the carrier (first-order information), suggesting that these neurons are specialized in processing SOM and that the input to them is cortical (Mareschal & Baker, 1999). Findings from different studies suggest that the area in which SOM is mainly processed is located at the level of V2 or higher (but see Chaudhuri & Albright, 1997). For example, Nishida, Ashida, and Sato (1994) demonstrated that the motion aftereffects of SOM can completely transfer from one eye to the other, while

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only 50% of motion aftereffects for FOM can transfer between the eyes. Since V1 is ocular selective, this finding suggests that the neural process for SOM is located in a higher (binocular) area. Furthermore, an fMRI study showed SOM to be processed in V2 or higher (Dumoulin, Baker, Hess, & Evans, 2003), while another fMRI study indicated that V3/Vp exhibit a stronger response to SOM than to FOM (Smith, Greenlee, Singh, Kraemer, & Hennig, 1998). In a cat study, only very few neurons in A17 (comparable to human V1) responded to SOM, whereas more than half of all neurons in A18 responded to SOM (Zhou & Baker, 1993). However, in subsequent processing stages, the information of FOM and SOM is thought to converge. Albright (1992) found that in the monkey brain, the middle temporal (MT) visual area responded with directional selectivity to both FOM and SOM. Evidence for the role of MT in processing both FOM and SOM also comes from other monkey and human studies (Churan & Ilg, 2001; Dumoulin et al., 2003; Geesaman & Andersen, 1996; O'Keefe and Movshon, 1998).

The two-stream model is also supported by developmental studies. Since directional selectivity to FOM appeared as early as V1 (Anstis & Duncan, 1983; Grunewald & Mingolla, 1998), but directional selectivity to SOM was found in V2 or higher (which ontologically develops later than V1), it is conceivable that young children have relatively poor sensitivity to SOM. Recently, Ellemberg and co-workers found the threshold for discrimination of SOM direction to be higher for 5-year-olds compared to adults, whereas the thresholds for FOM were almost the same between the two groups (Ellemberg et al., 2003; Ellemberg et al., 2004). Moreover, it is unknown exactly when infants become sensitive to SOM (but see Braddick, Atkinson, & Hood, 1996). Evidence for the two-stream model also comes from clinical work. MacKay et al. (2005) reported that children born with very low birth weights continued to exhibit deficits in the processing of SOM at the age of 5–8 years. Since the processing of SOM appears to be largely dependent on the higher visual cortical areas, a diagnosis using SOM sensitivity in infants might be helpful in the early identification and intervention of some higher visual cortical damages. Braddick et al. (1996) reviewed an experiment by Braddick, Atkinson, and Wattam-Bell (1995) that investigated whether infants can perceive SOM. Stimuli consisting of FOM, SOM and control non-directional flickering¹ were presented to 8–10 and 16–20-week-olds. Using the preferential looking paradigm, a pair of movies (either FOM and a control stimulus, or SOM and a control stimulus) was presented to the infants. Braddick et al. (1995) reported that both age groups looked longer at FOM and SOM than at the control stimulus. However, they did not demonstrate directional sensitivity.

¹ The control stimuli consisted of the strips of horizontally alternating flickering and static areas. Based on this, the texture of static area drifted for FOM stimulus, and the boundaries of flickering and static areas shifted for SOM stimulus.

Since motion is primarily defined by its direction, a requirement to prove the sensitivity to motion is a demonstration that the response to motion is direction dependent. This stricter definition also invalidates the possibility that participants responded to different components included in SOM stimuli that are not defining for motion perception. It is well known that FOM induces robust optokinetic nystagmus or responses (OKN or OKR). When FOM stimuli are presented in a large visual field, this even occurs for infants (e.g., Rosander & von Hofsten, 2000; Valmaggia et al., 2004). Smooth pursuit eye movements (SPEM) for FOM begin to appear at the age of 2 months (e.g., von Hofsten & Rosander, 1997), and their quality becomes almost adult-like around 5 months of age (Rosander & von Hofsten, 2000; Rosander & von Hofsten, 2002; von Hofsten & Rosander, 1996; von Hofsten & Rosander, 1997). Several studies have revealed that the perceived motion of a first-order stimulus is closely related to SPEM (e.g., Beutter & Stone, 2000; Dobkins, Stoner, & Albright, 1998). Stone and Krauzlis (2003) further demonstrated that the perception of motion direction and the direction of SPEM covary on a trial-by-trial basis, suggesting that SPEM and the perception of motion share the same neural mechanism. It is worth noting that both SPEM and the slow phase of OKN belong to the subclass of slow eye movements (SEM), and that their underlying neural systems largely overlap at the cortical level (Konen, Kleiser, Seitz, & Bremmer, 2005). Although adult monkey and human studies demonstrate SPEM to SOM (Benson & Guo, 1999; Butzer, Ilg, & Zanker, 1997; Guo & Benson, 1998; Lindner & Ilg, 2000), little is known about whether SOM induces SEM in infants.

In this paper, we investigate the directional sensitivity to SOM in infants by using SEM as an index of infants' sensitivity to SOM. In Experiment 1, we presented 10-month-old infants with a small first-order or second-order moving visual target. These stimuli were expected to induce tracking behavior. The directional sensitivity was assessed by means of gain, that is, the eye movement speed relative to the target speed. The gain was calculated in two ways, using all eye movement (AEM), or using only SEM. By analyzing AEM, we could estimate the visibility of the target. That is, if a participant can clearly see the target and track it, then the AEM gain is close to 1, and from this we can conclude that the subjective visibility is high. However, this does not necessarily mean that the participant actually perceives the motion itself, since AEM contains SEM and saccades, and saccades can be made intentionally as well as unintentionally; if they are made intentionally, the direction is apparently unrelated to motion perception. If infants follow the target by making saccades, they might just have detected the salient area in the screen and tracked it. By analyzing SEM, however, we gain a good measure of motion perception.

A small SOM target stimulus might be insufficient to evoke SEM (both OKN and SPEM); this could be due to the insufficient amount of motion signal in the original

small stimulus. Therefore, in Experiment 2, we presented wide angle moving gratings to the participants as the previous adult human and animal studies have demonstrated that SOM induces SEM less efficiently than FOM in terms of gain and/or latency (Butzer et al., 1997; Guo & Benson, 1998; Harris & Smith, 1992; Harris & Smith, 2000; Hawken & Gegenfurtner, 2001). It might thus be possible that infants fail to track SOM even if they can sense SOM. Therefore, we presented the participants in Experiment 2A with wide angle moving gratings defined either by luminance (FOM) or flickering (SOM). By increasing the amount of motion information in the stimuli, we expected SEM (especially OKN) to be induced. In order to further tap into the interaction between FOM and SOM, we presented the participants in Experiment 2B with mixtures of FOM and SOM gratings. This mixture provided us with the opportunity to directly compare the relative strength of FOM and SOM in terms of the factor inducing SEM (Harris & Smith, 2000). Thus, under these conditions, FOM and SOM either moved in the same or opposite direction with respect to each other. Additionally, the depth of luminance (modulation depth) was manipulated. In all the experiments, infants' performance was compared to that of an adult group.

2. General methods

2.1. Subjects

Ten-month-old infants were recruited from a large metropolitan area and contacted by mail, and adult subjects were recruited from the students of Uppsala University. The study was conducted in accordance with the ethical standards specified in the 1964 Declaration of Helsinki and was approved by the ethics committee at Uppsala University. Before each experiment, the adult participants and the families of the participating infants were informed about the purpose of the study and signed a consent form. The infants and their parents received a token worth 100 SwKr as compensation, and adult participants received either a movie ticket or a certificate for their participation in our experiments. In Experiment 1, 15 healthy, full-term 10-month-old infants (9 males and 6 females) participated. Their mean age \pm standard deviation was 303 ± 6 days. Nine adults (6 females and 3 males; mean age, 25.6 ± 2.6 years) also participated in the experiment as a control group. In Experiment 2A, another 26 healthy, full-term 10-month-old infants (12 males and 14 females; Mean age, 300 ± 8 days) participated. Fourteen adults (9 females and 5 males; Mean age, 26.0 ± 3.5 years) also participated in the experiment as a control group. In Experiment 2B, 14 healthy, full-term 10-month-old infants (10 males and 4 females; Mean age, 307 ± 7 days) were newly recruited and participated. Eight adults (5 females and 3 males; 25.8 ± 2.7 years) participated in the experiment as a control group.

2.2. Apparatus and stimuli

The experiment was conducted in a quiet and dark room. Visual stimuli were presented on a 17-inch LCD display that was a part of a cornea reflection eye-tracking system (Tobii 1750, Tobii Corp.) that measures the direction of each eye separately at 50 Hz. Gamma-correction was performed with a colorimeter (Spider2Pro, Color Vision). Sounds were presented from a 7-cm full-range loudspeaker located just below the display with a moderate loudness level. The distance between the participants

and the display was set at approximately 60 cm in order to facilitate efficient tracking of their eyes. At this distance, the display subtended $30^\circ \times 24^\circ$.

All stimuli were MATLAB-generated (MathWorks) and converted into avi files compressed by Microsoft video 1 codec with the quality of 100%. The frame rate was set at 30 Hz, whereas the refresh rate of the LCD was set at 60 Hz. For Experiment 1, FOM and SOM stimuli consisted of small targets. In Experiment 2A, FOM and SOM stimuli consisted of wide pure gratings, while the FOM and SOM stimuli in Experiment 2B consisted of wide mixed gratings.

2.2.1. Small target stimuli (Experiment 1)

The first-order stimulus consisted of a white disk (referred to as the target) with a diameter of 2.3° , moving in front of a gray background. The luminance of the gray background was 35 cd/m^2 and that of target was twice the luminance of the background (Weber contrast: 100%). The target moved back and forth in the horizontal direction during the presentation period. The target started from the left (9.0° left of the center of the display) and inverted its velocity at the right (9.0° right of the center); the speed of the target was either $3.8^\circ/\text{s}$ (slow) or $15.0^\circ/\text{s}$ (fast). The stimulus duration was 9.5 s. In order to obtain the same amount of data for the different conditions, the duration was maintained constant; thus, the target moved back and forth once when the target speed was slow, and four times when the speed was fast.

The second-order stimulus was composed of two-dimensional, temporally modulated random noise, the luminance of which was binary. Each noise element subtended $7.5 \times 7.5'$, and was assigned independently with a probability of 1/2 to be either "white" or "black"; the noise contrast (Michelson contrast) was set at 100%. The size and speed of the target and the background were the same as that of the first-order stimulus. Two types of SOM were used. In the dynamic target SOM (dtSOM) condition, the dots in the target area were flickering and the dots in the background were static. In the static target SOM (stSOM) condition, flickering and static areas were mutually replaced. In these cases, each dot in the flickering area reversed its luminance polarity with a probability of 1/6 for every refresh; thus, the mean flickering rate was 30/6 (i.e., 5 times/s). These stimuli are described as being second-order (Cavanagh & Mather, 1989) and are non-Fourier because they can be shown to be microbalanced (Chubb & Sperling, 1988). The 1/6 probability was selected in order to avoid the incomplete luminance change caused by the relatively slow onset and offset of the LCD display whilst still maintaining SOM. Note that the response time of the LCD monitor was 8 ms. There was no statistical difference between the mean luminance of the static area and that of the flickering area. The space- and time-average luminance of the stimuli was the same as the luminance of gray in the first stimulus (35 cd/m^2). As a control, a no-motion condition was introduced for all types of motion. Here, the target appeared at the center of the background without moving. Thus, these three types of motion could have two velocities or be stationary, resulting in a total number of nine trials.

2.2.2. Wide pure grating stimuli (Experiment 2A)

The first-order stimuli consisted of vertical, luminance-modulated sinusoidal gratings ($.32 \text{ cycle/}^\circ$) subtending a full-screen (30° wide by 24° high, viewed from a distance of 60 cm). The stimuli drifted either left or right for 8.0 s at a velocity of $0^\circ/\text{s}$ (static), $3.9^\circ/\text{s}$ (slow), $7.8^\circ/\text{s}$ (medium) and $15.6^\circ/\text{s}$ (fast). The modulation depth of the luminance (Michelson contrast) was defined as

$$\text{Modulation depth} = (L_{\max} - L_{\min}) / (L_{\max} + L_{\min}) \quad (1)$$

where L_{\max} and L_{\min} are the maximum and minimum local luminance, respectively. We set the modulation depth to 100%. The space- and time-average luminances of the stimuli were maintained at 35 cd/m^2 . The temporally modulated second-order grating stimuli consisted of two-dimensional random noise, and vertical strips of flickering and static areas. The properties of the flickering were identical to those of small target stim-

uli. The strips alternated horizontally with a cycle of .32 cycle/°. The square wave modulation of flickering and 100% modulation depth were selected in order to optimize the perception of SOM, which means that the probability of flickering within a stripe is the same, but the frequency is either 0 or 5 times/s.

Both the FOM and SOM were presented at four velocities. With the exception of the static condition, every motion had a direction: either left or right. Thus, there were a total of 14 combinations.

2.2.3. Wide mixed grating stimuli (Experiment 2B)

The stimuli contained both first- and second-order motion cues subtending the full-screen. The stimuli consisted of static two-dimensional random noise (referred to as the carrier), the luminance of which was binary. Each noise element subtended $7.5 \times 7.5'$. The first-order component was generated by adding the noise carrier to a vertical luminance-modulated sinusoidal grating of .32 cycle/°. The modulation depth of the grating was either low (20%) or high (50%). This grating drifted either left or right for 8.0 s at a velocity of $3.9^\circ/\text{s}$. The second-order component consisted of a vertical, square-wave grating (.32 cycle/°) comprising alternating vertical strips in which the noise flickered at 5 times/s on average, or did not flicker. In order to avoid a constant phase difference between FOM and SOM in the same direction, the drift speed of SOM was doubled to $7.8^\circ/\text{s}$. The mean luminance of the two components was adjusted such that in the final images all had the same mean luminance when combined, irrespective of contrast. There were two types of motion, each of which moved left or right, and two levels of modulation depth, resulting in a total of eight combinations.

2.3. Procedure

Each infant sat in a baby seat on the lap of a parent. The adult participants sat in a chair in front of the display without assistance and were instructed to watch the screen. Lights were turned off and the calibration procedure for the eye tracker was started. We used a 9-point calibration procedure. A short expanding-contracting movie with accompanying sounds appeared within a 3×3 grid on the display, and when the experimenter was certain that the participant was looking at it, he pushed a key and proceeded to the next calibration point. The order was randomized. If the calibration data was poor or was missing for certain calibration points, the eye tracker presented those calibration points again. Completing the calibration procedure took 1 min on average. Subsequently, test stimuli were presented serially. Between the test stimuli, small short movies with accompanying sounds were shown in the middle of the screen as attention-getters. These movies were shown until the participants looked at the center of the screen. Every test stimulus was presented once to each participant and the order was counterbalanced by means of the random rotation method (Latin square).

2.4. Data analyses

For each trial, participants were included if they looked at the stimulus for more than 1 s. For that purpose, we calculated a looking time with a large area of interest (AOI) that totally covered the monitor. In order to evaluate the looking time at the target as accurately as possible, a small AOI was defined. When the small target moved horizontally, the width of the AOI was the same as the screen: 30° . However, in order to prevent all gazes being counted as “gaze at a target,” the AOI was narrowed in the vertical dimension (± 100 pixels from the center of the target, corresponding to 6.3°). For the no-motion condition, the AOI was 100×100 pixels ($3.1^\circ \times 3.1^\circ$), which precisely covered the target at the center of the screen. This improved the accuracy of looking time estimation in the no-motion condition. When the grating stimuli were presented, however, the AOI corresponded to the whole display.

AEM gain was calculated relative to the velocity of the small target. SEM gain was also calculated for the small target. However, for the gratings, SEM gain was only calculated relative to the drifting velocity, since in this case we wanted to omit saccades. In order to calculate SEM gain,

the trace of gaze points was differentiated by an algorithm that removed the fast eye movements by their velocity (cut-off velocity: $38^\circ/\text{s}$). This cut-off velocity was selected to cut out the saccades as close to their base as possible. The remaining eye movements were then averaged. Although we could not discriminate smooth pursuit from the slow phase of OKN, both responses indicate the same event, namely, that motion is detected. The factor of motion direction was collapsed by averaging the two directions.

Finally, repeated measures ANOVAs were conducted. Post-hoc pairwise *t*-tests (Bonferroni correction) were also performed if necessary. Under some conditions, one-sample *t*-tests were performed in order to verify whether looking time/gain was statistically positive or negative.

3. Results

3.1. Experiment 1: Small target motion

Six of the infants were excluded from the analysis of the results due to short looking times, leaving the data of 9 infants (6 males and 3 females) to be analyzed.

3.1.1. Infants

The overall looking time was $4.56 \pm .44$ s (Mean \pm SE) out of 9.5 s of stimulus presentation. The results were analyzed using a two-way repeated measures ANOVA with Motion Type and Target Speed as factors. There was a main effect of Motion Type, $F(2, 16) = 10.31$, $p = .001$ and $\eta^2 = .56$. A post-hoc pairwise *t*-test revealed that infants looked longer at the dtSOM stimuli ($6.24 \pm .51$ s) than at either the stSOM stimuli ($2.89 \pm .71$ s; $p < .01$) or the FOM stimuli ($4.54 \pm .60$ s; $p < .05$). There was no effect of Target Speed and no interaction between Motion Type and Target Speed. Next, in order to test whether the infants could detect the target, we focused on the looking time under the three no-motion conditions. We compared the looking times under these three conditions and found that the times differed between motion types, $F(2, 16) = 13.26$, $p < .001$ and $\eta^2 = .62$. The looking time in the dtSOM condition was longer than that in the stSOM condition ($p < .005$); however, there were no significant differences between the other pairs. Since the AOI precisely covered the target in the no-motion condition, a significant looking time in the AOI indicates the detection of the target. We found that the looking times in the AOI were significant for both the FOM and dtSOM conditions, $t(8) = 3.20$, $p < .05$ and $t(8) = 8.96$, $p < .001$, respectively. However, in the stSOM condition, the looking time was not significantly different from 0, suggesting that infants did not detect the target.

Fig. 1A shows the mean AEM gains as a function of Motion Type and the Target Speed. A two-way repeated measures ANOVA with factors Motion Type and Target Speed was conducted on AEM gain and we found that Motion Type affected the AEM gains, $F(2, 16) = 172.81$, $p < .001$ and $\eta^2 = .96$. Post-hoc pairwise *t*-tests revealed that AEM gain was highest in the FOM condition and lowest in the stSOM condition. Target Speed affected the AEM gains; we found that the AEM gain was higher when the

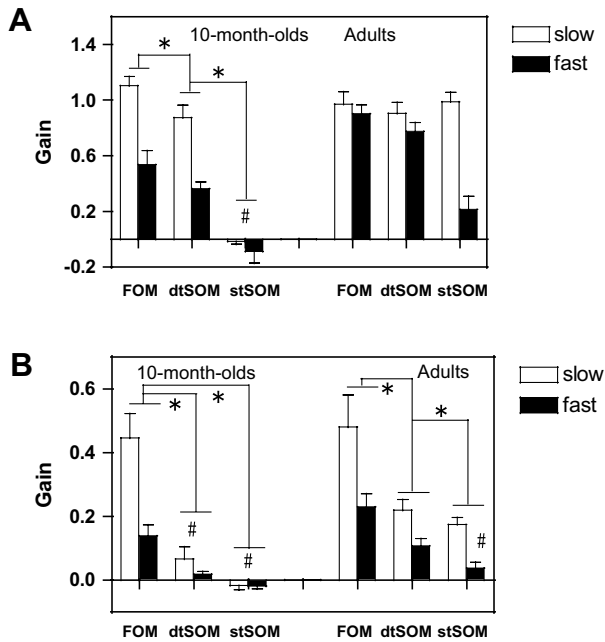


Fig. 1. Gains as a function of Motion Type and Target Speed for Experiment 1. AEM gains (A) and SEM gains (B) for 10-month-olds and adults. White and black bars indicate AEM gains at slow and fast target speeds, respectively. Error bars indicate Standard Error of the Mean. * indicates a significant difference between a pair ($p < .05$), and # indicates that the corresponding bars were not significantly different from 0 ($p < .05$).

target moved slower, $F(1, 8) = 27.04$, $p = .001$ and $\eta^2 = .77$. The interaction between Target Speed and Motion Type was also significant, $F(2, 16) = 8.71$, $p < .005$ and $\eta^2 = .52$. Post-hoc analyses were performed to investigate the effect of Target Speed on gain for each motion type. The AEM gain for the slow Target Speed condition was higher than for the fast target speed condition in the FOM and dtSOM conditions ($p = .001$ and $.002$, respectively). However, in the stSOM condition, AEM gains were not significantly different between the two speeds. We conducted a one-sample t -test to test whether the gain in the stSOM condition was significantly different from 0 and found that it was not.

Fig. 1B shows the mean SEM gain as a function of Motion Type and Target Speed. A two-way repeated measures ANOVA with factors Motion Type and Target Speed revealed that the Motion Type affected SEM gain, $F(2, 16) = 30.57$, $p < .001$ and $\eta^2 = .79$. Post-hoc pairwise t -tests revealed that SEM gain in the FOM condition was higher than in the dtSOM and stSOM conditions ($p = .002$ and $.001$, respectively). Target Speed also affected the SEM gain; we found that the SEM gain was higher when the target moved slowly, $F(1, 8) = 21.05$, $p < .005$ and $\eta^2 = .73$. We also found an interaction effect between Motion Type and Target Speed, $F(2, 16) = 15.15$, $p < .001$ and $\eta^2 = .65$. Post-hoc analyses were performed in order to investigate the effect of Target Speed on SEM gain for each motion type. We found that in the FOM condition, the SEM gain was higher for slow target speed than for fast

target speed ($p = .001$). However, in the other motion type conditions, SEM gain did not differ significantly between the two speeds. Since the gains in the dtSOM and stSOM conditions were close to 0, a one-sample t -test was performed; this revealed that the gains were not significantly different from 0.

3.1.2. Adults

The mean looking time for adults was $7.10 \pm .30$ s (Mean \pm SE). A two-way repeated measures ANOVA revealed that there was neither a main effect for either Motion Type or Target Speed, nor a significant interaction. The looking times in the three no-motion conditions were then investigated. Each of these was found to be significantly different from 0: $t(8) = 6.60$, $p < .001$ for the FOM condition; $t(8) = 11.56$, $p < .001$ for the dtSOM condition and $t(8) = 5.42$, $p = .001$ for the stSOM condition. This suggests that adults could detect the target in all of the no-motion conditions.

Fig. 1A also shows the mean AEM gain for the adult participants. A two-way repeated measures ANOVA revealed that there was a main effect of Motion Type, $F(2, 16) = 10.83$, $p = .001$ and $\eta^2 = .58$. The AEM gain in the stSOM condition was lower than that in both the FOM and dtSOM conditions ($p < .05$ for both conditions). Since the gains in the stSOM condition were close to 0, we conducted a one-sample t -test and found that the gain in that motion type condition was marginal, $t(8) = 2.27$, $p = .053$, when the target moved fast. The effect of Target Speed was also significant; the AEM gain was higher when the target moved slowly, $F(1, 8) = 41.40$, $p < .001$ and $\eta^2 = .84$. The interaction between Motion Type and Target Speed was also significant, $F(2, 16) = 14.81$, $p < .001$ and $\eta^2 = .65$. Post-hoc analyses were performed in order to investigate the effect of Target Speed on AEM gain for each motion type. We found that in the stSOM condition, the AEM gain for the slow target speed was higher than that for the fast target speed ($p < .001$). However, in the FOM and the dtSOM conditions, the AEM gain did not significantly differ between the two speeds.

Fig. 1B shows the mean SEM gains for the adult participants. A two-way repeated measures ANOVA revealed that there was a main effect of Motion Type, $F(2, 16) = 12.51$, $p = .001$ and $\eta^2 = .61$. The gain was highest in the FOM condition and lowest in the stSOM condition. (pairwise t -tests using Bonferroni correction revealed all of these to be $p < .05$). Target Speed also affected the SEM gains, $F(1, 8) = 28.44$, $p = .001$ and $\eta^2 = .78$, but no interaction effect was found. Since the gain in the slow stSOM condition was close to 0, a one-sample t -test was performed; this was not significantly different from 0.

3.2. Experiment 2A: Wide pure gratings

3.2.1. Infants

Of the total of 26 infants, the data obtained from 12 infants were excluded due to insufficient looking; therefore,

the analysis was based on data from the remaining 14 infants (8 males and 6 females). The mean looking time was $5.07 \pm .31$ s (Mean \pm SE) out of 8.0 s of stimulus presentation. A two-way repeated measures ANOVA with Motion Type (FOM and SOM) and Drift Speed (static, slow, medium and fast) as factors revealed that 10-month-olds looked longer at SOM stimuli ($5.78 \pm .40$ s) than at FOM stimuli ($4.37 \pm .30$ s), $F(1, 13) = 16.14$, $p = .001$ and $\eta^2 = .55$. There was no significant effect of Drift Speed and no interaction effect. In the static condition, the mean velocity of eye movements was not significantly different from 0° /s.

Fig. 2 shows the mean gain as a function of Motion Type and Drift Speed. A two-way repeated measures ANOVA with factors Motion Type (FOM and SOM) and Drift Speed (slow, medium, and fast) revealed that the gain was higher in the FOM condition than in the SOM condition, $F(1, 13) = 157.48$, $p < .001$ and $\eta^2 = .92$. Drift Speed affected the gain, $F(2, 26) = 38.77$, $p < .001$ and $\eta^2 = .75$, and there was an interaction between Motion Type and Drift Speed, $F(2, 26) = 34.71$, $p < .001$ and $\eta^2 = .73$. Post-hoc analyses were performed in order to investigate the effect of Drift Speed on gain for each motion type. We found the gain in the FOM condition was lower for the fast drift speed compared to the slow ($p < .001$) and medium ($p < .001$) drift speeds. However, in the SOM condition, gains were not significantly different for the three drift speeds, and the gain in the SOM condition was not significantly different from 0.

3.2.2. Adults

The mean looking time for adults was $7.26 \pm .24$ s. A two-way repeated measures ANOVA revealed no main or interaction effects. In the static condition, the mean velocity of eye movements was not significantly faster than 0° /s.

Fig. 2 shows the mean gain as a function of Motion Type and Drift Speed. A two-way repeated measures ANOVA was conducted on gain. It was found that the gain was higher in the FOM condition than in the SOM condition, $F(1, 13) = 43.27$, $p < .001$ and $\eta^2 = .77$. Drift Speed

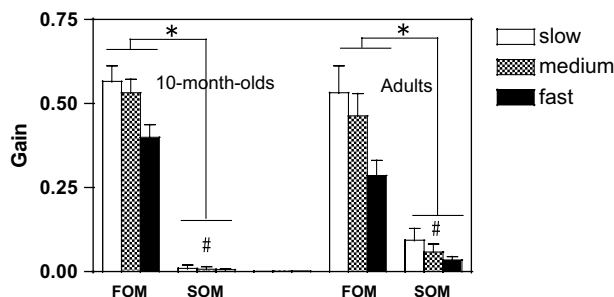


Fig. 2. Gains as a function of Motion Type and Drift Speed. Data are from group A of Experiment 2, for 10-month-olds and adults. White, checked and black bars indicate SEM gains at slow, medium and fast drift speeds, respectively. Error bars indicate Standard Error of the Mean. * indicates a significant difference between a pair ($p < .05$), and # indicates that the corresponding bars were not significantly different from 0 ($p < .05$).

affected the gains, $F(2, 26) = 23.02$, $p < .001$ and $\eta^2 = .64$. We also found an interaction between Motion Type and Drift Speed, $F(2, 26) = 28.82$, $p < .001$ and $\eta^2 = .69$. Post-hoc analyses were performed in order to investigate the effect of Drift Speed on gain for each motion type. For the FOM condition, we found the gain of fast drift speed to be lower than that for the slow ($p < .001$) and medium ($p < .001$) drift speeds, while the gain of medium drift speed was lower than for the slow drift speed ($p < .01$). However, in the SOM condition, gains were not significantly different for the three drift speeds. Further analyses revealed that the gain in the SOM condition differed significantly from 0, $t(41) = 4.24$, $p < .001$.

3.3. Experiment 2B: Wide mixed gratings

3.3.1. Infants

Four infants were excluded from the data analysis due to short looking times, leaving the data from 8 infants (5 males and 3 females) to be analyzed. The mean looking time for infants was $5.98 \pm .57$ s out of the 8.0 s of stimulus presentation. A two-way repeated measures ANOVA on looking time with the factors Motion Direction (same direction and opposite direction) and Contrast of FOM (low and high) was conducted. We found that the infants looked at stimuli presented in the opposite direction (6.19 s) longer than those presented in the same direction (5.78 s), $F(1, 7) = 14.02$, $p < .01$ and $\eta^2 = .67$. There was no main effect of Contrast, and the interaction was not significant. A two-way repeated measures ANOVA on gain revealed a main effect of Motion Direction, $F(1, 7) = 6.07$, $p < .05$ and $\eta^2 = .46$, and a main effect of Contrast, $F(1, 7) = 12.53$, $p < .01$ and $\eta^2 = .64$. The interaction effect was marginal, $F(1, 7) = 4.48$, $p = .07$ and $\eta^2 = .39$. We conducted a post hoc pairwise *t*-test in order to examine whether the effect of Motion Direction on gain could be modified by the FOM contrast. As shown in Fig. 3, we found that the effect of Motion Direction on gain was significant in the low contrast condition ($p < .05$), but not in the high contrast condition. Further examination of the

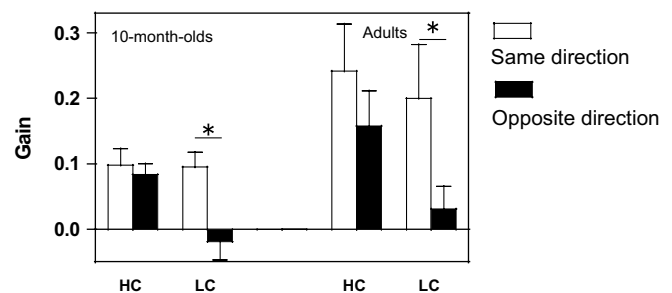


Fig. 3. Gains as a function of Contrast of FOM and Motion Direction. Data are from group B of Experiment 2, for 10-month-olds and adults. LC, low contrast; HC, high contrast. White and black bars indicate relative motion directions of FOM and SOM (same or opposite direction), respectively. Error bars indicate Standard Error of the Mean. * indicates a significant difference between a pair ($p < .05$).

gains in the low FOM contrast condition revealed that the gains were significantly different from 0 (one-sample *t*-test) when the direction was the same, $t(7) = 4.96$, $p < .005$, whereas it was not significant when the direction was opposite.

3.3.2. Adults

The mean looking time for adults was $7.70 \pm .13$ s. A two-way repeated measures ANOVA on looking time was conducted; however, we found no main or interaction effects.

A two-way repeated measures ANOVA on gain revealed a main effect of Motion Direction, $F(1, 7) = 5.56$, $p = .05$ and $\eta^2 = .44$, and a main effect of the Contrast, $F(1, 7) = 9.13$, $p < .05$ and $\eta^2 = .57$. There was no significant interaction effect. However, as shown in Fig. 3, when the FOM contrast was low, the gain in the opposite direction condition was significantly smaller than that in the same direction ($p < .05$), although this difference was not significant for the high FOM contrast. Further examination of the gains in the low contrast FOM by means of a one-sample *t*-test revealed that the gain was significantly positive when the direction was the same, $t(7) = 2.93$, $p < .05$, whereas it was not significant when the direction was opposite.

4. Discussion

4.1. Visibility

When small target motion was presented (Experiment 1), infants looked longer at the dtSOM stimulus than at the FOM and stSOM stimuli. One simple explanation for this observation, without assuming differential sensitivity to FOM and SOM, is that infants were simply more sensitive to the flickering. The higher saliency of flickering in the SOM can result in longer looking times. Thus, in the dtSOM condition, infants might have preferred the flickering *target*, which resulted in the increased looking time. In line with this reasoning, the flickering *background* in the stSOM condition was also more salient, resulting in a decrease in looking time, as the flickering background is not a part of the AOI. This idea is also supported by the looking time in the no-motion conditions: The duration of looking at a stSOM target was not statistically different from 0. These results are important in that infants are sensitive to flickering, which is an ability necessary for sensing SOM.

The next issue is the difference in visibility between FOM and SOM. As shown in Fig. 1A, the AEM gain was almost one when the FOM/dtSOM targets moved slowly, and although the gains became smaller when the targets moved fast, the decrease was almost the same for the FOM and the dtSOM conditions. These similar tendencies suggest that the visibility of SOM is largely comparable to FOM. The decrease in AEM gain as a function of target speed appears to contrast with the findings of Gredeback,

von Hofsten, Karlsson, and Aus (2005). These authors reported that the gain of AEM to first-order motion stimuli did not significantly decrease as target velocity increased in the range of 5–20°/s. This disparity probably stems from the different types of targets used in the two studies. Gredeback et al. (2005) used a happy face, which is known to attract an infant's gaze, as the target, whereas relatively simple images were used in our case.

In the stSOM condition, infants' AEM gains were not significantly positive; however, this was not surprising since, as noted above, the looking time for the stSOM condition was not significantly different from 0. Adults could follow the target very well when it moved slowly (AEM gain was approximately 1); however, the performance markedly decreased when it moved fast. This is also congruent with the subjective reports by participants who often said that they lost track of the target at high speed.

4.2. SOM sensitivity

When small target motion was presented, infants smoothly tracked the FOM but not the SOM (neither dtSOM nor stSOM). This was also the case when the wide gratings with greater motion signal were presented. Does this mean that infants have no sensitivity to SOM? The first explanation for this observation, which we think probable, is that infants could perceive SOM but could not track it smoothly. Actually, the SEM gain in the SOM condition for adults was considerably smaller compared to the gain in the FOM condition, although the participants reported that they clearly saw the SOM stimuli. In addition, previous studies have indeed demonstrated that SOM stimuli were very poor at evoking SEM (Harris & Smith, 1992; Harris & Smith, 2000), that the latency of eye movements in response to SOM is greater than that to FOM (Butzer et al., 1997; Hawken & Gegenfurtner, 2001), and that the initial direction of eye movements was largely dominated by FOM (Lindner & Ilg, 2000). These previous studies suggest that FOM, and not SOM, is the dominant factor in controlling eye movements.

Another explanation for the absence of the smooth tracking of SOM can be sought in terms of visibility, as FOM and SOM are not equated for visibility. However, we consider that this explanation is unlikely. Although the SEM gains in the dtSOM condition were close to 0, the AEM gains in the same condition were far from 0 and largely comparable to the AEM gains in the FOM condition (Fig. 1A and B). If visibility is the only factor required to explain the lack of SEM induced by SOM, then the AEM gain should also be close to 0.

An alternative explanation for the lack of the smooth tracking of SOM is that 10-month-olds are not directionally sensitive to SOM. However, this explanation is also unlikely because it cannot explain the results of the mixed grating motion experiment. Here, we found indirect evidence for infants' sensitivity to SOM, that is, the gain for the infants as well as for the adults was markedly smaller

when FOM and SOM drifted in opposite directions, compared to when they drifted in the same direction (see Fig. 3). This effect was only observed when the FOM contrast was low, which is consistent with a previous study on adult participants (Harris & Smith, 2000). Harris and Smith (2000) found that a large visual field of SOM gratings elicited SEM. However, the same authors previously reported the reverse (Harris & Smith, 1992). They explained this inconsistency in terms of the instructions given to participants (Harris & Smith, 2000). In their earlier study, the participants were instructed to fixate on the center of the screen, whereas in the later study, they asked participants to attempt to look straight at the screen, but not attempt to suppress “involuntary eye movements”. In the present experiment, adult participants were asked neither to fixate nor to suppress involuntary eye movements. Thus, it appears that the SEM induced by a large visual field of SOM gratings is so weak and fragile that the instructions can sufficiently suppress the SEM response (Harris & Smith, 2000). Again this suggests that FOM is the dominant factor in controlling eye movements.

One might argue that the flickering dots act as noise in the process of sensing the motion signal, causing the decrease of gain. However, this does not explain why the gain was dependent on the relative direction of FOM and SOM because there is no physical difference between the amount of flickering in the same and opposite direction conditions. In terms of looking time, when FOM and SOM drifted in opposite directions, the mean looking time was significantly longer compared to when they drifted in the same direction. This suggests that infants did discriminate between FOM and SOM direction.

Therefore, it is clear that infants smoothly tracked FOM, although they did not smoothly track SOM. However, 10-month-olds are sensitive to SOM. Evidence for this comes in a somewhat indirect manner; the SEM response to FOM was modified by the direction of the co-occurring SOM.

4.3. Implication for the two-stream processing model

According to some two-stream processing models, SOM is processed with a cascade of filters (linear–nonlinear–linear filters) and SOM direction can be extracted at the final linear filter that would be located in V2 or in the higher visual cortex. There are, however, some studies in which the SOM-induced neural activity was observed as early as in V1 (e.g., Barraclough, Tinsley, Webb, Vincent, & Derrington, 2006; Nishida, Sasaki, Murakami, Watanabe, & Tootell, 2003). This could imply that nonlinear processes already occur in subcortical areas such as the lateral geniculate nucleus (LGN). As the LGN has neuromorphologically matured at 9 months after birth (Garey & Courten, 1983), 10-month-old infants might have shown the same responses to SOM as to FOM. However, we did not find tracking to pure SOM at that age, refuting the subcortical two-stream processing model and supporting the notion

that the nonlinear processes necessary for the processing of SOM occur at a cortical level.

5. Conclusion

There are many studies showing that very young infants can smoothly follow FOM in the form of objects (Aslin, 1981; Rosander & von Hofsten, 2000; Rosander & von Hofsten, 2002; von Hofsten & Rosander, 1996; von Hofsten & Rosander, 1997); however, to our knowledge, there has been no study that has investigated the directional sensitivity to SOM in infants. Although we do not demonstrate the age at which infants become sensitive to pure SOM, a sprout was already observed as early as 10 months of age. In line with the previous findings showing that sensitivity to SOM is lower for 5-year-old children compared to adults (Elleberg et al., 2003), we demonstrate that the development of the directional sensitivity to SOM is considerably slower than the sensitivity to FOM.

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