THE DEVELOPMENT OF SENSITIVITY TO MOTION

THE DEVELOPMENT OF SENSITIVITY TO FIRST- AND SECOND-ORDER LOCAL MOTION

By

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Preface

This thesis is comprised of three manuscripts produced in collaboration with my supervisors Drs. Terri Lewis and Daphne Maurer. Dr. Dave Ellemberg is also a co-author of Chapter 2.

For Chapter 2, Dr. Dave Ellemberg was responsible for the experimental design of Experiment 1, while I was responsible for the experimental design of Experiment 2. I was directly responsible for all other aspects of data collection, analysis, as well as interpreting the results of each experiment. I was also responsible for developing the criteria of a custom VPIXX testing program required for Experiment 2.

For Chapter 3, I was directly responsible for the experimental design, data collection and analysis, as well as interpreting the findings. I developed the testing method that I used with 3-year-olds. Both Chapter 2 and 3 are in preparation for submission to Vision Research.

For Chapter 4, I was directly responsible for the experimental design, data collection, as well as the analysis and interpretation of the results. Chapter 4 is in preparation for submission to the Journal of Vision.

I am the first author of all three manuscripts and I was responsible for their preparation.

Abstract

The purpose of this thesis is to determine the timeline of the development of sensitivity to first-order (luminance-defined) versus second-order (contrast-defined) motion and to compare how sensitivity to motion varies with temporal frequency (flicker rate), spatial frequency (stripe size), and velocity. In Chapter 2, I demonstrate that infants' sensitivity to drifting gratings is more adult-like for second-order than first-order stimuli. Moreover, the evidence suggests that infants choose a moving over a stationary grating based on their sensitivity to grating flicker rather than its direction. In Chapter 3, I demonstrate that sensitivity to second-order motion is more adult-like than sensitivity to first-order motion at all ages tested. Children reach adult-like levels of sensitivity to motion at 7 years when stimuli are second-order, but are still worse than adults at 10 years when stimuli are first-order. Furthermore, sensitivity to motion varies with temporal frequency when stimuli are first-order, but spatial frequency when stimuli are second-order. These results are consistent with the hypothesis that first-order motion is processed using low-level motion mechanisms, while second-order motion is processed using a feature tracking mechanism. In Chapter 4, I explored sensitivity to second-order motion in 5-year-olds and adults using directional and non-directional motion tasks. Children's sensitivity to motion is more immature when temporal frequency is relatively low, but only for the directional motion tasks. All participants perform better on the non-directional than the directional task, but only when temporal frequency is relatively high. These results are consistent with Seiffert and Cavanagh's (1998) findings that second-order motion is processed by a feature tracking mechanism. Combined, these findings are consistent with the idea that first- and second-order motion are processed, at least in part, by different neural mechanisms.

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This work was completed with the help of many undergraduate students and volunteers, as well as the participation of hundreds of parents and children. Thank you for taking the time to make this research possible.

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CHAPTER 1
Introduction

Motion perception helps us to make sense of a world full of moving people and objects. It helps us to segment objects from the background (Braddick, 1993), to see where they are in depth (Rogers & Graham, 1979), and to keep track of our position as we move through the world (Previc, 1998). In the rare case of brain damage preventing the perception of motion, the world appears as a series of still images, with objects in it changing location unpredictably (Zihl, von Cramon, & Mai, 1983).

Broadly speaking, motion can be defined as being local or global. Local motion occurs when all the elements making up a section of a stimulus, or an entire stimulus, move in the same direction. A simple example of local motion is the motion of a solid object or a point of light moving across space. Global motion is more complex because it contains different directions of local motion, with some local cues to motion moving in the same direction as the global, or predominate, direction of motion, and other local cues to motion moving in directions that differ from the global direction of motion. One example of global motion is a person walking. The direction in which the person is walking is the global direction of motion. This direction is perceived easily despite the fact that, at any one time, the various local motions of the person's body can move in directions that differ from the global direction of motion as the person lifts up his feet, swings his arms, or moves his head. Global motion can also occur when no elements have that local direction of motion but the vector sum of the local motions signals the global direction, as when 50% of elements move northwest and the other 50% move southwest, signaling a westwardly direction of global motion.

The cues that produce motion are commonly categorized as first-order or second-order. First-order cues to motion are the result of spatiotemporal changes in luminance boundaries, whereas second-order cues to motion are the result of spatiotemporal variations of boundaries created by physical characteristics other than luminance, such as contrast, texture, or size without an overall change in mean luminance across boundaries (see *Figure 1*).

As with most perceptual abilities, infants are much less sensitive to motion than adults (e.g., Dobkins & Teller, 1996). Although sensitivity to motion improves rapidly during infancy, it continues to show more gradual improvements well into childhood (Bertone, Hanck, Cornish, & Faubert, 2008; Parrish, Giaschi, Boden, & Dougherty, 2005). The main goal of this thesis is to examine the development of sensitivity to first- and second-order local motion from infancy to adulthood. Doing so is important for characterizing the nature of the child's visual world and is the first step toward understanding the mechanisms driving development. As well, data on the development of sensitivity to local motion may be helpful in understanding the neural mechanisms that are responsible for local motion perception. For example, capabilities that develop at different rates may be, at least in part, mediated by different neural mechanisms. To place the work in context, I will first provide a brief review of the visual pathways involved in motion and form perception, followed by a more detailed review of the candidate models of first- and second-order motion processing. Although second-order vision has been studied extensively in the lab, relatively few studies have addressed second-order information in natural scenes. Thus, I will also review evidence that supports the ecological validity of second-order vision. Finally, I will review what is currently known about the development of sensitivity to first- and second-order form and motion in infants and children and further describe the purpose of this thesis.

1.1 Functional Organization of the Visual System

Here, I will describe the dominant projections of the retinogeniculocortical pathway that are important for motion and form perception. It should be noted that, in addition to the pathways described here, there is a complex array of feedforward and feedback connections throughout the visual system, much of which we still have only a partial understanding.

The retinogeniculocortical pathway of the visual system includes the retina, the lateral geniculate nucleus (LGN) and the striate cortex (area V1, also termed primary visual cortex). Projections from this pathway extend further to a number of extrastriate cortical areas, including areas MT (also known as area V5) and V4 (see below). The primary function of the retinogeniculocortical pathway is to process the elements of what we commonly think of as seeing –motion, shape, pattern and colour (Daw, 2006). Other visual pathways involve retinal projections to the superior colliculus, the pretectum, and the suprachiasmatic nucleus, and are involved, respectively, in the control of eye movements, the pupil, and diurnal rhythms (Daw, 2006).

The process of converting light into visual signals that are interpreted by the brain begins in the retina. The retina lines the back of the eye and is composed of several distinct layers including photoreceptors (rods and cones), intermediate layers of interconnecting neurons, and a final layer of retinal ganglion cells (Dowling & Boycott, 1966; Kaplan, Lee, & Shapley, 1990). The retinal ganglion cells of each eye project to separate layers of the LGN. The LGN can be considered as a gateway for visual signals between the retina and cortex, as little processing occurs in the LGN (Daw, 2006). The LGN projects primarily onto layers 4Cα and 4Cβ of the striate cortex (area V1), where cells respond selectively to a variety of stimulus aspects, such as orientation, motion, colour, and temporal frequency (Hawken, Shapely, & Grosof, 1996; Livingston & Hubel, 1988; Vidyasagar, Kulikowski, Lipnicki, &

Dreher, 2002). It is in the visual cortex that vision first becomes binocular with input from each eye being combined in layers 2,3,5, and 6 of V1, while cells in layer 4 are predominately monocular (Wiesel, 1982; Daw, 2006). V1 projects primarily onto area V2, which projects onto extrastriate areas V4 (Livingstone & Hubel, 1988; Xiao, Zych, & Felleman, 1999) and MT (Livingston & Hubel, 1988; Maunsel & van Essen, 1983; Shipp & Zeki, 1989). Area V1 also projects directly onto MT (Born & Bradley, 2005). Area V4 is predominately involved in colour and form perception, while MT is predominately involved in motion and depth perception (van Essen & Maunsell, 1983).

In the subcortical areas, magnocellular (M), parvocellular (P) and, more recently, koniocellular (K) pathways have been identified by selective staining and tracing techniques as well as by their different response properties (Hendry & Reid, 2000). As shown in *Figure 2*, The M pathway carries luminance signals from the larger parasol ganglion cells in the retina to the M layers of the LGN (Callaway, 2005), which then project to layer 4Cα of area V1 (Livingston & Hubel, 1988). The P pathway can be traced from the smaller midget ganglion cells of the retina that can be characterized by red-green colour opponency to the P layers of the LGN (Callaway, 2005). The P layers of the LGN project to layer 4Cβ in area V1 (Livingston & Hubel, 1988). The more recently discovered K pathway likely originates, at least in part, from bistratified retinal ganglion cells characterized by blue–ON receptive fields (Callaway, 2005). The K layers of the LGN are small and intercalated between the M and P layers (Hendry & Reid, 2000). Signals from the K layers of the LGN likely provide input to layers 1 (Hendry & Reid, 2000) and layer 4A (Sincich & Horton, 2005) of area V1. Part of the difficulty in mapping the K pathways is that it makes up a small proportion of the cells and projections between the retina, LGN, and V1 (Hendry & Reid, 2000; Callaway, 2005).

Prior to the discovery of the K pathway, early views of the visual system favoured parallel processing streams that were segregated in terms of both physiology and function starting at the P and M division at the retina and that maintained segregation even in the extrastriate cortical areas (e.g., Livingstone & Hubel, 1988). However, improvements in staining and tracing techniques indicate that the segregation between the streams is not maintained after input to area V1. Beginning in V1, extensive mixing of the M, P, and K pathways occurs (Merrigan & Maunsel, 1993; Nassi & Callaway 2006; Vidyasagar et al., 2002; see Sincich & Horton, 2005 for a review).

Processing in the cortical visual areas is divided into the dorsal and ventral streams, with the dorsal steam characterized as the motion pathway (Zeki et al., 1991) and the ventral stream characterized as the form and colour pathway (Zeki, 1978, Zeki et al., 1991). From V1, the dorsal stream projects to V2 thick stripes then to area MT and beyond.

Conversely, the ventral stream projects from V1 to thin and pale stripes in area V2 to area V4 and beyond (see *Figure* 2). Goodale and Milner (2000) have also characterized the dorsal stream as the 'vision-for action' system and the ventral stream as the 'vision-for-perception' system.

Positron emission topography shows that neurons that are selective for direction of motion are found in the highest concentrations in areas V1 and MT (Zeki et al., 1991). Neurons in both V1 and MT are also tuned for speed (Perrone & Thiele, 2002; Priebe, Lisberger & Movshon, 2006). In a recent review of MT function, Born and Bradley (2005) describe the primary functions of area MT as the integration and segmentation of motion signals. MT integrates motion signals from V1 to allow for the unified perception of pattern and object motion and segregates motion signals that arise from different objects so that the motion of independent objects can perceived simultaneously without confusion.

1.2 Models of First- and Second-order Motion Perception

There is considerable behavioural, neuropsychological, and physiological evidence that first- and second-order motion are processed, at least in part, separately. For example, interleaved frames of first- and second-order motion do not integrate into an unambiguous percept of motion (Ledgeway & Smith, 1994), and motion adaptation aftereffects are observed when the adaptation and test stimulus are either both first-order or both second-order, but not when test and adaptation stimuli are of different types (Nishida, Ledgeway, & Edwards, 1997). Imaging results from visually normal individuals also show functional separation between the areas involved in processing first- and second-order motion (Dumoulin, Baker, Hess, & Evans, 2003), while individuals with cortical lesions can show a selective impairment for first- or second-order motion (Rizzo, Nawrot, Sparks, & Dawson, 2008; Vaina & Cowey, 1996; Vaina, Cowey, & Kennedy, 1999; Vaina, Makris, Kennedy, & Cowey, 1998).

Specifically, Dumoulin and colleagues (2003) found that, in visually normal individuals, first-order motion most strongly activated the early visual areas (V1) whereas second-order motion most strongly activated the higher visual areas (near V5). Similarly, Ashida and colleagues (Ashida, Lingau, Wall, & Smith, 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.

Results from patients also show a functional and anatomical separation between first- and second-order motion processing. Specifically, a selective impairment of the detection of second-order motion was demonstrated in a patient (FD) who had a cortical lesion just dorsal to area MT (Vaina & Cowey, 1996; Vaina et al., 1999). When stimuli were presented in the visual field contralateral to the lesion, FD was impaired on several second-order motion tasks but not on a first-order motion task. The opposite pattern of impairment (i.e., to first-order but not second-order motion detection) was found in another patient (RA) following a unilateral lesion close to the medial surface of the occipital lobe (Vaina et al., 1998). The lesion probably involved parts of V2 and V3, and may have disrupted connections between V1 and later dorsal regions (Vaina, et al., 1999). RA was impaired on a variety of tests of direction discrimination for both local and global first-order motion, whereas performance on similar second-order motion tests was normal compared to controls (Vaina et al., 1998). These results are consistent with a more recent study in which patients with unilateral focal lesions of the right or left cortex showed impairment in first-order but not second-order motion processing when compared to control subjects who had no lesions (Rizzo et al., 2008). Selective impairment of only first-order or second-order motion processing provides direct evidence that the pathways processing first- and second-order motion are at least partially segregated, both functionally and anatomically.

There are also differences in visual evoked potential (VEP) response and reaction time to first- versus second-order motion. In one study, Ellemberg, Lavoie et al. (2003) measured VEP latencies and reaction time for the onset of suprathreshold first- and second-order stimuli that were matched for visibility. Both VEP latencies and response times were slower for second-order than first-order motion. Similarly, Ledgeway and Hutchinson (2008) found that reaction time for a direction discrimination task was slower for second-order than first-order motion that where matched for visibility. This result was replicated for a variety of types of second-order motion and wide range of depth modulations (Ledgeway & Hutchinson, 2008).

A number of models can account for differences between first- versus second-order motion. The most prominent is the filter-rectify-filter model (Wilson, Ferrera, & Yo, 1992). In this model, first- and second-order motion are processed by low-level motion sensitive mechanisms. Second-order motion perception requires additional processing stages beyond what is required to process first-order motion. There is also evidence to suggest that a higher-level feature tracking mechanism may operate in parallel with low-level motion mechanisms (Cavanagh, 1992). Below, I review the filter-rectify-filter and feature tracking motion models, present evidence supporting them, and briefly review other motion models.

Filter-rectify-filter model: Low-level motion perception can be described by the motion energy model (Adelson & Bergen, 1985). Based on this model, motion is processed using spatiotemporally oriented receptive-fields or filters. Hence, a moving edge can be represented as an oriented bar on a space-time plot. The slope of the oriented bar represents the speed of the motion and the direction of slope (positive or negative) represents the direction of motion. Physiologically, this representation could be produced by combining the responses of at least two separate filters that are identical except for a shift in receptive field centre and a temporal delay. This type of motion energy detector is computationally equivalent to the elaborated Reichardt detector (Adelson & Bergen, 1985), so no distinction will be made here between those two types of mechanisms. The basic motion energy model has been supported by recordings in complex cells of cat V1 (Emerson, Bergen, & Adelson, 1992). Emerson and colleagues measured neural impulses of directionally sensitive complex cells in response to single and paired bars that were presented at the cells' preferred orientation. A stepwise progression of the oriented bars resulted in directionally selective responses. Space-time contour plots of the neural response showed a spatiotemporally oriented pattern that is consistent with predictions based on Adelson and Bergen's spatiotemporal oriented motion energy detectors.

Such motion energy, or Reichardt, detectors are the basis of motion extraction in Wilson and colleagues (1992) prominent filter-rectify-filter model of first- and second-order motion perception. In the filter-rectify-filter model, first- and second-order information are processed by two at least partially separate cortical mechanisms. The detection of first-order boundaries is carried out by orientation selective simple cells in area V1 that consist of an elongated central excitatory zone flanked on each side by inhibitory zones, which in turn are flanked by weaker secondary excitatory zones. This initial filtering is followed by a motion extraction phase, which can be modeled by Adelson and Bergen's (1985) motion-energy detectors.

The detection of second-order cues to motion also begins in area V1 with a similar oriented filtering stage, but unlike the detection of first-order cues to motion, additional processing is required before motion extraction takes place. In these additional stages, the output of the simple V1 cells is rectified (a non-linear operation) and further processed by a second larger oriented filter in cortical area V2 -- hence, the term, 'filter-rectify-filter'. Second-order motion is extracted following these additional rectify and filter stages. Finally, the first- and second-order pathways are combined into a pattern unit network, presumed by Wilson et al. to be area MT. The processing of second-order motion is thought to take longer as the result of the extra processing stages that occur in the second-order motion pathway.

Scott-Samuel and Smith (2000) provided a demonstration of the separate nature of the analysis of first- and second-order motion using the perception of transparency. Motion transparency is the perception of two (or more) directions of motion occurring simultaneously, with one signal superimposed on top of the other. As described by Scott-Samuel and Smith, this perception can be eliminated if local motion signals are balanced, such that the motion signals of any two oppositely drifting dots or pattern segments that fall into any one receptive field are equal. When this occurs, the motion signals cancel each other out and the result is a net signal of no motion, thus making it impossible to determine reliably the direction of motion of any single element in the display. Based on this logic, the elimination of the perception of transparency is an indication that locally balanced motion signals are processed by the same mechanism. If the motion signals are processed by different mechanisms that are not pooled, the perception of transparency will persist. Scott-Samuel and Smith found that that the perception of transparency was eliminated only when the signals were of the same type (i.e., both first-order or both second-order). However, when equally visible first- and second-order stimuli were combined to create a composite stimulus, thresholds to discriminate the direction of a single element in the display remained nearly perfect. This indicates that cancellation of motion signals did not occur, and thus, that different mechanisms were involved in processing first and second-order motion. These results support the, at least partial, separation of the processing of first- and second-order motion. Furthermore, these results are as expected if the processing of both types of signals begins with low-level motion sensitive cells, as described by the filter-rectify-filter model, although higher level cancellation of signals cannot be ruled out.

In a similar study, Ledgeway and Smith (1994) demonstrated that frames of first- and second-order motion could not be integrated to produce a percept of smooth motion. Specifically, they used motion sequences consisting of two alternating frames that were designed to yield an unambiguous percept of motion in a particular direction only if the motion signals of the separate frames were integrated together (see *Figure 3*). When the two frames were of the same type (i.e., either both first-order or both second-order), participants were able to judge the direction of the motion signal with nearly perfect accuracy, even if the second-order motion sequence consisted of two different types of second-order frames (i.e., boundaries defined by changes in contrast in one frame and by size in the other). However, when the motion sequences consisted of alternating first- and second-order frames, performance in the same task dropped to chance levels. Integration of the motion sequences and, subsequently, the perception of unambiguous motion was seen only when the frames in the motion sequence were of the same type.

It is likely that Ledgeway and Smith's (1994) results also reflect low-level mechanisms because the spatial displacements between frames were small enough (e.g., 0.125 deg) to favour lower-level motion rather than higher-level motion processes. Unlike Ledgeway and Smith, others have found that observers *can* perceive apparent motion of alternating disks that were defined by different stimulus attributes, including luminance and texture (Cavanagh, Arguin, & von Grunau, 1989). In that case, the spatial displacement between frames was much larger at 3-4 deg and the integration likely occurred at the level of MT neurons, whose receptive fields are many times larger than those of V1 neurons (approximately 10 times in a linear measure; Born & Bradley, 2005). MT neurons can respond to both first- and second-order motion. For example, in a study of macaque MT, O'Keefe and Movshon (1998) found that about a quarter of the sampled MT neurons were selective to both first- and second-order motion.

Feature Tracking: Another mechanism that has been implicated in motion perception, especially, but not exclusively, second-order motion processing, is feature tracking. This mechanism works first by extracting features and then by analyzing changes in their location (Derrington, Allen, & Delicato, 2004). Feature tracking has yet to be well defined; however, it is presumed to be a relatively high-level mechanism that is limited by the visual system's ability to extract spatial structure (Derrington et al., 2004). Conversely, motion energy detectors are low-level and automatic in nature. Furthermore, motion-energy mechanisms do not require position to be extracted for motion analysis to occur (Adelson & Bergen, 1985).

Smith and Ledgeway (2001) suggest that motion energy and feature tracking mechanisms operate in parallel, with the most sensitive mechanism underlying motion processing for a given stimulus parameter. For example, feature tracking has been linked to stimulus parameters such as element size of random dot kinematograms (Smith & Ledgeway, 2001), as well as temporal frequency/velocity and contrast of second-order gratings (Seiffert & Cavanagh, 1998; 1999; Ukkonen & Derrington, 2000). In a review, Derrington et al. (2004) suggested a number of differences in performance that should be found between feature tracking and low-level motion sensitive mechanisms. For example, conditions that make features harder to locate may decrease performance on motion tasks where feature tracking is used because the feature tracking mechanisms must locate features before tracking can occur. This includes conditions that have brief presentation times or a high temporal frequency. A motion energy detector should not be affected by these conditions because it calculates motion energy without extracting the position of the moving elements (Adelson & Bergen, 1985). Other differences that may be expected between a low-level motion mechanism and a feature tracking mechanism are longer processing times and higher attentional demand (Derrington et al., 2004).

A number of experiments have demonstrated that feature tracking mechanisms process second-order motion under some testing conditions but not others. For example, studies by Seiffert and Cavanagh (1998;

1999) reveal that displacement thresholds[1] for the detection and discrimination of second-order motion are roughly constant across a range of temporal frequencies/velocities, but only when contrast and speed of the stimuli are low (at 10 times contrast threshold and speeds of 2 Hz; equivalent to 5.5 -12 deg/sec for the radial stimulus used by Seiffert and Cavanagh). When contrast is higher than 10 times contrast thresholds (especially when 40 or 80 times threshold), and when motion, in addition to the oscillation of the radial grating, is above 2 Hz, displacement thresholds improve with increases in grating or oscillation temporal frequency/velocity. Displacement thresholds also improve with increases in temporal frequency/velocity for first-order stimuli, regardless of testing parameters. The finding that displacement thresholds for low contrast and low velocities of second-order motion do not vary with temporal frequency suggests that, under the conditions tested, second-order motion is processed by a system that is governed by minimum displacement or distance that the stimuli traveled (Seiffert & Cavanagh, 1998;1999). This is consistent with the way a feature tracking mechanism is expected to work. Regardless of the velocity, the stimulus must travel a certain distance before motion can be perceived (Seiffert & Cavanagh, 1998; 1999). The pattern of findings for first-order motion and for higher contrast and higher speed second-order motion is consistent with the operation of a mechanism that codes velocity/temporal frequency such as low-level motion detectors (Seiffert & Cavanagh, 1998; 1999).

Ukkonen and Derrington (2000) found a similar pattern of results for contrast of second-order gratings using a pedestal test. A pedestal is a static stimulus that is added to a drifting stimulus (e.g. a static grating added to a moving grating). A pedestal is expected to disrupt a feature tracking mechanism because the moving features are incorrectly matched to the stationary features, thereby making the grating appear to wobble back and forth. However, for a motion energy detector, the net motion signal is unchanged by the stationary pedestal because it ignores static stimuli, and motion processing remains unaffected, or is immune to the pedestal (Lu & Sperling, 2001). Ukkonen and Derrington found that accuracy on direction discrimination tasks were unaffected by the pedestal when the stimuli were first-order or high-contrast second-order. However, when the stimuli were low-contrast second-order, accuracy on the direction discrimination task was worse than conditions without the pedestal. Like the results of Seiffert and Cavanagh (1998; 1999), these results indicate that second-order motion may be processed by feature

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[1] Seiffert and Cavanaugh (1998) described thresholds in terms of displacement (deg of shift measured in phase) while Seiffert and Cavanaugh (1999) described thresholds in terms of amplitude (shift measured as percent of cycle). As both are very similar variations of a measure of spatial change, the term 'displacement thresholds' will be used in reference to both studies to avoid confusion.

tracking under some testing conditions and low-level motion mechanisms under other testing conditions.

Others have also reported results that are inconsistent with the filter-rectify-filter model of first- and second-order motion processing and suggest that feature tracking may be responsible for their findings. Allard and Faubert (2008) measured the effect of luminance- and contrast-modulated dynamic noise on sensitivity to direction of luminance- and contrast-modulated motion. When the temporal frequency of the grating was low (2Hz), a double dissociation occurred: sensitivity to motion was affected more when signal and noise were of the same type than when they were different. However, when temporal frequency was higher (8Hz), sensitivity to luminance- and contrast-modulated motion was affected similarly by both types of noise. Allard and Faubert concluded that the selective impairment of each motion type for the low temporal frequency condition was consistent with the idea that fundamentally different mechanisms processed first- and second-order motion, while common mechanisms processed the two motion types when temporal frequency was high. They suggested that second-order motion might be processed by a feature tracking mechanism when temporal frequency is low, but a motion-energy based mechanism when temporal frequency is high.

Other models of first- and second-order motion perception: Lu and Sperling (1995; 2001) have also modeled first- and second-order motion processes, though, unlike others, have included a third stream for the processing of third-order motion. The third-order motion stream was included to account for experimental results that are inconsistent with both first- and second-order motion mechanisms (Lu & Sperling, 2001). In this model, first- and second-order motion mechanisms are motion-energy based, primarily monocular, and fast, while the third-order motion mechanism is binocular, slow, and strongly influenced by attention. Feature based mechanisms are important in both second- and third-order processing.

According to Lu and Sperling (2001), the *first-order system* extracts motion using motion energy/elaborated Reichardt detectors. Their *second-order motion* system appears to be a hybrid of Wilson and colleagues (1992) filter-rectify-filter model and a feature tracking mechanism. Unlike the filter-rectify-filter model that is based on simple motion-sensitive mechanisms, Lu and Sperling posit that for second-order motion to be processed, features must be first extracted by texture grabbers that consist of linear spatial and linear temporal filters and a nonlinear transformation (e.g., full-wave rectification). Motion is then extracted from the output of a field of texture grabbers by elaborated Reichardt detectors.

The additional *third-order motion* system was included in the model of motion perception because some types of motion are invisible to first-and second-order processing (e.g., a drifting square that is defined differently in successive frames such as texture orientation in one frame, then contrast in the next, and so on). The third-order mechanism detects movement of what Lu and Sperling (2001) termed 'feature salience changes' in areas marked as figure versus ground. Rather than correlate the square in successive frames, a process that would involve a very complex point-by-point correlation, a single common attribute is extracted from all frames and then the motion of that attribute is computed. This could be done using a figure/ground computation based on a salience calculation whereby more salient features are perceived as figure and less salient features are perceived as ground. Motion is then computed using the standard algorithms. Like the other two systems, the third order system carries information about location, direction, and speed of motion, while information about the nature of the object is carried by a pattern-processing system (Lu & Sperling, 2001) the literature on motion perception has given little attention to the idea of third-order motion mechanisms, likely because the vast majority of evidence suggests the existence of two, but not three, motion mechanisms.

In contrast with postulations of two or three systems for motion perception (Lu & Sperling, 1995; 2001; Seiffert & Cavanagh, 1998; 1999; Smith & Ledgeway, 2001; Ukkonen & Derrington, 2000; Wilson et al., 1992), Benton (2004) has suggested that first- and second-order motion can be processed using only one mechanism. He showed that the direction of contrast-modulated stimuli could be extracted by a gradient-based motion mechanism, which is equivalent to low-level motion energy detectors, given that the correct initial filters are chosen (Benton, 2004). The gradient-based model includes a motion opponent stage followed by a contrast-normalization phase. Using this model, Benton demonstrated that the correct direction of contrast-modulated second-order motion could be indicated at the contrast-normalization phase. Benton (2004) contrasts this result with the two-channel hypothesis (e.g., filter-rectify-filter model) and argues that one processing stream can process first- and second-order motion without the additional step of rectification for second-order motion.

Benton's (2004) results complement the suggestion by Derrington and colleagues (2004) that there is no reason to assume that the visual system contains dedicated second-order motion mechanisms. Rather, Derrington and colleagues suggest that second-order motion may be processed by a mixture of feature tracking mechanisms and low-level motion mechanisms, such as elaborated Reichardt detectors, motion energy detectors, or gradient-based motion detectors, all which can be shown to be equivalent.

Benton's (2004) claim that first- and second-order motion can be encoded by the same mechanism has been criticized by some (e.g., Hutchinson & Ledgeway, 2006) in that a vast array of evidence suggests that first- and second-order motion are processed by separate mechanisms (see Section 1.2 Above; e.g., Ledgeway & Smith, 1994, Nishida, et al., 1997; Vaina & colleagues, 1996; 1998; 1999). Moreover, even in Benton's unified model, first- and second-order processing is split into separate stages of the gradient-based model, which may be equivalent to a two-process model (Schofield, Ledgeway, & Hutchinson, 2007). Nonetheless, as suggested by Benton and echoed by others (Allard & Faubert, 2008; Derrington et al., 2004), there may be some conditions where second-order motion is processed by something analogous to a gradient-based model rather than dedicated second-order mechanisms.

The studies in this thesis were not designed to distinguish among the theories of motion processing mechanisms, but the pattern of results supports the existence of two mechanisms, one of which involves feature tracking. Although there is some support for Lu and Sperling's (1995; 2001) three-stream approach and Benton's (2004) single channel approach to first- and second-order motion processing, consideration of these alternate models is beyond the scope of this thesis.

1.3 Ecological Validity of Second-Order Information

The perception of second-order motion and structure is generally studied using laboratory-generated stimuli that have little to no resemblance to any natural image. Baker (1999) has suggested that examples of real world second-order information can be seen in camouflaged animals or a soccer ball moving at a distance. Still, given the abundance of cues to motion and structure provided by differences in luminance and colour, one may question the importance of second-order information in the natural world.

Recent findings suggest the circumstances under which second-order information may be important in perception of the natural word. For example, based on results from a model of stimulus salience convolved with natural images and a behavioural study of the allocation of attention, Parkhurst and Niebur (2004) found evidence that both first- and second-order information guide overt attention to areas of a natural scene that, once attended, are processed in more detail. Similarly, Zanker (1997) found that performance on a direction discrimination task decreased with increasing eccentricity from the fovea for different types of second-order, but not first-order motion. An effect of eccentricity was not found for simple motion detection, nor for orientation discrimination, for either first- or second-order stimuli. Thus, adults are able to detect second-order motion and form over the whole visual field, but are limited to discriminating its direction in the central field where spatial resolution is best (Zanker, 1997). Given that the perception of second-order motion is specialized to the fovea, second-order motion processing may be adapted for detailed analysis of the visual scene (Zanker, 1997).

Natural images do contain significant second-order structure. Both Schofield (2000) and Johnson and Baker (2004) used biologically inspired models of how second-order vision works to determine if natural images contain any significant second-order structure. Both found that they do, although because of differences in how their models of second-order filters pooled the image signal, their results differed. Schofield's model pooled the signal's signed values, while Johnson and Baker's model pooled absolute values. Schofield found that natural images contained second-order structure that was independent of the first-order structure, and thus areas defining edges or texture, like grass, were enhanced beyond what first-order vision provided. In contrast, Johnson and Baker found that first- and second-order structure was significantly correlated in natural images. Later, Johnson, Prins, Kingdom, and Baker (2007) found that the degree of correlation affected performance on a spatial frequency discrimination task of orientation-modulated stimuli (which stimulus structure is wavier?). Although this task uses laboratory generated stimuli, it does allow investigation of how correlated and uncorrelated first- and second-order information may affect perception. Specifically, they found that when first- and second-order signals were 50% correlated, performance was equal to performance for the same task with first-order signal alone. Furthermore, when first- and second-order signals were 75 and 100% correlated, performance was better than when first-order signals were presented alone. Performance was worse than first-order alone if first- and second-order signals were not correlated and was at chance when stimuli were second-order alone.

Despite the difference in findings as to whether first- and second-order structure is correlated in natural images, results from the studies by Schofield (2000) and Johnson and colleagues (Johnson & Baker, 2004; Johnson et al., 2007) suggest that second-order structure does, in some way, add valuable information to enhance the perception of visual images. If first- and second-order information *is not* correlated, the enhancement is obvious: the image contains more information than if first-order information is all that is available. If the cues *are* correlated, task performance described by Johnson et al. (2007) suggests that this correlation combines to add information to the visual system, beyond what is provided by first-order, and especially second-order information alone. The finding that performance is at chance when second-order information is presented alone (Johnson et al., 2007) suggests that the visual system responds to natural structure where second-order components are correlated with, rather than independent from, first-order information. Similarly, as noted by Johnson and colleagues (2007), objects in the natural world tend to differ from the background on more than one dimension, suggesting that a correlation should be expected.

1.4 The Development of Sensitivity to First- and Second-Order Stimuli

Investigations of infants' sensitivity to first- and second-order information began with studies of the age at which they could first detect first- versus second-order form.

Such studies indicate that sensitivity to first-order cues to form are evident in the youngest age groups tested—in infants as young as 1-3 months of age (Atkinson & Braddick, 1992; Rieth & Sireteanu 1994; Sireteanu & Rieth, 1992). However, sensitivity to second-order form is not evident until about 3.5 to 4.5 months of age (Atkinson & Braddick,1992; Rieth & Sireteanu, 1994), or even as late as 9-12 months of age (Sireteanu & Rieth, 1992), depending upon testing parameters. Thus, sensitivity to first-order form emerges before sensitivity to second-order form.

The pattern of development is less clear for moving stimuli. Infants who were 8 – 12 and 16 – 20 weeks old showed significant preferences for both first- and second-order moving patterns over a moving control pattern in a forced-choice preferential looking task (Atkinson, Braddick, & Wattam-Bell, 1993; Braddick, Atkinson, & Hood, 1996). This indicates that infants as young as 2 months of age can detect both first- and second-order cues to motion. However, nothing can be concluded about the development of sensitivity to first- and second-order motion, as detection thresholds were not measured. Moreover, the first-order test pattern was a form-from-motion stimulus and thus likely involves higher-level integration than involved in the perception of first-order local motion.

Sensitivity to first- and second-order information has also been measured in older infants and children. Using forced-choice preferential looking, Thibault, Brosseau-Lachaine, Faubert, & Vital-Durand (2007) measured contrast thresholds for children ranging from just under 1 year to about 7 years of age. Regardless of age, infants and children could discriminate both first- and second-order moving gratings from a patch of static grey-scale noise. Furthermore they reported that contrast thresholds improved with age at an equal rate for first- and second-order stimuli over the age range tested. However, conclusions based on these results are limited because the test and control stimulus differed in form, flicker, and motion. Because any difference between a test and control stimulus could affect forced-choice preferential looking, results from this study may reflect sensitivity to form or flicker rather than motion.

Unlike the findings described by Thibault et al. (2007), the only two studies of sensitivity to direction of motion in children suggest that sensitivity to first- and second-order motion develop at different rates. Ellemberg, Lewis et al., (2003) reported that 5-year-olds' sensitivity to the direction of motion was more immature on second-order than first-order motion. However, a reanalysis of results shows that 5-year-olds' sensitivity to second-order motion is more adult-like than their sensitivity to first-order motion, at least when temporal frequency is relatively low. Conversely, Bertone et al., (2008) reported that at 5-6 years of age, children were more immature for second-order than first-order motion. However, they also reported that sensitivity to second-order motion became adult-like by 7-8 years age, while sensitivity to first-order motion was still not mature.

1.5 The Current Studies

Given the few reports that have addressed the development of sensitivity to first- and second-order motion and the inconsistent nature of the results, the main goal of this thesis is to measure sensitivity to first- and second-order motion over a wide range of ages from infancy to adulthood. In addition to determining the developmental trajectories for sensitivity to first- and second-order motion, I varied the parameters of the stimulus to probe the nature of the developing mechanisms. Specifically, I studied the effects of motion velocity, temporal frequency (flicker rate), and spatial frequency (stripe size) on sensitivity to first- and second-order motion in adults and children in order to probe properties of the underlying mechanisms and hence possibly allow conclusions about the source of any immaturity.

Chapter 2 describes studies measuring sensitivity to drifting gratings in infants at 3 and 6 months of age and sensitivity to direction of motion at 3 months of age. Chapter 3 addresses sensitivity to first- and second-order motion from 3 years of age to adulthood, as well as how the factors of temporal frequency, spatial frequency, and velocity affect these thresholds. Chapter 4 further examines the effect of temporal frequency, spatial frequency, and velocity on second-order motion mechanisms in 5-year-olds and adults. In all three chapters, sensitivity to motion was also compared to sensitivity to form. One reason for this comparison was to determine if immaturities to motion were related to immaturities to form. It is possible that children's sensitivity to motion could be limited by immaturities in sensitivity to the pattern that makes the moving stimulus, rather than by an immaturity of the motion system itself. The form data also allowed further comparison of the pattern of results for first- versus second-order stimuli.

In each study, I measured contrast thresholds for first- and second-order stimuli. Contrast thresholds are the most common measure of sensitivity to motion and were used in the three pervious studies of children's sensitivity to motion (Bertone et al., 2008; Ellemberg, Lewis, et al., 2003; Thibault et al., 2007) and a large array of studies of adults' sensitivity to motion (e.g., Cropper, 2005; Kiopres & Movshon, 1998; Ledgeway & Hess, 2002; Schofield et al., 2007). Contrast thresholds have the benefit of allowing sensitivity to motion to be quantified and compared at different ages. The stimuli consisted of luminance modulated (first-order) and contrast modulated (second-order) gratings. Although there are a number of varieties of second-order motion, I chose contrast-modulated second-order motion because it is the most common form of second-order motion studied in adults (e.g., Allard & Faubert, 2008; Allen, Ledgeway & Hess, 2004; Bertone et al., 2008; Ellemberg, Lewis, et al., 2003; Ledgeway & Hutchinson, 2005; 2008, Seiffert & Cavanagh, 1998; 1999; Thibault et al., 2007) and results may not generalize across all types of second-order stimuli (Ledgeway & Hutchinson, 2008).

In sum, the purpose of this thesis was to chart the development of first- and second-order motion mechanisms and to explore the effect of temporal frequency, spatial frequency, and velocity on sensitivity to first versus second-order motion. In the Discussion of each chapter and the General Discussion, I consider the implications of the findings for the existing models of the underlying mechanisms.

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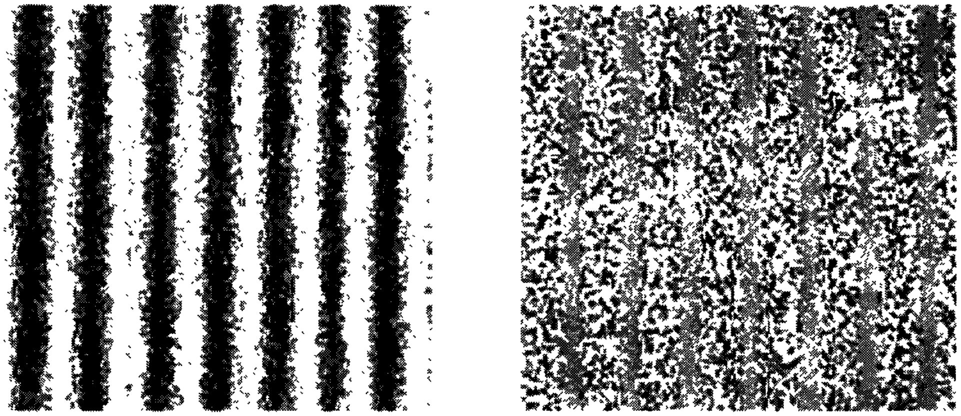

Figure 1.1. The left panel depicts a first-order stimulus. Adjacent stripes are defined by differences in luminance. The right panel depicts a second-order stimulus. The stripes are defined by a difference in the contrast of the pixels in each stripe. In this example, the outer stripes consist of high-contrast pixels, while the adjacent stripes consist of low-contrast pixels. The mean luminance of adjacent stripes is identical.

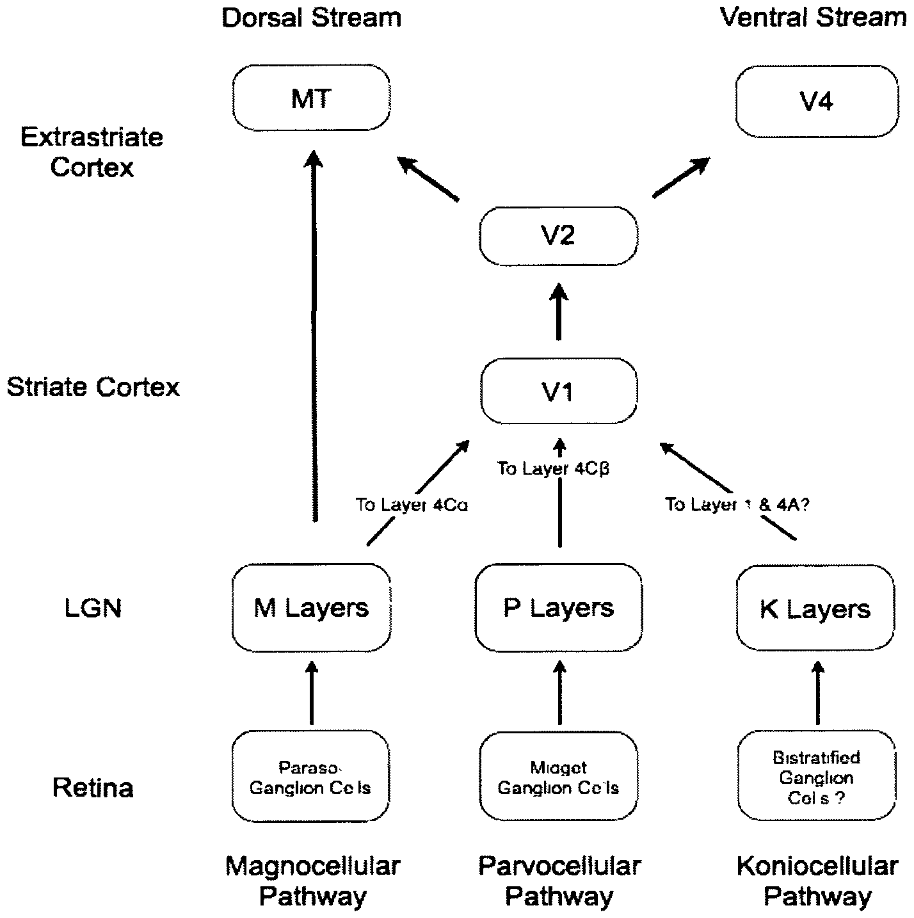

Figure 1.2. The dominant visual pathways involved in the perception of motion and form. Adapted from Born & Bradley, 2005; Callaway, 2005; Merrigan & Maunsell, 1993; Sincich & Horton, 2005. The M, P, and K pathways are limited to the retina, lateral geniculate nucleus (LGN) and the LGN projections to area V1. Extensive mixing of the M, P, and K pathways occurs in Area V1. The dorsal and ventral streams are cortical pathways that are involved in motion perception and form/colour perception, respectively.

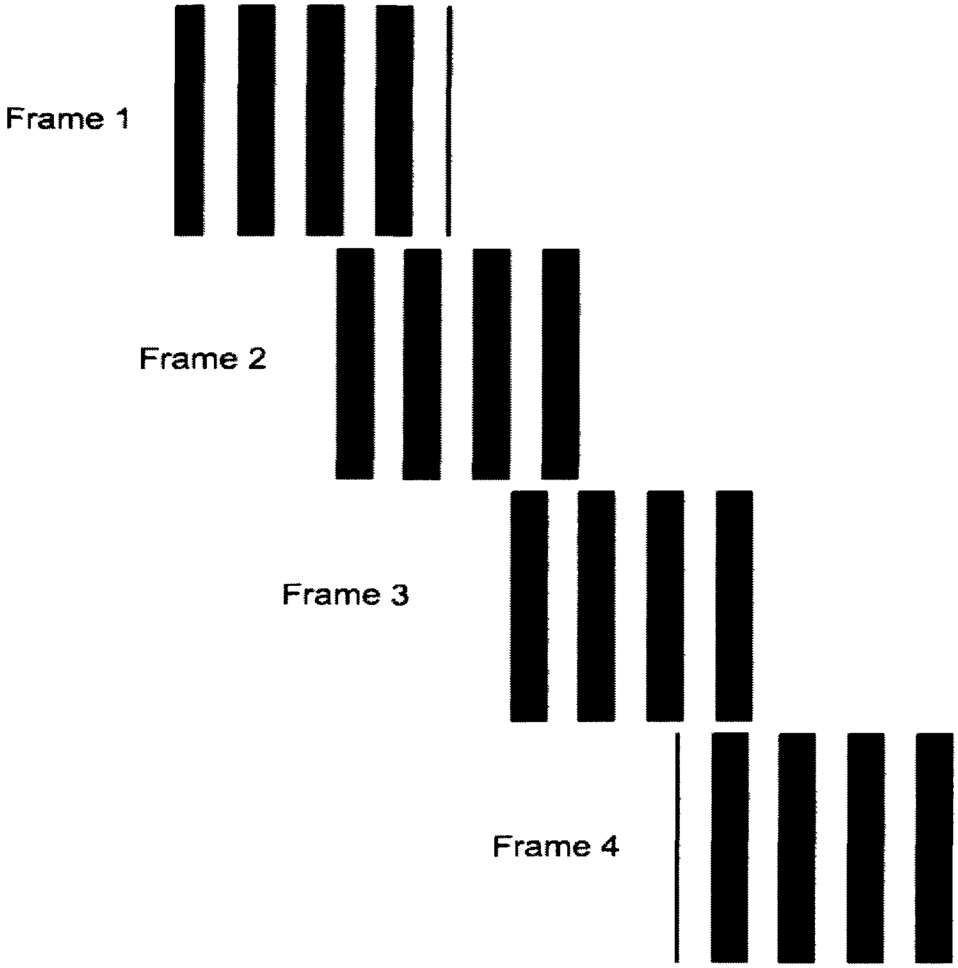

Figure 1.3. A schematic of Ledgeway and Smith's (1994) experiment. They presented sequential frames of first- and second-order gratings. The gratings were displaced by an equal amount in each frame. If all the frames were of the same type (i.e., all first-order or all second-order) participants perceived smooth motion that was consistent with the direction of the displacement - in this case, moving to the right. If the frames alternated between first-order and second-order stimuli (i.e., Frames 1 & 3 were first-order and Frames 2 & 4 were second-order) participants did not perceive smooth motion and were unable to determine the direction of displacement.

CHAPTER 2

Sensitivity to First- and Second-order Drifting Gratings During Infancy

V. L. Armstrong, T. L. Lewis, D. Ellemberg, & D. Maurer

2.1. Preamble

In the experiments in Chapter 2, I examined the development of infants' sensitivity to first- and second-order information. Specifically, in Experiment 1 I examined their contrast thresholds for discriminating a drifting from a static grating and in, Experiment 2, I tested their ability to discriminate direction of motion. Unlike previous studies, I chose stimuli that isolated sensitivity to flicker or motion from sensitivity to form. The results indicated that 3-month-olds show no evidence of sensitivity to direction of motion and hence likely discriminate static from moving patterns on the basis of flicker. Moreover, thresholds for second-order drifting gratings were more adult-like than thresholds for first-order drifting gratings. This pattern is unexpected, given current models of first- and second-order vision, but is consistent with recent findings from infant monkeys (Kiorpes et al., 2006) and children (Bertone et al., 2008). This is the first study to test for sensitivity to direction of second-order local motion in infants and the first study to compare contrast sensitivity for first- and second-order drifting gratings during early infancy.

2.2 Abstract

We used forced-choice preferential looking to estimate infants' discrimination thresholds for drifting versus stationary gratings. At 3 and 6 months of age, thresholds were more adult-like for second-order than first-order gratings. However, between these ages thresholds improved more for first-order than second-order gratings. We also tested 3-month-olds' sensitivity to *direction* of motion using habituation. Infants dishabituated to a change in first-order orientation, but not to a change in direction of first- nor second-order motion. Hence, results from Experiment 1 were likely driven by the perception of flicker rather than motion. Sensitivity to first- and second-order gratings develop at different rates.

2.3 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 arise from spatiotemporal variations that give rise to contrast or texture boundaries without a change in mean luminance.

The results of psychophysical (Chubb & Sperling, 1988; Ellemberg, Lewis et al., 2003; Ledgeway & Smith, 1994a), electrophysiological (Ellemberg, Lavoie et al., 2003; Zhou & Baker, 1993), human imaging (Dumoulin, Baker, Hess, & Evans, 2003; Smith, Greenlee, Sing, Kramer, & Hennig, 1998), and neuropsychological (Greenlee &

Smith, 1997; Vaina & Cowey, 1996; Vaina, Makris, Kennedy, & Cowey, 1998) experiments suggest that first- and second-order motion are processed, at least in part, by separate mechanisms. For example, adults do not integrate alternating frames containing first- and second-order local motion cues into an unambiguous percept of motion (Ledgeway & Smith, 1994a), 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 a clear segregation between the areas that are involved in the processing of first- and second-order motion (Dumoulin et al., 2003). Specifically, Dumoulin and colleagues found that first-order motion most strongly activated the early visual areas (V1) whereas second-order motion most strongly activated the higher visual areas (near V5).

The purpose of the current study was to evaluate sensitivity to first- and second-order cues to motion in infants. Several behavioural methods have been used to measure infants' ability to discriminate two stimuli. One method, forced-choice preferential looking, relies on an observer's judgment of infants' visual behaviour (e.g., direction of first eye movement, direction of most frequent fixations, or direction of the longest fixation) to provide evidence that infants can discriminate two stimuli. For example, infants look reliably longer at moving than stationary stimuli, suggesting they can tell the difference between the two (Volkmann & Dobson, 1976). However, it should be noted that an infant's visual behaviour may be based on any parameter that differs between a test and control stimulus, provided that the difference is salient to the infant. For example, if a drifting grating is paired with a static grey-scale noise field, as it was in a recent study by Thibault and colleagues (Thibault, Brosseau-Lachaine, Faubert, & Vital-Durand, 2007), then the test and control stimulus differ in form, flicker, and motion. Therefore, any one or combination of these cues could allow the infant to discriminate the drifting grating from the plain field. Furthermore forced-choice preferential looking does not allow one to test sensitivity to direction of motion, because infants do not have any robust looking preference for one direction of motion over another.

Another behavioural method that is used to measure infants' sensitivity to motion is habituation. This method takes advantage of the fact that infants will show recovery of attention if they can tell the difference between a habituated and a novel stimulus (Bornstein, 1985). In infant-controlled habituation, testing begins with a habituation phase during which infants view the same stimulus over a number of trials until mean looking time is reduced to a criterion, typically to 50% of the mean looking time measured at the beginning of the session. This reduction in looking time indicates that infants have become habituated, or lost interest, in the stimulus. The habituation phase is followed by a test phase during which looking times for both the habituated and a novel stimulus are measured. If infants look longer at the novel stimulus than the habituated stimulus (i.e., recover from habituation), we can conclude that they can tell the difference between the two stimuli. The benefit of this method is that one can test whether infants can discriminate between stimuli such as leftward versus rightward motion, where the difference between the stimuli would not result in preferential looking. One goal of the present study was to use forced-choice preferential looking to measure infants' sensitivity to moving versus stationary stimuli. A second goal was to use a habituation paradigm to determine whether the preferential looking was mediated by sensitivity to flicker, which is not directionally selective, or by direction of motion.

Wattam-Bell (1996abc) made considerable gains in understanding infants' sensitivity to first-order motion using both forced-choice preferential looking and habituation. In a number of experiments, Wattam-Bell used a segregated form-from-motion 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 patch of dots appears to have three horizontal stripes and will look different from a patch dots that move in a uniform direction, move incoherently, or are static. At 3 - 5 and 3 - 6 weeks of age, infants can discriminate a form-from-motion pattern from stationary dots and from a patch of dots moving incoherently, but at the same age, infants show no evidence of being able to discriminate a form-from-motion pattern from uniform motion or one direction of uniform motion from the opposite direction of motion (Wattam-Bell, 1996abc). By 6-8 weeks of age, infants can discriminate the form-from motion stimulus from uniform motion (Wattam-Bell 1996b), but still cannot discriminate uniform motion moving in one direction from uniform motion moving in the opposite direction at the same age or even at 9 -12 weeks of age (Wattam-Bell, 1996bc). There are no known published studies that have established the age at which infants demonstrate sensitivity to uniform motion using behavioural methods (see Section 2.6 General Discussion).

The differences in results that Wattam-Bell (1996abc) found for various test and control stimuli underscore the difficulty in interpreting infants' responses to moving stimuli versus a control stimulus. Wattam-Bell found that infants could discriminate the test and control stimulus when the control stimulus was static or incoherent, but not when it was uniform motion. When the comparison stimulus was static, only the form-from-motion stimulus contained temporal modulation; when the comparison stimulus moved incoherently, it did so with less energy at low temporal frequencies than the form-from-motion stimulus. However, in tasks with uniform motion, only directional information could be used to discriminate the test and control stimuli (Wattam-Bell, 1996bc). Wattam-Bell's findings suggest that even 3-6 week olds are able to perceive the temporal dynamics of motion, perhaps as flicker, but infants, even at 9 - 12 weeks, cannot discriminate differences in uniform direction of motion.

Given Wattam-Bell's (1996abc) findings, it must be reiterated that any difference between a test and control stimulus that allows an infant to discriminate one stimulus from another may be the basis for that discrimination. This is important to understand because the basis of the discrimination determines what one is measuring. That is, if discrimination is based on a response to differences in form, then the sensitivity that is measured reflects mechanisms that are sensitive to form. Likewise, if the discrimination is based on response to flicker, then the sensitivity that is measured reflects mechanisms that are sensitive to flicker. Furthermore, if the test and control stimulus differ on more than one parameter, the measure likely reflects the most sensitive mechanism. To complicate matters further, the most sensitive mechanism may change with age, such that the same task may be measuring the sensitivity of one mechanism in one age group, but the sensitivity of another mechanism in an older age group. If a discrimination is not based on a response to direction of motion, then measures cannot be generalized to reflect sensitivity to motion, simply because the system that was tested was not the motion system. There is clear evidence that different mechanisms mature at different rates (e.g, sensitivity to form emerges earlier than sensitivity to motion; Braddick, Birtles, Wattam-Bell, & Atkinson, 2005).

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

Thibault and colleague's (2007) results must be interpreted with caution. The task was designed to test infants' visual response to a drifting grating versus a uniform grey-scale noise field. Thus, infants may have responded to form, flicker, or motion in the drifting grating because the uniform noise field differed from the drifting grating on all three of these parameters. Furthermore, because the non-clinical 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]

For tests that require sensitivity to the direction of motion, the available evidence suggests that by 8 - 12 weeks, infants can detect directional information in both first- and second-order motion. Specifically, results from forced-choice preferential looking experiments indicate that both 8- to 12-week-olds and 16- to 20-week-olds discriminate motion patterns that produce either first-order form-from-motion or second-order vertical motion from a control pattern that moves, but not in any coherent direction (Atkinson, Braddick, & Wattam-Bell, 1993; Braddick, Atkinson, & Hood, 1996). Although the observer's mean percent correct responses were higher for first-order than for second-order stimuli at both ages tested, the authors were not able to draw any conclusions regarding the development of sensitivity to first- versus second-order stimuli, as the size of the difference between first- and second-order responses did not change with age and the authors did not measure thresholds.

Little else is known about infants' ability to perceive second-order stimuli. When stimuli are stationary, infants show evidence of detecting a change in a second-order pattern defined by texture at 12 weeks of age (Freedland & Dannemiller, 1990). However, other studies using different methods have found that sensitivity to second-order pattern does not emerge until 14 - 18 weeks of age (Atkinson & Braddick, 1992; Rieth & Sireteanu, 1994b) or even as late as 9 - 12 months of age (Rieth & Sireteanu, 1994a; Sireteanu & 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 & Braddick, 1992; Rieth & Sireteanu, 1994ab; Sireteanu & Rieth, 1992).

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

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[1] Trend analyses for first- and second-order conditions were done using a larger group of clinical controls (n=72). While we do recognize that the small group of typical controls show the same tendency in results as the larger group of clinical controls, this larger group was recruited at a vision clinic because of possible risk for visual disorder. Although these children did perform normally on a number of visual screening tests, their possible risk of visual disorder suggests that they may not be an appropriate sample for the purpose of assessing typical visual development.

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 a drifting grating from an identical stationary grating. We tested infants at 3 months of age because results from directional motion tests are mixed at this age (Wattam-Bell, 1996abc). For comparison, we also tested an older group of 6-month-olds.

The forced-choice preferential looking method of Experiment 1 allowed us to quantify sensitivity to first- and second-order stimuli, but did not allow us to determine if results were based on perceived differences in flicker or in direction. To determine if 3-month-olds are sensitive to *direction* of first-order and second-order local motion, 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.

2.4 Experiment 1: Forced-Choice Preferential Looking

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 as well as to determine how the size of immaturities changes from 3 to 6 months of age.

Methods

Participants

The participants were 24 3-month-olds (3.00 - 3.99 months), 24 6-month-olds (6.00 - 6.99 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 and five 6-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 bonus points on their class grade for participation.

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 x 768. The stimuli were two 0.5 cy/deg vertical sinusoidal gratings, each contained within a 10.2 cm square (15 x 15 deg square when viewed from 50 cm). Each display consisted of two identical gratings whose inner edges were separated by a 3.4 cm (5 deg) gap. One grating drifted outward at 6 deg/sec, while the other remained stationary. The gratings were surrounded by a grey background. Each grating was either luminance-modulated (first-order) or contrast-modulated (second-order) and was like those described by Ellemberg and colleagues (Ellemberg, Lewis, et al., 2003; Ellemberg, Lavoie, et al., 2003). Specifically, the carrier consisted of static two-dimensional random binary noise, the luminance of which was binary. Each noise element subtended 2 x 2 arc min, and was assigned independently with a probability of 0.5 to be either 'light' or 'dark'. 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) was defined as:

$$\text{Depth modulation} = (L_{max}-L_{min})/(L_{max}+L_{min}),$$

where L_{max} and L_{min} are defined as the maximum and minimum mean local luminance in the stimulus.

For contrast-modulated stimuli, the same luminance-modulated sinusoidal grating was multiplied by, rather than added to, the carrier 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 (depth modulation) was defined as:

$$\text{Depth modulation} = (C_{max}-C_{min})/(C_{max}+C_{min}),$$

where C_{max} and C_{min} are defined as the maximum and minimum mean local contrasts in the stimulus.

The mean luminance of the stimuli at maximum contrast was 72 cd/m^2 for both the luminance- and contrast-modulated stimuli. The background had a mean luminance of 74 cd/m^2.

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 first- versus second-order stimuli. Motion type was tested between-subjects at 3 months of age and within-subjects at 6 months of age. 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 luminance- or contrast-modulations for each type of stimulus (see Table 1 for modulations tested).

A separate group of 6-month-olds was tested on higher depth modulation values because the first group of 6-month-olds performed above chance on all contrast-modulations we tested, thus preventing us from estimating their threshold for second-order stimuli.

Procedure

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

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 in 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 to see a clear view of the infant's eyes. This feature 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 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, used any reliable cue provided by the infant (e.g., 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. Each test consisted of 16 trails. 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). The experimenter's accuracy was measured for each 3-month-old on one stimulus type, and each 6-month-old on both types of stimuli, with the order of test counterbalanced across participants. We estimated group thresholds for infants based on the experimenter's accuracy for each modulation tested.

A second experimenter made independent forced-choice decisions as to the side of the moving grating for half of the 12 infants tested per stimulus type (2) and age group (3) for a total of 36 infants. The second experimenter agreed with the primary experimenter on at least 75% of the trials for each infant. The mean reliability was 86%, (range of means for the 6 groups: 77 - 91%; range for individual infant: 75 - 100%). Only the data from the first experimenter were used in the final analyses.

Adults were tested using the same display. However, adults, unlike infants, provided an individual threshold for both first- and second-order stimuli. 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, participants 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 within ±0.1 log units. 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- (50%) or contrast-modulation (100%), 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 up to three blocks of four test trials, again at maximum depth modulation. To be included in the study, participants had to respond correctly on all four trials in a test block. Participants received verbal feedback for this phase. All participants met this criterion in the first test block.

After the criterion phase, participants completed the initial phases of 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.

Data Analysis

For each infant and each modulation tested we measured the number of trials during which the experimenter correctly guessed the side of the drifting grating based on the infant's responses. This measurement was expressed as the experimenter's percent correct responses. The percent correct responses were averaged across subjects to give a group psychometric function that related accuracy to the luminance- and contrast-modulations tested. This resulted in four mean accuracy scores per test group that spanned a range of luminance- or contrast-modulations (see Table 1 for ranges tested). We performed one sample t-tests to determine if performance differed from chance (50%) at each modulation depth. For each group of infants, four 1-tailed t-tests were performed for each type of motion and alpha was set to 0.0125 for each test to maintain a family-wise Type I error rate of 0.05. We estimated group thresholds by determining the lowest luminance- and contrast-modulations that resulted in above chance experimenter accuracy. Estimated thresholds were compared to adults' mean thresholds to determine how many times worse infants were compared to adults. This ratio allowed us to compare development for first- versus second-order stimuli.

Although others have used more stringent criteria to determine infants' thresholds for sensitivity to moving stimuli, (e.g., Aslin & Shea, 1990, used a criterion of 75%) or have used the same threshold criterion for infants and adults, (e.g., Thibault et al., 2007), we chose the current approach because any result significantly above chance is a clear indication that the infant 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, Kuefner, Westerlund, & Nelson, 2006), texture segmentation (e.g., Rieth & Siretenau, 1994ab), and motion detection (Braddick et al., 1996) and has been used to measure grating acuity in infants (Teller, 1979) and animals (Wilkinson, 1995). A more strict 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 was 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 at each age are more or less mature for first-order versus second-order stimuli and whether sensitivity for the two stimulus types changes similarly between 3 and 6 months of age. 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.

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 (*p*s < .005), but did not differ from chance when luminance-modulation was 0.7 log units (5%) (*p* = .048, alpha = .0125). For one group of 6-month-olds tested with luminance-modulations ranging from 0.5 - 1.4 log units (3 - 24%) and another group of 6-month-olds tested with luminance-modulations ranging from 0.1 - 1 log units (1.25 - 10%) the experimenter's accuracy was significantly above chance when the luminance-modulation was 0.7 log units (5%) or higher (*p*s < .01). When luminance-modulation was 0.5 log units (3%) the experimenter's accuracy was marginally, but not significantly, above chance (*p* = .014, alpha = 0.0125). Based on these results, we estimate first-order thresholds to be between 0.7 and 1 log unit at 3 months of age, and between 0.5 and 0.7 log units at 6 months of age.

For second-order gratings, the experimenter's accuracy was above chance for 3-month-olds' 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 or lower (*p*s > .08). The experimenter's accuracy for one group of 6-month-olds tested with contrast-modulations ranging from 1.85 - 2 log units (70 - 100%) was above chance for all modulations tested (*p*s < .005). However the experimenter's accuracy for the other group of 6-month-olds tested with contrast-modulations ranging from 1.7 - 1.9 log units (50 - 80%) did not differ from chance for any modulation tested (*p*s > .027). Thus we estimate that thresholds for second-order gratings are between 1.95 and 2 log units at 3-months of age, and around 1.85 - 1.9 log units at 6 months of age.

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; a direct comparison of first- and second-order thresholds is not meaningful.

Discussion

Similar to many previous studies (e.g., Aslin & Shea 1990; Volkmann & Dobson, 1976), we found that infants discriminated a moving grating from a stationary grating of the same spatial frequency and orientation. Unlike previous studies, which used a uniform noise field as the control stimulus, the visual behaviour that infants showed in Experiment 1 could not have been based on form (that is, a preference for stripes over noise). In the current experiment, both choices contained stripes, but only one choice was moving. Therefore, infants' discrimination must have been based on sensitivity to motion and/or flicker. Experiment 1 also provides a quantification of infants' sensitivity to first- and second-order drifting gratings because we measured infants' sensitivity to first-and second-order stimuli over a range of modulation values. That quantification showed that both 3- and 6-month-olds' sensitivity to second-order motion was more adult-like than their sensitivity to first-order motion.

Between 3 and 6 months of age, infants' sensitivity to drifting first-order gratings doubles: it changes from about 16 - 32 times to 10 - 16 times worse than adults' mean threshold at 3 and 6 months of age, respectively. Sensitivity to second-order drifting gratings also improves, but less dramatically: it changes from about 2.8 - 3.2 times to 2.2 - 2.5 times worse than adults' mean threshold at 3 and 6 months of age, respectively.

Adults' mean first-order thresholds were -0.5 log units (0.3%), while their mean second-order thresholds were 1.5 log units (32%). Although the relative difference between first- and second-order thresholds is much larger than reported by some (Ledgeway & Smith 1994b; Smith, Hess, & Baker, 1994), these values are very similar to values reported by Ledgeway and Hutchinson (2005). Specifically, Ledgeway and Hutchinson conducted a systematic study of the spatial and temporal sensitivity functions for first- and second-order motion. For conditions tested with static noise, and temporal frequencies of 2 and 4 Hz (temporal frequency in the current study was 3 Hz), individual thresholds were about 0.2 - 0.3% modulation for first-order motion and 10 - 25% for contrast-modulated second-order motion. Second-order thresholds were generally much higher for the 4 Hz condition than the 2 Hz condition, and showed greater individual differences than first-order thresholds. The same pattern of results was found for luminance and contrast modulations of dynamic noise, although thresholds were higher than with static noise (Ledgeway & Hutchinson, 2005; Hutchinson & Ledgeway, 2006). The values reported by Ledgeway and Hutchinson for the static noise conditions are very similar to the values that we found in the present study, especially since the present study tested naïve subjects with a threshold criterion of 82% whereas Ledgeway and Hutchinson tested experienced psychophysical observers with a threshold criterion of 79%.

Given the current results, it is difficult to predict if adult-like sensitivity is reached for one stimulus type before the other. If infants' sensitivity to first- and second-order stimuli develops along a similar time line as monkeys', we would expect second-order thresholds to reach adult-like values before first-order thresholds. 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 reached adult-like levels until the monkeys were 40 weeks of age (Kiorpes, Gavlin, & El-Shamayleh, 2006).

Results from studies of sensitivity to direction of motion also support the idea that sensitivity to second-order motion becomes adult-like before sensitivity to first-order motion. A reanalysis of the data reported by Ellemberg, Lewis, and colleagues (2003) was conducted to compare mean thresholds of children and adults rather than immaturity scores as calulated by Ellemberg and colleagues. This reanalysis indicates that 5-year-olds' sensitivity to second-order motion was more adult-like than their sensitivity to first-order motion, at least when the velocity and temporal frequency were relatively low at 1.5 deg/sec and 1.5 Hz. Under that condition, 5-year-olds' sensitivity to second-order motion was only 1.4 times worse than adults', while their sensitivity to first-order motion was 2.4 times worse than adults. When the velocity and temporal frequency were higher at 6 deg/sec and 6 Hz, 5-year-olds were 2.6 times worse than adults for both first- and second-order motion.

In a similar study, Bertone, Hanck, Cornish, and Faubert (2008) found that children reached adult-like thresholds for second-order before first-order motion. However, unlike us, they reported that 5- to 6-year-olds were more immature for second-order than first-order motion. Bertone et al. calculated how many times worse children's thresholds were compared to adults by *dividing* logged thresholds. Log scores cannot be divided meaningfully. A log score is an exponent with a base of 10. For example, log units 3 and 2.5 represent 10^3 and $10^{2.5}$,respectivly. Thus, if 3 and 2.5 are divided, the result is 1.2; however $10^3/10^{2.5} = 3.16$. The ratios of log scores can be correctly calculated by either by *dividing* unlogged thresholds to get a ratio of 'times worse' than adults (given our previous example: 1000 / 316 = 3.16 x worse), or by *subtracting* the logged thresholds to get the number of log units worse than adults (3 - 2.5 = 0.5 log units worse; $10^{0.5} = 3.16$).

When we recalculated how many times worse children's thresholds were compared to adults' thresholds by dividing Bertone and colleagues' (2008) *unlogged*, rather than the logged data, we found that the 5- to 6-year-olds tested by Bertone et al. were in fact more immature for first-order than second-order motion, a pattern like that reported here for our preferential looking task. Specifically, their 5- to 6-year-olds were 3.3 times worse than adults for first-order motion, and only 2.6 times worse than adults for second-order motion. Thus, results from all age groups of children tested by Bertone et al. are in agreement with our finding that infants' immaturity is larger for first-order than second-order drifting gratings.

Finally, data from Thibault and colleagues' (2007) study of sensitivity to first- and second-order drifting gratings also suggest that children's thresholds may be more adult-like for second- than first-order stimuli. Although they reported that thresholds for clinical controls matured at about the same rate for first- and second-order stimuli, it is apparent from their data that individual thresholds for children in the extra-clinical group (typically developing controls) continued to improved after 30 months of age for first-order but not second-order stimuli. For second-order stimuli, individual thresholds remain relatively constant after about 30 months of age. This suggests that sensitivity to second-order information asymptotes before sensitivity to first-order information.

Given the predominant filter-rectify-filter model of first- and second-order motion processing (Wilson, Ferrera, & Yo, 1992), it is paradoxical that infants' sensitivity to first-order information is worse that than their sensitivity to second-order information. The second stage of Wilson's filter-rectify-filter model (where second-order motion is extracted) is dependent upon output of the first stage of the model (where first-order motion is extracted), so it might be expected that adult-like first-order vision would be required to reach adult-like levels of second-order vision. One explanation of why this may not be necessary lies in the fact that adults are much less sensitive to second-order motion than first-order motion. This idea can be difficult to evaluate: the thresholds cannot be compared directly because they are measured in different units. However, there is evidence that second-order mechanisms are less directionally selective than first-order motion mechanisms (Ledgeway & Hess, 2002), and that reaction times to the onset of motion are slower for second-order than first-order stimuli (Ellemberg, Lavoie et al., 2003). Furthermore, human observers are less efficient at detecting contrast-modulations than luminance-modulations compared to an ideal observer (Manahilov, Simpson, & Calvert, 2005). If second-order mechanisms are less efficient or less sensitive than first-order mechanisms, then adult-like sensitivity to first-order motion may not be required to reach adult-like sensitivity to second-order motion. Thus, less neural development may be required to reach adult-like levels of second-order processing than first-order processing (Bertone et al., 2008).

There was one anomaly in the infants' results: the experimenter's accuracy for 6-month-olds tested on second-order stimuli with contrast-modulations values ranging from 1.85 - 2 log units were above chance for all modulations tested, but the experimenter's accuracy for a separate group tested with contrast values ranging from 1.7 - 1.9 log units did not differ from chance for any modulation tested, even though two of the values contained in the first test range were the same as two values contained in the second test range (1.85 and 1.9 log units). We do not believe that the difference was caused by a problem in the testing method because there were no anomalies in results for the first-order condition. The difference between groups may reflect the variability of infants' responding and/or individual differences in the rate of visual development.

An additional possibility is that the pattern of results for the two groups of 6-month-olds depends on context, specifically whether or not the range of the values tested includes ones well above the infants' group threshold. The contrast modulations of 1.85 and 1.9 log units (70 - 80%) were intermixed with very low modulations in one group, and very high modulations in the other group. The experimenter's accuracy for stimulus modulations of 1.85 and 1.9 were significantly above chance when these values were at the lower end of the range of contrast-modulations tested, but did not differ from chance when they were the highest two modulations tested. We suggest that this pattern of findings arose because contrast-modulations of 1.85 and 1.9 (70 & 80%) were at or near 6-month-olds' threshold. When these modulations were at the lower end of the test range, the higher modulations may have been readily visible and primed the infant to expect, and look for, a grating in each display, and thus performance was above chance for every test value. However, when modulations of 1.85 and 1.9 log units (70 - 80%) were the most visible ones in the display, the infant may not have readily perceived any cues to flicker/motion on the display and lost interest more quickly than when the stimuli were at higher modulations.

In sum, we used forced-choice preferential looking to measure the minimum luminance- and contrast-modulation that allowed infants to provide evidence of discriminating drifting from stationary gratings. Based on our results, we estimate infants' first-order thresholds to be between 0.7 and 1.0 log units (5 and 10%) at 3 months and 0.5 and 0.7 log units (3 and 5%) at 6 months. In comparison to adults' mean threshold of -0.5 log units (0.32%), these estimates are 16 - 32 times worse than those of adults for 3-month-olds, but only 10 - 16 times worse than those of adults for 6-month-olds. For second-order gratings, we estimate infants' thresholds to be between 1.95 and 2 log units (90 - 100%) at 3 months and 1.85 - 1.90 log units (70 - 80%) by 6 months. In comparison to adults' mean threshold of 1.5 log units (31.4%), these estimates are only about 2.8 - 3.2 times and 2.2 - 2.5 times worse than adults, respectively. Our finding of different rates of development for first-order and second-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 (e.g., Ellemberg, Lavoie et al., 2003; Ledgeway & Smith, 1994a; Vaina & Cowey, 1996).

2.5 Experiment 2: Habituation

One limitation of the current forced-choice preferential looking method is that infants may have discriminated the drifting from the stationary stimulus either because they perceived the actual drifting motion of the grating or because they perceived only the flicker. To determine if infants are sensitive to motion, the paradigm must be capable of demonstrating that infants discriminate between stimuli that have different directions of motion.

In Experiment 2, we tested infants' sensitivity to the direction of first- and second-order motion using a habituation design. We habituated 3-months-olds to one direction of motion (left or right) and tested whether they recovered attention to the opposite direction of motion. We tested only 3-month-olds in this experiment because, in the past, we have found that 6-month-olds do not give reliable results in a habituation design using simple 2-dimensional stimuli, perhaps because of their faster saccades and short periods of sustained interest in such simple stimuli.

Similar to previous studies (Wattam-Bell,1996bc), 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 (first-order orientation) shown previously to be discriminable even by 1-month-olds who were tested with a similar habituation paradigm (Maurer & Martello, 1980).

Methods

Participants

The participants were 40 3-month-olds (3.00 - 3.99 months). 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).

Apparatus & 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 displayable luminance-modulation (50%) or contrast-modulation (100%).

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 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 a 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. 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 habituation and test phase. 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. The order of the first test stimulus (habituated first or novel first) was counterbalanced across infants. 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 90 deg differences in the orientation of sequentially presented luminance-modulated gratings (Maurer & 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 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 subjects 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) 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 various stimuli, ranging in interest from faces to stationary gratings. Each stimulus remained on the screen for 10 seconds. The experimenters made independent judgements of the infants' on and off looks. These looking times were significantly and positively correlated, $r \geq .95$, for each infant.

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 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.

Results

Infants required 6 - 70 trials to become habituated to the moving stimuli (overall mean = 21 trials; first-order stimuli: mean = 20 trails, range = 6 - 58 trials; second-order stimuli: mean = 21 trials, range = 6 - 70 trails). 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 versus the novel direction of motion, $t(17) = 0.14$, $p = .444$, Cohen's d = 0.05. However, there was a significant difference between the familiar direction of motion versus 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 versus the novel direction of motion, $t(17) = 0.87$, $p = .199$, Cohen's d = 0.21 nor the familiar direction of motion versus the novel orientation, $t(17) = 1.6$, $p = .064$, 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.

Discussion

Using a habituation technique, we found that 3-month-old infants recovered attention to a change in orientation of first-order gratings but not to a change in orientation in second-order gratings. This finding is consistent with earlier reports that demonstrated that sensitivity to first-order pattern emerges within the first 3 months of life (Atkinson & Braddick, 1992; Rieth & Sireteanu, 1994b; Sireteanu & Rieth, 1992) while sensitivity to second-order pattern emerges at 14 - 18 weeks of age (Atkinson & Braddick, 1992; Rieth & Sireteanu, 1994b) or 9 - 12 months of age (Sireteanu & Rieth, 1992; Sireteanu & Rieth, 1994a). 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.

It is interesting that infants could discriminate the moving grating from the stationary grating in Experiment 1, but in Experiment 2, show no evidence that they dishabituate to a change in orientation for second-order stimuli. There are two explanations for result. First, in Experiment 1, the forced-preferential looking results may have been based on the perception of flicker or motion; perception of the pattern of the stationary control stimulus is not necessary for this discrimination. This explanation is consistent with evidence suggesting that sensitivity to second-order structure emerges as early as 14 - 18 weeks of age (Atkinson & Braddick, 1992; Rieth & Sireteanu, 1994b) while sensitivity to first-order structure emerges earlier (Atkinson & Braddick, 1992; Rieth & Sireteanu, 1994b).

A second explanation as to why infants did not show evidence of sensitivity to second-order structure in Experiment 2 may be that, although they can detect the second-order pattern, they are unable to discriminate the two orientations of the second-order gratings. Even adults have shown better performance 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, Dupont, Vogels, Bormans, & Mortelmans, 1997). Furthermore, adults require less contrast to detect than to discriminate complex gratings when the ratio of the grating spatial frequency is small (less than 3 cyc/deg) (Furchner, Thomas, & Campbell, 1977). The same pattern of results holds true for more complex visual tasks. Specifically, d' measures for object detection are better than object discrimination in natural scenes (Rohaly, Ahumada, & Watson, 1997), while contrast thresholds are better for letter detection than letter identification (Pelli, Burns, Farell, & Moore-Page, 2006).

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. Therefore, we conclude that at 3 months of age, infants do not demonstrate sensitivity to the direction of first- or second-order drifting gratings under the conditions tested in this study. Similarly, in the only other published studies using habituation to test infants' sensitivity to stimuli that moved in a uniform direction of motion, Wattam-Bell found that 6- to 8-week-olds (1996b) and 9- to 12-week-olds (1996c) failed to recover attention to a change in direction of motion. These findings suggest that 3-month-olds in Experiment 1 may have discriminated the static and moving stimuli on the basis of flicker rather than motion *per se.* This is a very important distinction because it suggests that our thresholds measured sensitivity to first- and second-order flicker, not sensitivity to second-order motion. Thus, we cannot generalize the results in Experiment 1 to the development of first- and second-order motion *per se.*

2.6 General Discussion

Using a forced-choice preferential looking procedure in Experiment 1, we found that sensitivity to both first- and second-order drifting gratings improves between 3 and 6 months of age. Thresholds improved more rapidly for first- than second-order motion. However, at both ages, infants' sensitivity to the drifting grating was still more adult-like for second-order than first-order stimuli. Because stimulus discrimination in Experiment 1 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 direction of first- or second-order motion. While these results do not give conclusive evidence that 3-month-olds are not sensitive to direction of motion, they raise the possibility 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 (e.g., Regal, 1981). Although evidence from VEP studies suggests that cortical sensitivity to direction of motion emerges at about 2 - 3 months of age (Braddick, Birtles, Wattam-Bell, & Atkinson, 2005; Wattam-Bell, 1991), older infants have not been tested with behavioural methods distinguishing flicker from uniform motion, in part because the habitation technique is no longer effective with simple stimuli.

Studies of the perception of motion in infants and adults have used shearing, referential, and uniform motion. Shearing motion can be seen when a stimulus has regions or segments that move in opposite directions to each other, such that the two regions appear to shear against each other. Referential motion generally contains one area of the stimulus that is moving, and other flanking segments that are stationary, so that the moving regions of the stimulus can be seen to move in relation or in reference to the stationary regions. Uniform motion occurs when the whole stimulus moves or translates in one uniform direction, without reference to any stationary or oppositely moving regions of the stimulus.

Previous results do indicate that infants 3 months of age and younger are sensitive to direction, but only when shearing motion is used. Recall, Wattam-Bell (1996b) found that infants as young as 6 - 8 weeks of age can discriminate a segregated form-from-motion stimulus from a patch of uniform motion. However, at the same age, and even at 9 - 12 weeks of age, infants showed 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 1996bc). 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 referential motion, where stationary segments flanked the moving centre strip. Taken together, these findings suggest that sensitivity to shearing motion develops prior to sensitivity to referential motion, which in turn develops before sensitivity to uniform motion. 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 directional sensitivity without such a reference. Another possibility may be that there were differences in temporal dynamics between the shearing or referential stimuli and the uniform stimulus that can account for these results. In the present study, the paired presentation of drifting versus stationary gratings in Experiment 1 did not produce referential motion because the stationary grating was separated by a 5 deg gap from the moving grating. Rather, it is likely that infants' thresholds in Experiment 1 reflect mechanisms sensitive to flicker rather than motion.

The idea that sensitivity to shearing motion develops before sensitivity to uniform motion contradicts the conclusions in a review of the literature by Banton and Bertenthal (1997): based on evidence from optokinetic nystagmus (OKN), they concluded that sensitivity to uniform motion is the first type of motion sensitivity to emerge in infancy and that it develops before sensitivity to shearing motion. OKN is a reflexive series of eye movements in response to motion, in which the eyes follow one part of a repetitive pattern and then saccade back to follow another part of the pattern. These reflexive eye movements are likely controlled by sub-cortical mechanisms during early infancy (Atkinson & Braddick, 1981; Braddick et al., 1992; van Hof-van Duin & Mohn, 1983). In contrast, behavioural methods, like preferential looking, likely reflect cortical motion mechanisms (Atkinson & Braddick, 1981).

Consistent with the notion that OKN reflects sub-cortical motion mechanisms, while behavioural measures reflect cortical motion mechanisms, Mason, Braddick, and Wattam-Bell (2003) demonstrated that measures of sensitivity to motion differed when the measures were based on OKN versus preferential looking. Specifically, they found that OKN measures of motion coherence thresholds were stable between 6 and 27 weeks of age, and at all ages were better than those obtained from preferential looking. Preferential looking measures resulted in motion coherence thresholds that improved over the same age range. Thus, if OKN measures of sensitivity to motion are discounted, Banton and

Bertenthal's (1997) conclusion that sensitivity to uniform motion emerges before sensitivity to shearing motion no longer holds true. Rather, evidence suggests that sensitivity to shearing motion emerges prior to sensitivity to uniform motion. Consistent with this interpretation, OKN is present at birth even in pre-term babies (reviewed by van Hof-van Duin & Mohn, 1984), but sensitivity to uniform motion as measured by cortical VEPs is not evident until about 8-12 weeks of age (Braddick et al., 2005; Wattam-Bell, 1991).

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 (1996abc) 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 5.6Hz; 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.

At the very least, our results show that, at 3 months of age, infants can discriminate first- and second-order drifting gratings from stationary gratings and this sensitivity improves between 3 and 6 months of age. Furthermore, development for first- and second-order drifting gratings occurs at different rates, consistent with the hypothesis that different mechanisms mediate sensitivity to these types of motion. At 3 months of age, the ability to discriminate moving from stationary stimuli appears to depend on infants' sensitivity to flicker rather than on their sensitivity to motion, for both first- and second-order stimuli, at least for stimuli moving at a relatively slow speed.

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Table 2.1

Luminance- and contrast-modulations tested for each group of 3- and 6-month-olds (log units of percent modulation).

3-month-olds	**6-month-olds (Group 1)**	**6-month-olds (Group 2)**
Luminance Modulations		
0.7	0.5	0.1
1	0.8	0.4
1.2	1.1	0.7
1.6	1.4	1
Contrast Modulations		
1.85	1.85	1.7
1.9	1.9	1.78
1.95	1.95	1.85
2	2	1.9

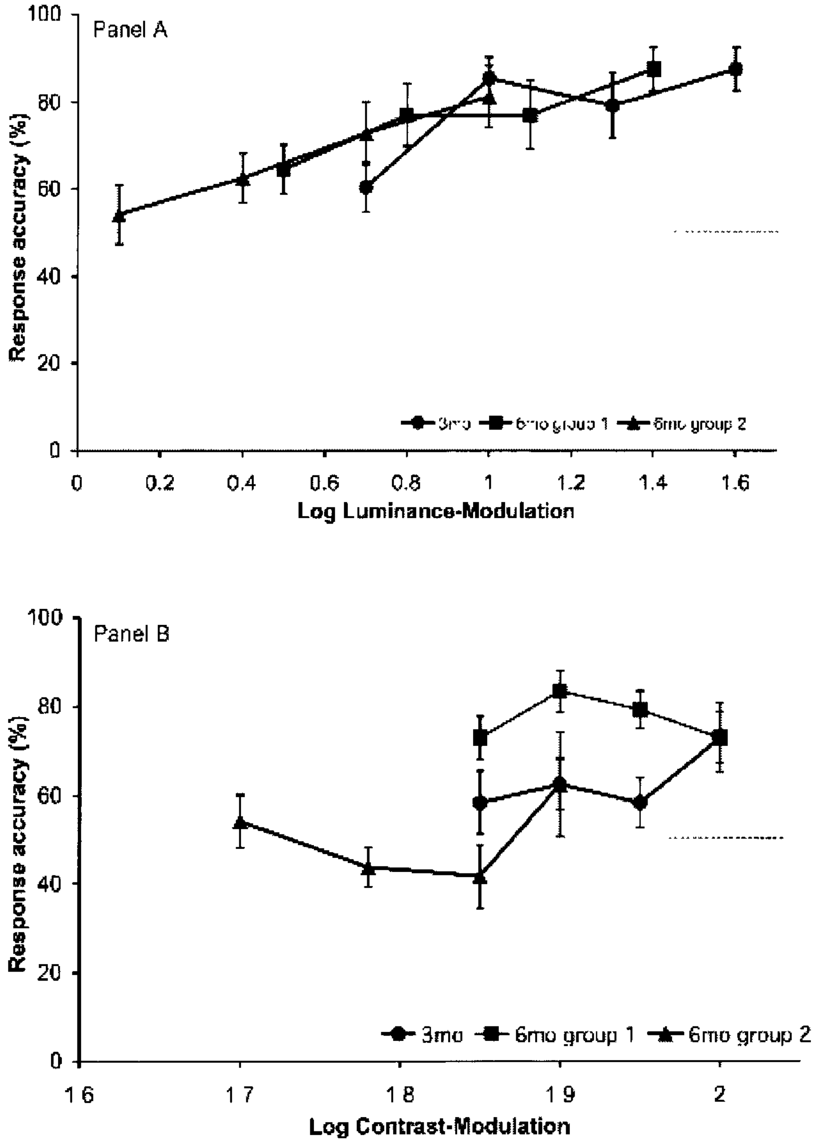

Figure 2.1. Experimenter's accuracy (mean percent of correct responses) (± 1 S.E.) for moving versus stationary first-order gratings (Panel A) and second-order gratings (Panel B). The x-axis denotes log of percent depth modulation tested. Accuracy was measured at 3 months (circles) and at 6 months of age (Group 1: squares, Group 2: triangles). Adults tested with the same stimuli had a mean log threshold of -0.5 log units for first-order stimuli and 1.48 log units for second-order

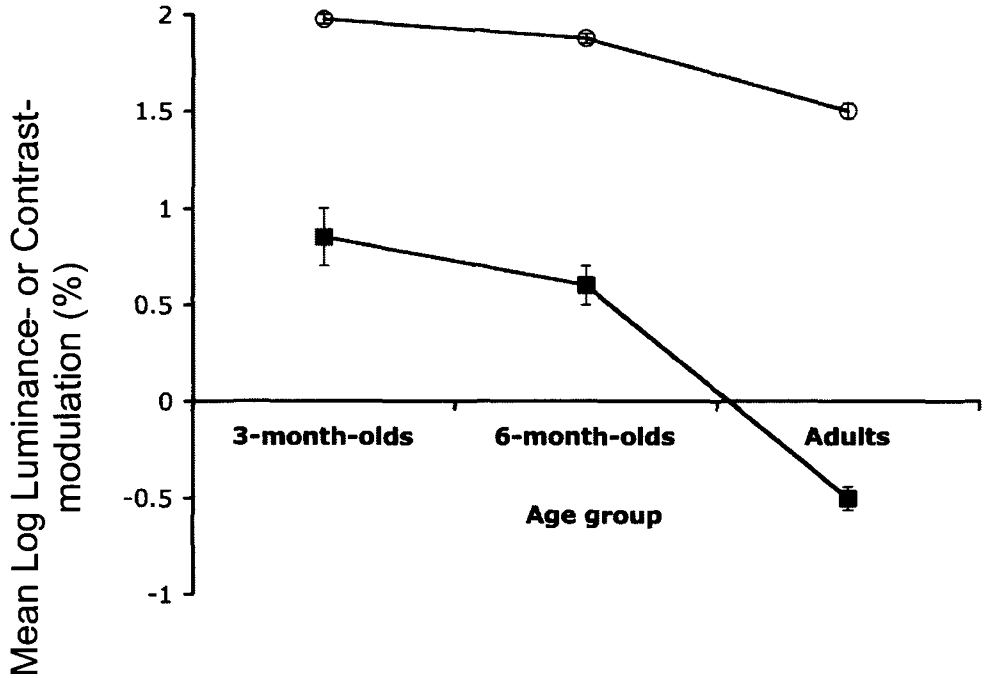

Figure 2.2. Infants' estimated log thresholds and adults' mean log thresholds for first-order (squares) and second-order (circles) stimuli. Error bars denote the estimated range of the threshold for infants and standard error of the mean for adults. In some cases error bars are smaller than the symbol marking

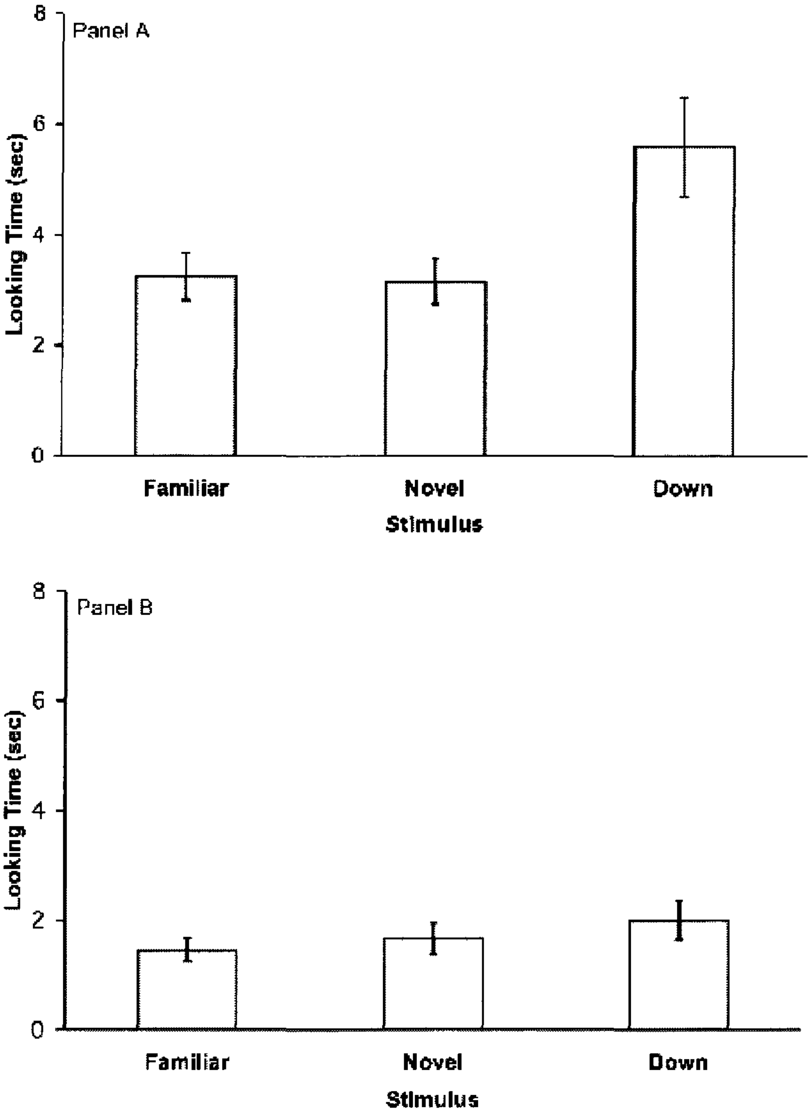

Figure 2.3. Three-month-olds' looking times (± 1 S.E.) during the test phase after habituation to vertical gratings moving leftward or rightward. Results are for vertical gratings moving in the habituated direction, vertical gratings moving in a novel opposite direction, and horizontal gratings moving downward (both a novel orientation and direction of motion). 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.

CHAPTER 3

Sensitivity to First- and Second-order Motion and Form in Children and Adults

V. L. Armstrong, T. L. Lewis, & D. Maurer

3.1 Preamble

In Chapter 3, I compared contrast thresholds for first- versus second-order motion and form in children aged 3, 5, 7, and 10 years and adults. I also varied the grating velocity, temporal frequency, and spatial frequency to determine how changes in these factors affect sensitivity to motion. Here, I establish a timeline of development of sensitivity to first- and second-order motion and, like Bertone et al. (2008) show that sensitivity to second-order motion reaches adult-like levels before sensitivity to first-order motion. This pattern of results is consistent across ages tested in both Chapters 2 and 3. Moreover, changes in temporal and spatial frequency had different effects on thresholds for first- versus second-order motion and the relationship between form and motion thresholds differed for first- versus second-order stimuli. These differences indicate that first- and second-order stimuli are processed, at least in part, by different mechanisms. This is the first study to measure sensitivity to direction of first- and second-order motion in 3-year-olds and the first to show that the pattern of more adult-like sensitivity to second-order than first-order motion is consistent between 3 and 10 years of age.

3.2 Abstract

We compared the sensitivity of adults and children aged 3 to 10 years for first- and second-order motion and form. For first-order stimuli, sensitivity was better for motion than form and motion thresholds varied with temporal frequency. For second-order stimuli, sensitivity was better for form than motion and motion thresholds varied with spatial frequency. Children's thresholds were adult-like before age 10 except for first-order motion. Thresholds became adult-like earlier for form than for motion and for second-order than for first-order stimuli. The results suggest that the mechanisms underlying the processing of first- and second-order stimuli develop at different rates.

3.3. Introduction

Cues to motion are provided by any physical parameter for which spatial location varies with time. Changes in boundaries that are defined by luminance are a first-order cue to motion. Changes in boundaries that are defined by parameters other than luminance, such as contrast or texture, are a second-order cue to motion.

A large body of evidence indicates that the mechanisms that process first- and second-order cues to motion are, in part, separate. For example, adults do not integrate alternating frames containing first- and second-order cues to local motion into an unambiguous percept of motion (Ledgeway & Smith, 1994), and their sensitivity to first- or second-order local motion is not affected by adaptation to motion of the other type (Nishida, Ledgeway, & Edwards, 1997). Further, both the latency of the visual evoked potential 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). In addition, a functional magnetic resonance imaging study demonstrated a clear segregation between the neural areas that are active during the processing of first- and second-order motion: Dumoulin, Baker, Hess, and Evans (2003) found that first-order motion most strongly activated early visual areas (V1) whereas second-order motion most strongly activated higher visual areas near V5.

To date only three studies have examined sensitivity to both first- and second-order local motion in typically-developing children and adults. In the first, Ellemberg, Lewis, et al. (2003) measured sensitivity to the direction of first- and second-order local motion in adults and 5-year-olds by measuring contrast thresholds for leftward and rightward drifting gratings. They reported that 5-year-olds' thresholds were worse than adults' regardless of motion type, but the difference between 5-year-olds' and adults' thresholds was greater for second-order motion than for first-order motion, a pattern suggesting that sensitivity to second-order motion may be slower to mature.

In a study using similar methods, Bertone, Hanck, Cornish, and Faubert (2008) measured sensitivity to the direction of first- and second-order local motion in children ranging from 5 to 10 years of age. In agreement with Ellemberg, Lewis, et al. (2003), Bertone et al. reported that at 5-6 years of age, children were more immature for second-order than first-order motion. However, they also reported that sensitivity to second-order motion became adult-like by 7-8 years age, an age at which sensitivity to first-order motion was still not mature.

In the third study, Thibault, Brosseau-Lachaine, Faubert, and Vital-Durand (2007) measured sensitivity to first- and second-order drifting gratings in children ranging from less than 1 year to almost 7 years of age using a forced-choice preferential looking method. Unlike the other two studies, Thibault et al. reported that thresholds improved at an equal rate for first- and second-order motion. However, because the stimuli were a drifting grating versus grey-scale noise, the looking preferences measured by Thibault et al. may have been based on the detection of the pattern or flicker rather than the movement of the drifting grating. Nevertheless, together, the results from the three studies describing the trajectory of development for sensitivity to first-order versus second-order motion raise the possibility that the relative rates of development differ during different periods of development.

In the current study, our first goal was to measure children's sensitivity to direction of first-order and second-order motion across a wide age range. To do so, we measured sensitivity to the direction of first- and second-order motion in children at ages 3, 5, 7, and 10 years, and in adults. We compared the relationship of the children's thresholds to those of adults for each type of motion, rather than directly comparing the thresholds for first- and second-order motion.

Also of interest is how the parameters of temporal frequency, spatial frequency, and velocity affect sensitivity to motion in children compared to adults. These parameters affect sensitivity to motion in adults. For example, the minimum stimulus duration required to discriminate the direction of both first- and second-order motion increases as temporal frequency increases (Ledgeway & Hess, 2002). Furthermore, temporal and spatial sensitivity functions differ for first and second-order stimuli. They are bandpass for first-order motion and lowpass for second-order motion (Hutchinson & Ledgeway, 2006).

In a study of the effect of velocity and temporal frequency on children's sensitivity to the direction of first- and second-order local motion, Ellemberg, Lewis, et al. (2003) reported that the difference between thresholds in 5-year-olds and adults varied with temporal frequency and velocity, but only for second-order stimuli. Because both temporal frequency and velocity varied together, it was not possible to determine which parameter or parameters are responsible for this difference. Distinguishing the effects of temporal frequency, spatial frequency, and velocity at each age for each type of motion was our second goal. To do so, we tested three conditions for each motion type, using key comparisons on each dimension so that each parameter was equated across two of the three conditions (see Table 1). The particular values were similar to those in Ellemberg, Lewis, et al., who used a spatial frequency of 1 cyc/deg, temporal frequencies of 1.5 and 6 Hz, and velocities of 1.5 and 6 deg/sec. For each set of parameters, we varied depth modulation across trials to determine the minimum luminance (first-order) or contrast (second-order) for which observers could correctly identify the direction of local motion.

Our final goal was to ensure that children's sensitivity to direction of motion was not limited by poor sensitivity to the pattern of the moving stimulus. If children are unable to see the form of the stimulus, then they may have reduced sensitivity to its motion, even if the motion mechanisms per se, are adult-like. We measured sensitivity to first- and second-order form in children using a horizontal/vertical discrimination task. On each trial, a stationary grating was presented in a vertical or a horizontal orientation. The task was to indicate the orientation of the grating (horizontal or vertical). Depth modulation was varied over trials to determine the minimum amplitude for which observers could identify correctly the orientation of the grating. We then compared the pattern of thresholds across stimulus parameters and age for the form task to those for the motion task.

For 5-year-olds, 7-year-olds, 10-year-olds, and adults, participants were asked to indicate the direction of motion (left/right) or orientation of the grating (horizontal/vertical) and received auditory and visual feedback about the accuracy of their responses. Depth modulation varied over trials to determine an individual threshold for each condition for each participant. To extend the developmental trajectory to a younger age, we added animals as reinforces for the 3-year-olds and shortened the procedure. Because, as in all developmental studies, there is no way to assure that the procedure is equally sensitive at all ages, our conclusions are based on comparisons of the pattern of results across age and among conditions.

3.4 Methods

Participants

A total of 280 participants were included in this study, 56 in each of the following five age groups: 3-year-olds (range = 3.5 - 3.75 yrs), 5-year-olds (5.0 yrs ±3 mo), 7-year-olds (7.0 yrs ±3 mo), 10-year-olds (10.0 yrs ±3 mo), and adults (median age = 18 yrs, range 18 - 21 yrs). Adults were recruited from a pool of undergraduate students registered in Introductory Psychology at McMaster University and received research participation credits in their class grade. Children were recruited using contact information provided by parents who expressed interest in participating in our studies at the time of the child's birth. Most children had participated in earlier studies at McMaster University. All participants in the final sample had normal visual histories according to self or parental report and all wore optical correction, if prescribed. An additional 30 participants were excluded from the final sample because they were uncooperative (16 3-year-olds, seven 5-year-olds, and one 7-year-old), because they failed a criterion designed to test understanding of the task (six 3-year-olds), or because the parent looked at the stimuli and influenced the child's responses (four 3-year-olds; see Procedure).

Apparatus and Stimuli

The stimuli were generated by an Apple Macintosh G4 computer by means of VPixx software^{TM} and were displayed on a 53.3 cm Sony Trinitron Monitor. The monitor had a frame rate of 75 Hz and pixel resolution of 1024 x 768. The stimulus was a sinusoidal grating contained within a 15 x 15 deg square at a viewing distance of 50 cm (absolute size: 13.2 x 13.2 cm square). For motion tests, the grating was vertical and drifted to the left or to the right. For form tests, the grating remained stationary and was either horizontal or vertical.

Grating velocities and spatial frequencies are listed in Table 1. Because temporal frequency is the product of spatial frequency and velocity (TF = SF x V), changing one value, while holding another constant, results in a change of the third parameter. However, with three conditions, each parameter can be equated over two of the conditions. As shown in Table 1, Conditions 2 and 3 had equal temporal frequencies, Conditions 1 and 2 had equal spatial frequencies, and Conditions 1 and 3 had equal velocities. This selection of values allowed us to evaluate the separate contributions of temporal frequency, spatial frequency, and velocity.

The gratings were luminance-modulated (first-order) or contrast-modulated (second-order) and were identical to those described by Ellemberg, Lavoie et al. (2003) and Ellemberg, Lewis et al., (2003). The carrier was static two-dimensional unmodulated noise like that described by Smith and Ledgeway (1997). Each noise element subtended 2 x 2 arc min, and was assigned independently with a probably of 0.5 to be either 'light' or 'dark'. 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 (depth modulation or Michelson contrast) was defined as:

$$\text{Depth modulation} = (L_{max}-L_{min})/L_{max}+L_{min}),$$

where L_{max} and L_{min} are defined as the maximum and minimum mean local luminance contrasts in the stimulus.

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 (depth modulation) was defined as:

$$\text{Depth modulation} = (C_{max}-C_{min})/(C_{max}+C_{min}),$$

where C_{max} and C_{min} are defined as the maximum and minimum mean local contrasts in the stimulus. Mean luminance at maximum contrast was 10 cd/m^2 for both luminance- and contrast-modulated stimuli. For the luminance-modulated stimulus, the light region had a maximum luminance of 13 cd/m^2, while the dark region had a minimum luminance of 7 cd/m^2, resulting in a maximum Michelson contrast of 30%. 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 background was grey with a mean luminance of 10 cd/m^2.

Procedure

The procedures were explained and informed consent was obtained from adults and from parents of the children. Assent was obtained from the children age 7 and older. The experimental protocol was approved by the McMaster Research Ethics Board.

Each participant was seated 50 cm away from the computer monitor. All but the 3-year-olds sat with their chin positioned on a chin rest, which ensured that a constant testing distance would be maintained. Parents who remained in the testing room were asked to sit out of their child's sight and to remain silent throughout testing. Each participant provided two thresholds, one for first-order and one for second-order stimuli tested in one of the four conditions (the form condition or the motion condition with one of the 3 combinations of spatial frequency, temporal frequency, and velocity—see Table 1). One quarter of the participants at each age completed each of the four conditions.

The 3-year-olds sat in a chair by themselves or, if necessary, on their parent's lap during testing. A chin rest was not used with this age group because it made testing more difficult; however, the experimenter monitored the child's viewing distance throughout the experiment and the child was repositioned as required to keep the distance near 50 cm. As for the older children, parents were asked not to aid in their child's decisions in any way and those holding a 3-year-old during the test were asked to look down at their child rather than at the monitor so that they would be blind to the specific stimulus shown on a trial. Four children were excluded from the final sample because their parents looked at the display and tried to help their child. We did not give the parents occluding glasses because they distracted the 3-year-olds.

Participants 5-years and older: For the direction discrimination task, participants were told that they would see one square containing stripes moving left or right and that the task would be to indicate the direction of movement. For the horizontal/vertical discrimination task, participants were told that they would see one square and that the stripes would be vertical/standing up or horizontal/lying sideways and that the task would be to indicate the orientation of the stripes. In all cases, participants could respond verbally or with hand gestures (e.g., pointing left or right, or holding a hand vertically or horizontally, as required by the task).

At the beginning of each trial, participants were asked to fixate on a 3 deg black dot that appeared in the centre of the screen. The black dot was then replaced by the stimulus. The experimenter, who could not see the display, watched the participant's eyes to ensure that they were directed toward the computer screen and entered responses on a computer keyboard.

Prior to testing, participants were presented with two demonstration trials with the gratings at maximum luminance-modulation (50%) or contrast-modulation (100%). The order of test type (first-order first or second-order first) was counterbalanced across participants. For each task, the demonstration consisted of one trial for each of the two alternative choices (left/right for motion tasks or horizontal/vertical for the form task). To verify that the participants understood the task, they were presented with a criterion phase consisting of up to three blocks of four test trials, again at maximum depth modulation. To be included in the study, participants had to respond correctly on all four trials in a test block. Participants received verbal feedback for this phase. All participants 5-years and older met this criterion, usually in the first test block.

Upon completion of the criterion phase, participants 5 years and older were given a practice staircase with feedback after each trial. The contrast of the grating(s) 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 within ±0.1 log units. Feedback consisted of a high-pitched tone paired with a happy face for a correct response and a low-pitched tone paired with a sad face for an incorrect response. The happy and sad faces appeared in a 15 x 15 deg square in the centre of the monitor and remained on the screen for 250 ms. Practice was terminated after the luminance- or contrast-modulation was reduced to the point where two incorrect responses occurred consecutively. Participants then completed the test phase with feedback. Thresholds were defined as the minimum luminance-modulation (first-order) or contrast-modulation (second-order) necessary to respond correctly 82% of the time. The order of first test type (first-order or second-order) was counterbalanced over participants. The entire testing session lasted 30-45 minutes.

Three-year-olds: For the motion tasks with 3-year-olds, black boxes were placed on the left and right sides of the computer monitor. When lit from within, a puppy and a monkey were visible in the left and right boxes, respectively. During the demonstration, participants were told that the stripes would go either toward the puppy (for leftward moving stripes) or the monkey (for rightward moving stripes). Each direction was displayed and the appropriate toy was illuminated. The child was then asked to complete the criterion phase to the same standard as the older participants. Three-year-olds responded by pointing to or verbally naming the animal that they thought would light up. The experimenter stood directly behind the computer monitor so that she could not see the stimuli (and thereby bias the child's response) but still had a full view of the child's eye gaze. As children of this age group almost always looked toward the animal they expected to light up, the direction of eye gaze was used as a check of verbal and pointing responses. Children of this age often looked toward one animal while saying or pointing to another. When eye gaze and other responses were not in agreement, the researcher confirmed the response by asking the child, "Which one do you mean, the puppy (pointing to puppy) or the monkey (pointing to monkey)?" This question always disambiguated the response. Gaze direction was used as the key response for a few shyer children who would not point or talk.

For the horizontal/vertical task, the child was given two cards with black stripes on a white background to aid responding. A transparent, coloured cartoon of a giraffe was superimposed on the card with vertical stripes. Likewise, a transparent, coloured cartoon of a long skinny dog (a 'wiener' dog) was superimposed on the horizontal stripes. These animals were chosen to give the cards a specific orientation and to match the orientation of the stripes that made up the stimulus: vertical stripes were 'giraffe stripes' and horizontal stripes were 'doggie stripes'. This allowed children to respond either by naming the stripes, pointing to the matching card, or even simply looking at the matching card.

Three-year-olds completed the demonstration and criterion phases, but not a practice phase. Pilot testing indicated that practice increased fatigue for children of this age group, thus lowering performance on test phases. The goal of testing was to optimize the performance from all participants, so that the best measures of sensitivity to motion/form could be obtained, regardless of age. Other than the differences described above in determining the participants' choice of alternatives and in the stimuli used for reinforcement, the test phase for 3-year-olds was identical to that for older subjects. A small number of 3-year-olds required two testing sessions, while all other participants completed testing in one session.

3.5 Results

Thresholds were multiplied by 100 and logged to be transformed into log percent luminance- or contrast-modulation. Outliers were replaced using a procedure outlined by Kirk (1999): data points that were ± 2.5 standard deviations from the cell mean were replaced with the cell mean. There were ten outliers: every age group had at least one outlying data point, and no cell had more than one outlier. Analyses were conducted separately for first- and second-order stimuli because their thresholds cannot be meaningfully compared directly. For each type of motion, we conducted a five (age) by three (condition) way ANOVA. For the comparison of thresholds for motion versus horizontal/vertical discrimination we conducted a 5 (age) by 2 (condition) way ANOVA separately for first-order and second-order stimuli, using the motion conditions with the same spatial frequency as the form condition. Post Hoc Analyses were conducted on the significant main effects. Partial eta squared (η_p^2) values were used for estimates of association strength between the independent and dependent variables. This measure is calculated as follows:

$$\eta_p^2 = SS_{effect} / (SS_{effect} + SS_{error})$$

and, unlike classic η^2 , it excludes variance attributable to other factors (Pierce, Block, & Aguinis, 2004). For differences analyzed with t-tests, effect size was estimated by calculating Cohen's d statistic.

First-order motion: A five (age) by three (condition) way ANOVA revealed significant main effects of age, $F(4,195) = 46.1$, $p < .001$, $\eta_p^2 = .49$, and of condition, $F(2, 195) = 105.7$, $p < .001$, $\eta_p^2 = .52$, but no significant age by condition interaction, $F(8,195) = 1.3$, $p = .24$, $\eta_p^2 = .05$

(see Figure 1).

A one-tailed Dunnett's test was used to examine the overall effect of age. Children's thresholds were significantly worse than adults' at every age tested (*p*s < .01; see Table 2 for full statistics). Although the age by condition interaction was not significant, it should be noted that the thresholds of 10-year-olds are closer to those of adults in some conditions than in others. For Condition 1, the difference was not significant, *t*(26) = 0.6, *p* =.6, Cohen's d = 0.2, while for Condition 2, there was a trend toward a significant difference, *t*(26) = 1.9, *p* = .07, Cohen's d = 0.72, and for Condition 3, the difference was significant, *t*(26) = 4.3, *p* < .001, Cohen's d = 1.56. These differences will be considered below in more detail. The main effect of condition was analyzed using Tukey's HSD. The results indicate that the threshold for Condition 1 was better than thresholds for Condition 2 and Condition 3, *t*(138) = 13.6, *p* <.001, Cohen's d = 1.7 and *t*(138) = 11.4, *p* <.001, Cohen's d = 1.3, respectively, while there was no significant difference between the thresholds for Conditions 2 and 3, *t*(138) = 2.2, *p* =.08, Cohen's d = 0.3. Conditions 2 and 3 had equal temporal frequencies of 1.5 Hz, while Condition 1 had a temporal frequency of 6 Hz.

Second-order motion: The five (age) by three (condition) way ANOVA revealed a significant main effects of age, *F*(4,195) = 47.4, *p* < .001, η_p^2= .49, and of condition *F*(2,195) = 26.1, *p* < .001, η_p^2 = .21, but no significant age x condition interaction, *F*(8, 195) = 1.4, *p* = .21, η_p^2= .05 (see Figure 2). A one-tailed Dunnett's post-hoc analysis revealed that 3- and 5-year-olds' thresholds were significantly higher (worse) than the adults' mean threshold (*p*s <.001) while 7- and 10-year-olds' thresholds were no different than the adults' mean threshold (*p*s =.47 and .93 respectively; see Table 2 for full statistics). Tukey's post-hoc analysis of the effect of condition revealed that thresholds for Conditions 1 and 2 were not different from each other, *t*(138) = 1.5, *p* = .3, Cohen's d = 0.2, but both were higher than the threshold for Condition 3, *t*(138) = 6.7, *p* <.001, Cohen's d = 0.8 and *t*(138)=5.3, *p* < .001, Cohen's d = 0.6, respectively for Conditions 1 vs. 3 and 2 vs. 3. Conditions 1 and 2 had equal spatial frequencies of 1 cyc/deg, while Condition 3 had a spatial frequency of 0.25 cyc/deg.

First-order form: The results for the Form Condition were compared to the results from the motion conditions with the same spatial frequency, namely, Motion Condition 1 and Motion Condition 2 in two separate five (age) by two (condition) way ANOVAs (see Figure 1). For Form versus Motion Condition 1, there were significant main effects of age and condition, *F*(4,130) = 35.4, *p* < .001, η_p^2 = .52 and *F*(1,130) = 837.5, *p* < .001, η_p^2= .87 for age and condition, respectively, but no significant interaction, *F*(1,130) = 0.8, *p* = .55, η_p^2 = .02 . A one-tailed Dunnett's test on the form thresholds revealed that mean thresholds for 3-, 5-, and 7-year-olds were significantly worse than the mean threshold for adults (*p*s <

.005) while the mean threshold for 10-year-olds was no different than the mean threshold for adults (see Table 2 for full statistics).

The main effect of condition indicates that thresholds for motion were better than thresholds for form. We found the same pattern of results for the Form Condition versus Motion Condition 2. There were significant main effects of age, $F(4,130) = 34.1$, $p < .001$, $\eta_p^2 = .51$ and condition, $F(1,130) = 298.1$, $p < .001$, $\eta_p^2 = .70$, but no significant interaction, $F(4,130) = 0.6$, $p = .66$, $\eta_p^2 = .02$.

Second-order form: As in the first-order comparison, the results for the Form Condition were compared to the results from Motion Condition 1 and Motion Condition 2 in two separate five (age) by two (condition) way ANOVAs (see Figure 2). We found significant main effects of age, $F(4,130) = 21.8$, $p < .001$, $\eta_p^2 = .4$ and condition $F(1,130) = 159.0$, $p < .001$, $\eta_p^2 = .55$, but no significant interaction for Form versus Motion Condition 1, $F(4,130) = 0.4$, $p = .79$, $\eta_p^2 = .01$. A one-tailed Dunnett's analysis of the effect of age on form thresholds revealed that 3-year-olds' mean threshold was worse than adults' mean threshold ($p < .01$) while thresholds for 5-, 7- and 10-year-olds were no different than those of adults (see Table 2 for full statistics). Here, the significant main effect of condition indicates that form thresholds were better than motion thresholds. We found the same pattern of results when the Form Condition was compared to Motion Condition 2. There were significant main effects of age and condition, $F(4,130) = 19.6$, $p < .001$, $\eta_p^2 = .38$ and $F(1,130) = 112.0$, $p < .001$, $\eta_p^2 = .46$, respectively, but no significant interaction $F(4,130) = 0.8$, $p = .52$, $\eta_p^2 = .02$.

Trend analysis: For first-order motion, trend analysis revealed a significant linear relationship between age and log mean threshold ($p < .001$), indicating that log thresholds improved as age increased. As can be seen in *Figure* 1, it appears that the rate of improvement was faster for younger children than older children. This was supported by a significant quadratic relationship between log mean thresholds and age ($p <.001$). Despite the finding that 10-year-olds' thresholds were closer to adults' in some condition than in others, the pattern of results at each age were the same when trends were analyzed for each condition separately (Condition 1, 2, and 3 linear trends: $ps < .001$; quadratic trends, $p < .01$, $p < .001$, and $p < .05$, respectively). For second-order motion, trend analysis revealed significant linear ($p < .001$) and quadratic ($p < .05$) relationships between age and log mean thresholds, indicating that thresholds improved with age, though at a faster rate for younger children than older children (see Figure 2). The linear and quadratic relationships between age and log mean thresholds were also significant for first- and second-order form ($ps < .001$). As for motion, as age increased, thresholds improved, though at a faster rate for younger than older children.

To examine the differences between first- and second-order developmental trajectories, we compared how much worse the children's mean thresholds were relative to the adults' mean threshold for each condition. This comparison can be done either by dividing unlogged thresholds to get a ratio of 'times worse' than adults, or by subtracting the logged thresholds to get the number of log units worse than adults. The calculations are mathematically equivalent. We chose to use unlogged data to calculate 'times worse' than adults because this is easier to conceptualize than log units worse. As shown in Table 3, children's thresholds were elevated above adults' thresholds more for first-order stimuli than second-order stimuli and this was true for every condition tested, especially for 3- and 5-year-olds.

3.6 Discussion

The current study had three main goals: (1) to determine and compare the developmental trajectories of sensitivity to the direction of first-order and second-order motion; (2) to examine the effects of temporal frequency, spatial-frequency, and velocity on sensitivity to first-order and second-order motion; and (3) to examine if sensitivity to motion in children is limited by poor sensitivity to form. To accomplish these goals, we measured sensitivity to first-order and second-order motion and form in adults and compared it to that of children at four different ages.

Non-visual factors, such as differences between children and adults in motivation or in ability to pay attention, may have contributed to the difference in thresholds between children and adults. However, this is unlikely to be the only explanation. Non-visual factors cannot account for the fact that children reached adult-like levels of sensitivity to motion at different ages for different conditions and the two motion types. For example, children were adult-like by 7 years for all second-order motion conditions, but were immature even at age 10 for first-order motion. Similarly, thresholds for second-order form were adult-like by 5 years of age, whereas they were adult-like for first-order form only at age 10. There also was evidence for a greater immaturity for first-order motion in Condition 3 at age 10 than the other two conditions. For each condition, the first and second-order motion task was the same and the measure was a threshold. Yet the extent of children's immaturities differed across conditions. Even the youngest age group tested, though immature on every condition, was more immature on some conditions than others (see Table 3). Thus, it is unlikely that the age differences in the current experiment were caused solely by differences in motivation and/or attention.

Developmental Trajectory for Motion: For first-order motion, children were still immature at age 10. For all second-order motion conditions, children were adult-like by 7 years of age. Furthermore, at younger ages, children's thresholds were elevated above adults' thresholds more for first-order motion than second-order motion (Table 3).

The results suggest that visual immaturities are greater for first-order than second-order motion, especially at 3 and 5 years of age.

Our results are similar to those of Bertone et al. (2008), who found that children attained adult-like thresholds for second-order motion before first-order motion. They suggested that second-order mechanisms are less efficient than first-order mechanisms even in adults and for that reason have a shorter developmental trajectory. In agreement with this hypothesis, Ledgeway and Hess (2002) found evidence that second-order motion mechanisms are less directionally selective than first-order motion mechanisms. The differences between thresholds for first- and second-order stimuli found in the current study are consistent with these claims. In the current experiment, adults were extremely sensitive to first-order motion, requiring only about 0.3 - 0.8% luminance modulation to discriminate the direction of a drifting first-order grating. In comparison, adults required around 20 - 35% contrast-modulation to discriminate the direction of a second-order grating. If second-order mechanisms are less sensitive than 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).

Like us, Bertone et al. (2008) found that children reached adult-like thresholds for second-order before first-order motion. However, unlike us, they reported that 5-6 year olds were more immature for second-order than first-order motion. We found that, regardless of age, children were more immature for first-order than second-order motion, and this immaturity is especially large at 3 and 5 years of age. One explanation we can offer to account for these discrepancies is that threshold elevations in the Bertone et al. (2008) study were calculated differently than in the present study. Bertone et al. calculated how many times worse children's thresholds were compared to adults by dividing logged thresholds. As discussed previously, the comparison must be done either by dividing unlogged thresholds to get a ratio of 'times worse' than adults, or by subtracting the logged thresholds to get the number of log units worse than adults. Log scores cannot be divided meaningfully. When we recalculated how many times worse children's thresholds were compared to adults' thresholds by dividing Bertone and colleagues' *unlogged*, rather than the logged data, we found that the 5- to 6-year-olds tested by Bertone et al. were in fact more immature for first-order than second-order motion, a pattern like that reported here. Specifically, their 5-6 year-olds were 3.3 times worse than adults for first-order motion, and only 2.6 times worse than adults for second-order motion. Thus, results from the study by Bertone et al. are in agreement with our findings that children's immaturity is larger for second-order than first-order motion when the analyses are conducted in the same way.

Ellemberg, Lewis, et al. (2003) reported that 5-year-olds' sensitivity to second-order motion was more immature than sensitivity to first-order motion. A re-analysis of those results using the analyses described in the current paper indicates that, like the current findings, children were more immature for first-order than second-order motion, at least when temporal frequency is relatively low. Specifically when temporal frequency and velocity were 1.5 Hz and 1.5 deg/sec, respectively, 5-year-olds were only 1.4 times worse than adults for second-order motion but 2.4 times worse than adults for first-order motion. When temporal frequency and velocity were 6 Hz and 6 deg/sec, respectively, the recalculation shows that 5-year-olds were 2.6 times worse than adults for both first-order and second-order motion.

In summary, after these recalculations, all three studies (Bertone et al., 2008; Ellemberg, Lewis, et al., 2003; the current study) agree that sensitivity to second-order motion reaches adult-like levels during childhood more quickly than does sensitivity to first-order motion. This contrasts with the pattern reported by Thibault et al. (2007) who measured sensitivity to drifting gratings in children ranging from less than 1 year to almost 7 years of age. Thibault et al. measured sensitivity to motion using looking preferences for a grating drifting at 4 deg/sec versus grey-scale noise. Unlike us, they reported that sensitivity to first- and second-order motion matured at equal rates. We suspect that the difference in findings is related directly to differences in the tasks. We used a direction discrimination task which necessarily involves the directional motion system. In contrast, the looking preference task used by Thibault et al. could just as easily reflect sensitivity to flicker or form rather than sensitivity to motion. This is because looking preferences can result from any perceived differences between a test and control stimulus. In the case of Thibault and colleagues, the test stimulus differed from the control stimulus in form (stripes versus grey-scale noise), flicker (present versus absent), and motion (present versus absent). Thus, the preferences may have been based on any one or combination of these differences. The current study eliminates these confounds by using a stimulus that differed only in direction of motion.

Effects of temporal frequency, spatial frequency, and velocity: Our second goal was to determine what parameters might limit sensitivity to motion. Thresholds for first-order motion were similar in the two conditions that had a temporal frequency of 1.5 Hz, despite significant differences in spatial frequency and velocity between those two conditions. Thresholds were better for the condition with the higher temporal frequency (6Hz) rather than the lower temporal frequency (1.5 Hz). The pattern of results differed for second-order motion. Second-order motion thresholds were similar when spatial frequency was 1 cyc/deg, despite very different temporal frequencies and velocities in the two conditions. Thresholds were better when spatial frequency was reduced to 0.25 cyc/deg. Sensitivity to second-order motion increased as spatial-frequency decreased. These patterns were evident at every age from 3 years to adulthood, a result indicating that the basic tuning of first-order and second-order mechanisms is adult-like by 3 years of age.

Seiffert and Cavanagh (1998) found that displacement thresholds for first-order motion decreased (i.e., sensitivity improved) when temporal frequency increased from 0.1 to 1-2 Hz. Second-order thresholds were generally constant over the same range in temporal frequency. However, they did vary with minimum displacement, or distance travelled. They concluded that first-order stimuli are processed using traditional motion or velocity sensitive mechanisms (i.e., motion energy/Reichardt mechanisms) while second-order motion is processed using a feature/position tracking mechanism. Our results for first-order motion are consistent with this hypothesis: as would be expected for a motion-sensitive mechanism, thresholds improved as temporal frequency increased. Our finding of better sensitivity for second-order motion when spatial-frequency was lower (larger stripes) is also consistent with the feature tracking hypothesis. To track features, one must first locate them (Derrington, Allen, & Delicato, 2003). Therefore, one would expect better performance with larger features because large features or stripes generally should be easier to find and track than small features.

It should be noted that like Seiffert and Cavanagh (1998), we tested sensitivity to motion over a small range of temporal frequency, spatial-frequency, and velocity. As pointed out by Lu and Sperling (2001), results obtained with a small range of parameters may not generalize beyond the range tested. It should also be noted that our results were found using a contrast threshold task, and that results may differ if the task was one that used stimuli presented at supra-threshold contrasts (Seiffert & Cavanagh, 1999).

At all ages, variations in temporal frequency limit sensitivity to first-order motion, while pattern detail (spatial frequency) limits sensitivity to second-order motion, at least under the conditions tested here. The similar patterns across age imply that the neural mechanisms underlying the processing of first- and second-order motion have already differentiated by 3 years of age and that subsequent development involves only a quantitative change in their sensitivity. There is evidence that 10-year-olds are more mature for some first-order conditions than others. The results from trend analysis and the examination of children's immaturities suggest that this difference in first-order thresholds is quantitative rather than qualitative. In all conditions, the pattern of improvement with age in sensitivity to motion is the same.

Form versus Motion: It is interesting to note that similar patterns of results were obtained in the motion and form discrimination tasks, except for the fact that adult-like thresholds were found at earlier ages in the form task. As with the faster development for second-order than first-order motion, children reached adult-like thresholds only at 10 years of age for first-order form but were already adult-like at 5 years of age for second-order form. As with motion, younger children's thresholds were more elevated above adults' thresholds for first-order than second-order form, especially at 3 and 5 years of age. Relatively faster development of sensitivity for second-order than first-order information has also has been demonstrated in infant monkeys (Kiorpes, Gavlin, & El-Shamayleh, 2006) and children (Bertone et al., 2008) with similar behavioural tasks.

The results for form indicate that children's immature thresholds for motion cannot be attributed solely to poor sensitivity to the form carrying the motion signal. Specifically, children reached adult-like thresholds for both first- and second-order form before motion, and first-order motion thresholds were better than form thresholds at every age tested. The finding that children reached adult-like thresholds for form before motion is consistent with findings that infants show a significant visual evoked potential (VEP) response to orientation reversals at an earlier age than they show a significant VEP response to directional reversals (Braddick, Birtles, Wattam-Bell, & Atkinson, 2005).

We also compared the pattern of results for form and motion across first-order and second-order stimuli. In all groups, thresholds for first-order motion discrimination were lower than for first-order horizontal/vertical discrimination. However, the opposite result was obtained with second-order stimuli: horizontal/vertical discrimination thresholds were lower than motion discrimination thresholds. More simply, we can 'see' the direction of first-order motion even if we cannot see its form. However, we can see the direction of second-order motion only if we can see its form. This finding is also consistent with the idea that second-order motion is processed using a feature tracking mechanism. One must be able to see the feature before the feature can be tracked. Others have also found that second-order motion thresholds are worse than second-order orientation identification thresholds and use this finding as confirmation that the second-order motion stimuli do not contain first-order artifacts (Ledgeway & Hess, 2002).

In summary, we found differences in the pattern of results for first-order and second-order motion and form. Sensitivity to second-order motion and second-order form reach adult-like levels before sensitivity to first-order motion and first-order form; and younger children's thresholds are more immature for first-order than second-order stimuli. This is likely related to the fact that adults are relatively insensitive to second-order stimuli (Allen, Ledgeway, & Hess, 2004; Ledgeway & Hess, 2002). Thus, reaching adult-like levels of sensitivity to second-order stimuli likely requires less development compared to first-order motion. When stimuli were first-order, participants are more sensitive to motion than form and their sensitivity varies with temporal frequency, patterns consistent with mediation by a motion-sensitive mechanism. When stimuli were second-order participants are more sensitive to form than motion and sensitivity varies with spatial frequency, patterns consistent with mediation by a feature tracking mechanism. These patterns were evident at 3 years of age, the youngest age tested. Regardless of the underlying mechanisms, these results support that idea that there are differences in the mechanisms that process first-order and second-order motion and that these mechanisms develop at different rates.

3.7 References

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Table 3.1

The three motion conditions and form condition tested. Temporal frequency equals spatial frequency multiplied by velocity (TF =SF x V). Two of three motion conditions were equated for each parameter so that the effect of each parameter on motion thresholds could be evaluated.

Condition	Temporal Frequency	Spatial Frequency	Velocity
Motion 1	6	1	6
Motion 2	1.5	1	1.5
Motion 3	1.5	0.25	6
Form	NA	1	0

Table 3.2
Full statistics for Dunnett's 1-way analysis comparing thresholds for each age group (age in years) to adults for first-order (FO) and second-order (SO) stimuli.

Age	***t***	***p***	**Cohen's d**
FO motion (df=82)			
3	12.2	<.001	1.8
5	8.4	<.001	1.4
7	4.1	<.001	0.8
10	2.9	< .01	0.5
SO motion (df=82)			
3	10.7	<.001	1.7
5	6.8	<.001	1.1
7	0.8	0.5	0.1
10	-0.5	0.9	-0.1
FO form (df =26)			
3	8.3	<.001	4.0
5	5.9	<.001	1.8
7	3.3	<0.01	2.0
10	1.9	0.09	1.7
SO form (df=26)			
3	3.4	<.01	2.0
5	1.7	0.14	1.3
7	0.3	0.7	0.3
10	-1.9	1.0	-0.5

Table 3.3

The ratio of children's thresholds for each age (in years) to adults' thresholds (times worse) for each of the three Motion Conditions (C1, C2, and C3) and for the Form Condition. Each condition shows immaturity ratios for first-order stimuli (FO), immaturity ratios for second order stimuli (SO), and the ratio of immaturities for first-order to second-order. In each case, children (age in years) are more immature for first-order than second-order stimuli, especially at 3 and 5 years of age.

	Motion C1			Motion C2			Motion C3			Form		
Age	FO	SO	Ratio	FO	SO	Ratio	FO	SO	Ratio	FO	SO	Ratio
3	3.3	1.4	**1.9**	2.4	1.6	**0.8**	3.5	1.9	**1.6**	2.7	1.5	**1.2**
5	2.0	1.2	**0.8**	1.9	1.3	**0.6**	2.6	1.5	**1.1**	2.1	1.2	**0.9**
7	1.4	1.0	**0.4**	1.2	1.0	**0.2**	1.8	1.1	**0.7**	1.5	1.0	**0.5**
10	1.1	0.9	**0.2**	1.3	1.0	**0.3**	1.6	1.1	**0.5**	1.3	1.0	**0.3**

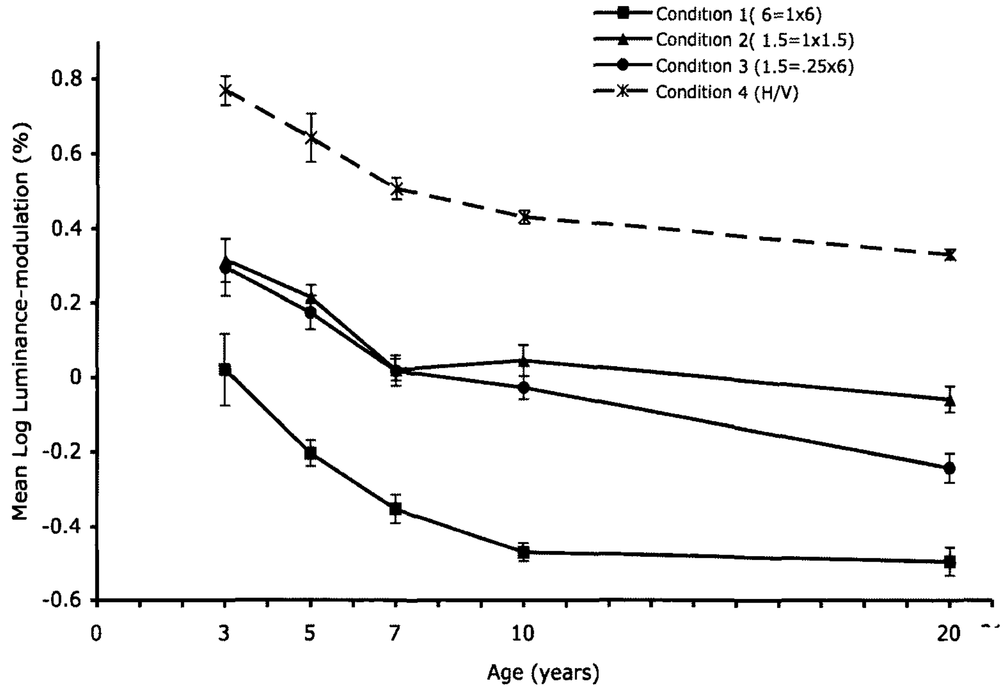

Figure 3.1. Mean log thresholds for first-order motion and form for children and adults. Thresholds represent the luminance-modulation required to identify the direction of motion (left or right) or orientation of form (horizontal or vertical) with 82% accuracy. The error bars represent ±1 standard error of the mean. Thresholds for the Form Condition were compared to motion conditions that had the same spatial frequency as the Form Condition, namely Motion Conditions 1 and 2.

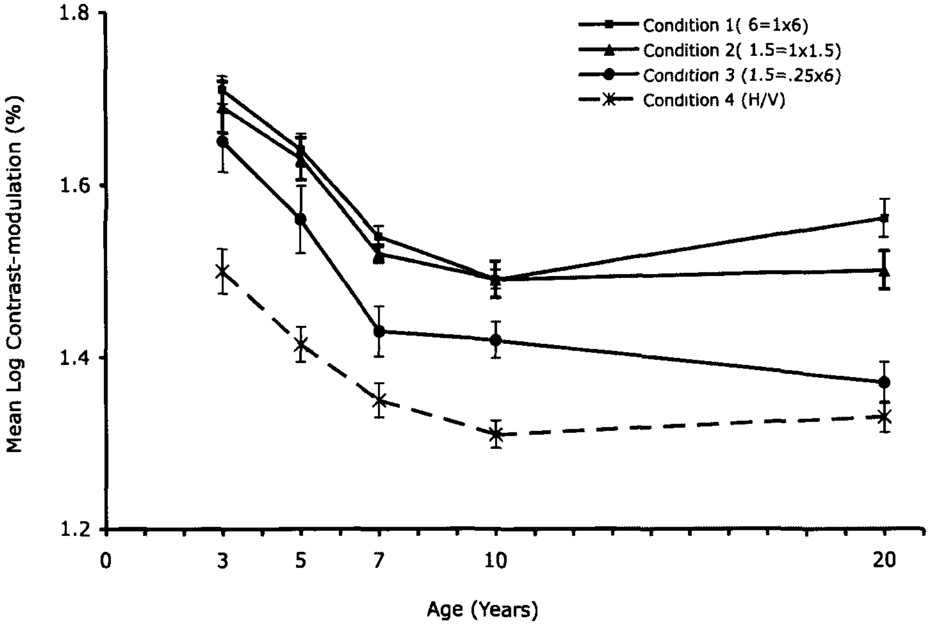

Figure 3.2. Mean log thresholds for second-order motion and form for children and adults. Thresholds represent contrast-modulation. Other details are as in Figure 1.

CHAPTER 4

Temporal Frequency Matters: Sensitivity to Drifting Contrast-modulated Stimuli in 5-year-olds and Adults.

V. L. Armstrong, T. L. Lewis, & D. Maurer

4.1 Preamble

In the research reported in Chapter 4, I examined sensitivity to second-order motion in 5-year-olds and adults by comparing thresholds on a directional motion task (discrimination of leftward and rightward drifting gratings) and a non-directional motion task (discrimination of drifting versus stationary gratings). I also examined the effect of temporal frequency, spatial frequency, and velocity on the two tasks, using a different range of values than those used in Chapter 3. Seiffert and Cavanagh (1998) found that adults' sensitivity to second-order was reduced at relatively high temporal frequencies, but only when the tasks required directional information. Here, I found the same pattern of interaction between temporal frequency and directional/nondirectional tasks in children and adults. Across the studies reported in Chapter 3 and in Chapter 4, I found that second-order order motion thresholds improve with both decreases in temporal frequency and spatial frequency. Conversely, thresholds for first-order motion tested in Chapter 3 improve with increases in temporal frequency. This is the first study to investigate second-order motion mechanisms in children. The results from Chapters 3 and 4 are consistent with evidence indicating that second-order-motion is processed using a feature tracking mechanism that is facilitated by slower temporal change (Seiffert & Cavanagh, 1998) and larger pattern detail (Smith & Ledgeway, 2001).

4.2 Abstract

We measured 5-year-olds' and adults' contrast thresholds for two second-order motion tasks, one directional and one non-directional. Participants were required to discriminate left from right motion for the directional task, and a drifting from a stationary grating for the non-directional task. Grating temporal frequency, spatial frequency, and velocity were varied across conditions. Regardless of task, adults' sensitivity to motion varied with temporal frequency: thresholds were better when temporal frequency was lower (0.75 Hz) than when it was higher (6 Hz). Thresholds for directional motion were significantly worse than thresholds for non-directional motion, but only when temporal frequency was relatively high (6 Hz). Children did not have adult-like thresholds for any condition tested. However, the size of the immaturity was greater in conditions with the lower temporal frequency (0.75 Hz). These results are consistent with the idea that, under the conditions tested, a feature tracking mechanism is used to process second-order motion.

4.3 Introduction

Although motion perception is typically thought to require the activation of direction-sensitive cells, motion can be perceived without such activation (Derrington, Allen, & Delicato, 2004). For example, one can detect motion with mechanisms that respond to flicker or a change in position (Seiffert & Cavanaugh, 1998). Although flickering stimuli can evoke the perception of motion in a particular direction (e.g., phi motion), only feature tracking and directionally sensitive mechanisms are capable of providing information about the actual direction of motion. Therefore, directional motion tasks, such as direction discrimination, may reflect the sensitivity of mechanisms that track the position of features or the sensitivity of mechanisms tuned to direction. However, non-directional motion tasks, such as the mere detection of motion, could reflect the sensitivity of mechanisms tuned to flicker, position, or direction.

Cues to motion can be provided by any physical parameter that changes spatial location over time. These parameters can consist of a boundary defined by a change in luminance, contrast, texture, element size, etc. When the boundary is defined by a change in luminance, it is termed a first-order cue to motion. When the parameter is defined by properties other than a change in luminance, it is termed a second-order cue to motion.

First- and second-order motion are processed, at least in part, by separate mechanisms, as evidenced by psychophysical (Chubb & Sperling, 1988; Ledgeway & Smith, 1994; Nishida, Ledgeway, & Edwards, 1997), electrophysiological (Ellemberg, Lavoie et al., 2003; Mareschal & Baker, 1998; 1999; Zhou & Baker, 1993), human imaging (Dumoulin, Baker, Hess, & Evans, 2003; Smith, Greenlee, Sing, Kramer, & Hennig, 1998), and neuropsychological (Greenlee & Smith, 1997; Vaina & Cowey, 1996; Vaina, Makris, Kennedy, & Cowey, 1998) data. For example, adults do not integrate alternating frames containing first- and second-order cues to local motion into an unambiguous percept of motion (Ledgeway & Smith, 1994), and their sensitivity to first- or second-order local motion is not affected by adaptation to motion of the other type (Nishida et al., 1997). Furthermore, both the latency of the visual evoked potential 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). Finally, a functional magnetic resonance imaging study demonstrated a clear segregation between the neural areas that are involved in the processing of first- and second-order motion (Dumoulin et al., 2003). Specifically, Dumoulin and colleagues found that first-order motion most strongly activated the early visual areas (V1) whereas second-order motion most strongly activated the higher visual areas (near V5).

The mechanisms involved in the detection of second-order motion are sensitive to different parameters than those involved in the perception of first-order motion (Seiffert & Cavanagh, 1998). For example, detection thresholds for first-order motion are dependent on minimum velocity, whereas those for second-order motion are dependent on minimum displacement or distance travelled, (Seiffert & Cavanagh, 1998), at least when the second-order stimulus contrast and speed are low (Seiffert & Cavanagh, 1999). Thus, Seiffert and Cavanagh concluded that first-order motion is best detected by a velocity-sensitive mechanism, while second-order motion is best detected by a position or feature tracking mechanism. The feature tracking mechanism works by first identifying a feature and then following the feature's change in position over time (Derrington et al., 2004).

Work in our lab suggests that 5-year-olds' sensitivity to direction of second-order motion may vary with temporal frequency and/or velocity. Ellemberg, Lewis, et al. (2003) reported that 5-year-olds' sensitivity to the direction of second-order motion was more immature when velocity and temporal frequency were relatively high (6 Hz and 6 deg/sec) than when they were relatively low (1.5 Hz and 1.5 deg/sec). Because both temporal frequency and velocity varied across conditions, it could not be determined if temporal frequency or velocity was responsible for this finding. To disambiguate the effects of temporal frequency and velocity, we conducted an experiment that equated temporal frequency, spatial frequency, and velocity across different conditions and measured children's and adults' thresholds for discriminating the direction of second-order motion (Chapter 3). Adults' second-order thresholds were better at the lower spatial frequency (0.25 cyc/deg) than at the higher spatial frequency (1 cyc/deg), but did not vary systemically with temporal frequency or velocity.

Unlike the results found in Chapter 3, others have shown that temporal frequency does have a large impact on sensitivity to second-order motion. Seiffert and Cavanagh (1998) found that when temporal frequency was 3-4 Hz, adults' displacement thresholds were much higher when measured using a directional motion task than a non-directional motion task. Because the non-directional motion task could be accomplished using flicker cues, this result suggests that adults may have used a flicker sensitive mechanism when temporal frequency was relatively high and a feature tracking mechanisms when temporal frequency was relatively low (Seiffert & Cavanagh, 1998). Consistent with this idea, adults' sensitivity to the direction of second-order motion is highest at temporal frequencies below 1 Hz and quickly declines as temporal frequency increases to 3 Hz and above (Derrington & Cox, 1998; Seiffert & Cavanagh, 1998, see Derrington et al., 2004 for a review).

Little is known about the development of second-order motion mechanisms. We examined whether children's sensitivity to directional and non-directional motion at high (6 Hz) and low (0.75 Hz) temporal frequencies follows the same pattern found in adults by Seiffert and Cavanagh (1998). We also re-examine our previous observation that sensitivity to second-order motion depends on spatial frequency (Chapter 3) by testing a wider range of spatial frequencies. Our goal was to compare 5-year-olds' and adults' sensitivity to second-order motion measured with a directional versus a non-directional motion task for various combinations of temporal frequency, spatial frequency, and velocity. In this experiment, spatial frequency was partially confounded with temporal frequency because examining each parameter independently required a prohibitively large number of participants. However, by having a small number of conditions with different combinations of temporal frequency and velocity (see Table 1), we were still able to examine the pattern of results for evidence of an effect of spatial frequency. We also measured sensitivity to second-order form using a horizontal/vertical discrimination task to ensure that developmental differences in motion perception were independent from any developmental differences in form perception.

4.4 Methods

Participants

The participants were 74 adults (mean age = 19.7 years, range = 18 - 28 years) and 74 5-year-olds (±3 months; mean = 5.04 years, range = 4.88 - 5.26 years) divided into 5 groups per age (see Table 2 for breakdown of ages by test group). Adults were recruited from a pool of undergraduate students registered in Introductory Psychology at McMaster University and received partial course credit for participation. The children were recruited using contact information provided by parents who expressed interest in participating in our studies at the time of the child's birth. Most of the children had participated previously in unrelated studies at McMaster University.

All participants had normal or corrected-to-normal visual acuity and no history of eye problems. For each of the two age groups, 64 participants completed one of four conditions for both the directional and non-directional motion task. The remaining 10 participants in each age group completed a horizontal/vertical pattern discrimination task. Fifty-two percent of the adults and 58% of the children were male. The breakdown of percent male in each group is shown in Table 2. Although there were an unequal number of males in each group, this was unlikely to have changed the results as thresholds were no different for males than females on the directional motion task, *t*(126) = 0.3, *p* = .8, Cohen's d = 0.05, the non-directional task, *t*(126) = 0.4, *p* =.7, Cohen's d = 0.06, nor the form task, *t*(18), = 0.7, *p* = .5, Cohen's d = .27.

An additional seven 5-year-olds were excluded from the study: five because they were unwilling to complete testing and two because of experimental error.

Apparatus and Stimuli

The stimuli were generated by a Macintosh G3 computer by means of VPixx software™, and were displayed on a 53.3 cm Sony Trinitron monitor. The monitor had a frame rate of 75 Hz and pixel resolution of 1024 x 768.

The stimuli were sinusoidal gratings contained within a 10.2 x 10.2 cm square (15 x 15 deg when viewed from 50 cm). All stimuli consisted of a static two-dimensional random noise carrier, the luminance of which was binary. Each noise element subtended 2 x 2 arc min, and was assigned independently with a probably of 0.5 to be either 'light' or 'dark'. The envelope of the test pattern consisted of a luminance-modulated sinusoidal grating that was multiplied by the carrier to create the contrast-modulated stimulus (e.g., Smith & Ledgeway, 1997). The stimulus consisted of a series of alternating regions of higher and lower contrast between noise dots, with every region having the same mean luminance. The amplitude of the contrast modulation (depth modulation or was defined as:

$$\text{Depth modulation} = (C_{max}-C_{min})/(C_{max}+C_{min}),$$

where C_{max} and C_{min} are the maximum and minimum mean local contrasts in the stimulus. The mean luminance of the stimuli was 13 cd/m^2. The monitor was calibrated every few weeks to ensure that the luminance of higher and lower contrast regions differed by less than 1 cd/m^2 when the grating was displayed at maximum contrast.

For the directional motion task, each display consisted of one vertical grating positioned in the centre of the monitor. The task on each trial was to say whether the grating drifted to the left or right. For the non-directional motion task, each display consisted of two identical vertical gratings on the left and right sides of the monitor; the inner edges of the gratings were separated by a 5° gap. One grating remained stationary while the other grating drifted outward, and the task was to indicate which side contained the drifting grating. We chose this task because it is a non-directional motion task that requires the same two-alternative forced choice decision (i.e., Left or Right) as the directional motion task. For both tasks, the temporal frequency, spatial frequency, and velocity of the grating varied across conditions as shown in Table 1. We chose the test temporal frequencies of 0.75 and 6 Hz because evidence suggests that sensitivity to the direction of second-order motion is best when temporal frequency is below 1 Hz and declines when temporal frequency is higher than 3Hz (Derrington & Cox, 1998; Seiffert & Cavanagh, 1998). Thus, we are most likely to tap the second-order mechanisms that are sensitive to direction of motion at the lower temporal frequency (0.75 Hz) and we are most likely to tap second-order mechanisms that are not sensitive to directional motion at the higher temporal frequency. These different underlying mechanisms make it likely that we will find a difference in sensitively to second-order motion at the two temporal frequencies.

For the horizontal/vertical orientation discrimination task, each display consisted of one stationary grating positioned in the centre of the monitor. The task on each trial was to say whether the grating was vertical or horizontal. The grating had a spatial frequency of 0.125 cyc/deg in one condition and 2 cyc/deg in the other condition. These spatial frequencies were chosen because they were the highest and lowest spatial frequencies tested in the motion tasks.

Procedure

The procedures were explained and informed consent was obtained from adults and from the parents of 5-year-olds. The experimental protocol was approved by the McMaster Research Ethics Board. Each participant was seated 50 cm away from the computer monitor with his or her chin positioned on a chin rest. Parents of 5-year-olds sat in the testing room out of their child's sight and were asked to remain silent throughout the testing.

Each participant provided two thresholds. Participants in the motion experiment provided one threshold for each motion task (directional and non-directional) for one of the four conditions listed in Table 1. Participants in the horizontal/vertical discrimination task provided one threshold for a spatial frequency of 0.125 cyc/deg and one for a spatial frequency of 2.0 cyc/deg.

For the directional motion task, the participant was told that he or she would see one square containing moving stripes. The task on each trial was to indicate which way the stripes moved, left or right. Many 5-year-olds could not accurately use the terms 'left' and 'right' to indicate the direction of motion, so they were asked to point in the direction that the stripes were moving. For the non-directional motion task, each participant was told that he or she would see two squares on each trial, one with stripes that would move outward and one with stripes that would remain stationary. The task on each trial was to point to the square that contained the moving stripes. Adults were given the option to respond by pointing or verbally, but all chose to respond verbally. For the horizontal/vertical discrimination task, each participant was told that he or she would see one square and that the stripes would be vertical/standing up or horizontal/lying sideways. The task on each trial was to indicate the position of the stripes. In all conditions, the stimuli remained on the screen until a response was made. An unlimited stimulus display was used because 5-year-olds' motion detection thresholds improve with display times up to as long as 1 sec (Ellemberg, Lewis, & Maurer, unpublished raw data*)*. Participants responded, as they preferred, either verbally or by using hand gestures (holding the hand vertically or horizontally).

At the beginning of each trial, participants were asked to fixate a 3 x 3 deg black dot that appeared in the centre of the screen. The back dot was then replaced by the stimulus. The experimenter, who was unaware of the particular display on each trial, entered responses on the keyboard and watched the participant's eyes continuously to ensure that he or she was looking at the computer screen. The contrast of the grating(s) 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 threhsold was within ±0.1 log units. Prior to testing, participants were presented with two demonstration trials with the gratings at maximum (100%) contrast-modulation. For each task, the demonstration consisted of one trial for each of the two alternative choices (left/right or horizontal/vertical). To verify that participants understood the task, they were presented with a criterion phase consisting of up to three blocks of four test trials, again at maximum depth modulation. To be included in the study, participants had to respond correctly on all four trials in a test block. Participants received verbal feedback for this phase. All participants met this criterion, usually in the first test block.

Upon completion of the criterion phase, participants were given a practice staircase with feedback after each trial. Feedback consisted of a high-pitched tone paired with a happy face for a correct response and a low-pitched tone paired with a sad face for an incorrect response. The happy and sad faces appeared in a 15 x 15 deg square in the centre of the monitor and remained on the screen for 250 ms. Practice was terminated after the contrast-modulation was reduced to the point where two incorrect responses occurred consecutively.

Participants then completed the test phase with feedback. In addition to feedback from the computer, children were praised periodically and reminded to watch carefully if necessary. Thresholds were defined as the minimum contrast modulation necessary to respond correctly 82% of the time.

The criterion, practice, and test phases were repeated for each testing condition. For the two motion tasks, the order of task type and condition was counterbalanced across participants. For the horizontal/vertical discrimination task, the order of spatial frequency was counterbalanced across participants. All adults and 5-year-olds completed the testing within one session that lasted less than 45 minutes.

Data Analysis

The raw data consisted of individual thresholds reported in proportion contrast-modulation. The data were multiplied by 100 to transform proportion contrast modulation thresholds into percent contrast modulation thresholds. The data were then logged and were expressed in terms of mean log thresholds (percent contrast modulation). An outlier procedure (Kirk, 1999) was used to replace extreme scores of the 5-year-olds and adults. Specifically, each individual threshold was converted to a z-score using the mean and standard deviation for that age and temporal frequency/velocity. Z-scores greater than +2.5 or less than –2.5 were replaced with the original group mean (i.e., the mean threshold for the condition before the removal of outliers). The analyses revealed two outlying data points: one adult tested on Condition 3 (6 = 1x6) with the non-directional motion task and one adult tested on Condition 4 (6 = 2x3) with the directional motion task. These two data points were replaced as described above and all subsequent analyses were conducted using this revised data set.

For the motion tasks, we conducted a two (Age) by two (Task) by four (Condition) way ANOVA with task type as a repeated measure. Post Hoc Analyses were conducted on the significant two-way ANOVAs. Partial eta squared (η_p^2) values were used for estimates of association strength between the independent and dependent variables. This measure is calculated as follows:

$$\eta_p^2 = SS_{effect} / (SS_{effect} + SS_{error})$$

and, unlike classic η^2, it excludes variance attributable to other factors (Pierce, Block, & Aguinis, 2004). For differences analyzed with t-tests, effect size was estimated by calculating Cohen's *d* statistic.

4.5 Results

Motion tasks: The data for the motion tasks are shown in *Figure 1*. The ANOVA revealed that the three-way interaction was not significant, $F(3,120)= 2.4$, $p =.07$, $\eta_p^2 =.06$. The two-way interactions will be discussed in turn below. The main effect of age was significant, $F(1, 120) = 200.7$, $p <.001$, $\eta_p^2 = .63$, indicating that thresholds were significantly lower in adults. The main effect of task also was significant, $F(1, 120) = 40.9$, $p < .001$, $\eta_p^2 = .27$, indicating that thresholds for non-directional tasks were lower than thresholds for directional tasks. The main effect of condition was not significant, $F(1,120) =2.7$, $p=.1$, $\eta_p^2 = .02$. There was no interaction between the effect of Age and Task, $F(1,120) = 2.7$, $p >.1$, $\eta_p^2 =.05$, but the Age x Condition and Task x Condition interactions were significant. These interactions are discussed in the following sections.

Age x Condition: The Age x Condition interaction was significant, $F(3, 120) = 9.6$, $p < .001$, $\eta_p^2= .19$. Separate one-way ANOVAs revealed that adult's thresholds varied with condition $F(3,63) = 16.8$, $p < .001$, $\eta_p^2 = .5$, while 5-year-olds' thresholds did not, $F(3,63) = 1.6$, $p = .21$, $\eta_p^2 = .07$. Pairwise Bonferroni post hoc t-test revealed that adults' thresholds were better for Condition 1 and 2 where temporal frequency and spatial frequencies were lower (0.75 Hz and 0.125 or 0.5 cyc/deg) than Conditions 3 and 4 where temporal frequency and spatial frequencies were higher (6 Hz and 1 or 2 cyc/deg, see Table 3a for statistics). Adults' thresholds for Conditions 1 versus 2 and thresholds for Condition 3 versus 4 were not significantly different (see Table 3a).

Five-year-olds were significantly worse than adults in every condition (see Table 3b). For Conditions 1 and 2, children's thresholds were 1.4 times worse than adults'. For Conditions 3 and 4, children's thresholds were 2.1 and 2.3 times worse than adults'. The effect of age, as measured by Cohen's d, was smaller when temporal frequency was 6 Hz than when temporal frequency was 0.75 Hz, and increased as spatial frequency decreased.

Task x Condition: The Task x Condition interaction was significant, $F(3, 124) = 114.3$, $p < .001$, $\eta_p^2 = .26$. Paired t-tests revealed that detection thresholds were better than discrimination thresholds (see Table 3c), but only when temporal frequency and spatial frequency were relatively high (6 Hz and 1 or 2 cyc/deg). When temporal frequency and spatial frequency were relatively low (0.75 Hz and 0.5 or 0.125 cyc/deg), there was no significant effect of task type.

Form tasks: For the horizontal/vertical discrimination task, we conducted a two (Age) by two (Spatial Frequency) ANOVA with spatial frequency as a repeated measure. The data for the horizontal/vertical discrimination are shown in *Figure 2a*. The two-way ANOVA revealed a significant main effect of age, $F(1, 18) = 14.7$, $p < .001$, $\eta_p^2 = .45$, indicating that 5-year-olds' thresholds were lower than adults'. Five-year-olds' horizontal/vertical discrimination thresholds were 1.4 times higher than those of adults. There also was a significant main effect of spatial frequency, $F(1, 18) = 16.7$, $p < .01$, $\eta_p^2 = .48$, indicating that thresholds were better at lower than higher spatial frequency. Overall, thresholds were 1.4 times lower when spatial frequency was 0.125 cyc/deg than when it was 2 cyc/deg. The Age x Spatial Frequency interaction was not significant, $F(1,18) = 0.2$, $p > .60$. Spatial frequency had the same effect of children's thresholds as it did on adults' thresholds. The results for the motion conditions with the same temporal frequencies are shown in *Figure 2b* for comparison.

4.6 Discussion

Overall, motion thresholds in adults varied with temporal frequency: thresholds were better when temporal frequency was lower (0.75 Hz) than when it was higher (6 Hz). Thresholds did not vary with velocity. These findings are consistent with findings that second-order motion mechanisms are most sensitive at lower temporal frequencies (below 1 Hz) and quickly become less sensitive as temporal frequency increases to 3 Hz and higher (Derrington and Cox, 1998; Seiffert, & Cavanagh, 1998).

Spatial frequency varied with temporal frequency and therefore, may be responsible for the effect of condition that we found in adults. However, there was no difference between motion thresholds in

Conditions 1 and 2, despite the fact that spatial frequency in those conditions differed by a factor of four. Likewise, thresholds in Conditions 2 and 3 did not differ even though spatial frequency doubled from 1 to 2 cyc/deg. For these reasons, we think it is unlikely that the effect of condition was caused solely by differences in spatial frequency.

Sensitivity to directional motion was significantly lower than sensitivity to non-directional motion, but only when temporal frequency and spatial frequency were relatively high (6 Hz and 1 or 2 cyc/deg). There was no difference between directional and non-directional motion thresholds when temporal frequency and spatial frequency were relatively low (0.75 Hz; 0.125 and 0.5 cyc/deg). Like the effect of condition, the effect of task on sensitivity to motion is likely attributable to changes in temporal frequency rather than spatial frequency because, as stated above, the thresholds for each task did not differ between Conditions 1 and 2, or between Conditions 3 and 4, even though spatial frequency differed in each case. Thus, this effect appears to be driven by an increase in directional motion thresholds when temporal frequency is relatively high.

Seiffert and Cavanagh (1998) reported a similar difference in thresholds for directional versus non-directional second-order motion tasks. They found that displacement thresholds for the detection of second-order motion (a non-directional task) changed little with temporal frequency. However, when the task required the perception of direction, thresholds were elevated when temporal frequency reached 3-4 Hz. They concluded that this difference in thresholds reflected poor sensitivity to direction of second-order motion at higher temporal frequencies, and that if the task allowed (i.e., if it was non-directional in nature) the more sensitive flicker processing mechanisms would predominate. Our findings are consistent with this explanation. Furthermore, our different findings for high and low temporal frequencies in the directional motion task is consistent with evidence that adults' sensitivity to direction of second-order motion is best when temporal frequency is below 1 Hz and quickly declines when temporal frequency is 3 Hz and above (Derrington and Cox, 1998; Seiffert & Cavanagh, 1998)

Low contrast second-order motion may be processed by a feature tracking mechanism, whereas high-contrast second-order motion may be processed by mechanisms that are similar to, or the same as, first-order motion mechanisms (Seiffert & Cavanagh, 1999; Ukkonen & Derrington, 2000). Although the precise mechanisms involved in feature tracking are ill-defined, it is generally thought that a feature must be identified before it can be tracked. It is likely that this identify-then-track process would take more time, and would be more demanding of attention, than low-level motion analysis, which is characterized as rapid and effortless (Derrington et al., 2004). In support of this view of feature tracking, visual evoked potentials and reaction times are slower in response to the onset of second-order than first-order motion (Ellemberg, Lavoie et al., 2003) and reaction times for discriminating the direction of motion is longer for second-order motion than first-order motion, regardless of the type of second-order motion tested (Ledgeway & Hutchinson, 2008). Similarly, tasks with multiple moving second-order objects require several seconds to perform the task, while the same tasks with first-order objects are rapid and effortless (Allen & Derrington, 2000).

Children did not have adult-like thresholds for any condition tested. However, the size of the immaturity was greater in conditions with lower temporal and spatial frequencies (0.75 Hz; 0.125 or 0.5 cy/deg), but unrelated to velocity. When temporal frequency was 0.75 Hz and spatial frequency was 0.125 and 0.5 cyc/deg, children were more than two times worse than adults. However, when temporal frequency was 6 Hz and spatial frequency was 1 or 2 cyc/deg, children were only 1.4 times worse than adults. Therefore, children's sensitivity to second-order motion was more immature when temporal frequency and spatial frequency were relatively low. We suspect that temporal frequency rather than spatial frequency may be primarily responsible for this difference in the size of immaturities. By 5 years of age, grating acuity is between 25 and 30 cyc/deg (Ellemberg, Lewis, Liu, & Maurer, 1999), far better than the smallest grating spatial frequency used here. Thus, children would have easily been able to detect the pattern of all the gratings that we tested.

Children's sensitivity to second-order motion did not vary across condition, although adults were more sensitive to motion at lower than higher temporal frequencies. Thus, the greater immaturity found for second-order motion found at low temporal frequencies was not caused by children having reduced sensitivity in the 0.75 Hz condition, but, instead, was because adults had higher sensitivity in the 0.75 Hz condition than in the 6 Hz condition. Thus, between 5 years of age and adulthood, sensitivity to second-order motion matures more for lower temporal frequencies than for higher temporal frequencies.

Our results are consistent with previous reports that age differences in visual sensitivity are greater at low than high temporal frequencies. For example, temporal contrast sensitivity of first-order homogeneous flickering field reaches adult-like levels earlier for higher temporal frequencies (20 and 30 Hz) than lower temporal frequencies (5 and 10 Hz) (Ellemberg et al., 1999). Furthermore, young infants are more sensitive to stimuli with higher than lower temporal frequencies/velocities (Aslin & Shea, 1990; Dannemiller & Freedland, 1989; Roessler & Dannemiller, 1997).

Similar to the current study, we found previously that 3- and 5-year-olds' sensitivity to direction of second-order motion was slightly, though not significantly, more immature at a lower (1.5 Hz) than at a higher temporal frequency (6 Hz) (Chapter 3). However, other results from our lab are inconsistent with our present findings. A reanalysis of the results reported by Ellemberg, Lewis et al. (2003) showed that 5-year-olds' sensitivity to second-order motion was more immature when temporal frequency and velocity were relatively high at 6 Hz and 6 deg/sec, respectively, than when temporal frequency and velocity were relatively low at 1.5 Hz and 1.5 deg/sec, respectively. The temporal frequencies tested in Chapter 3 and by Ellemberg, Lewis et al. (2003) were 1.5 and 6 Hz, whereas the current experiment used temporal frequencies of 0.75 and 6 Hz. The use of a lower temporal frequency (0.75 Hz rather than 1.5 Hz) that differs more from 6 Hz could explain why we found that children's immaturities to second-order motion were significantly larger for lower than higher temporal frequencies in the present study, but not in previous ones (Chapter 3; Ellemberg et al., 2003).

Another difference between the present findings and findings for children's and adults' sensitivity to the direction of second-order motion (Chapter 3) was that, in the current study, thresholds varied with changes in temporal frequency, but not spatial frequency, unless also accompanied by a change in temporal frequency, while in Chapter 3 thresholds varied with spatial frequency but not temporal frequency. Specifically, here we found that second-order motion thresholds were better when temporal frequency was 0.75 Hz than when it was 6Hz. In Chapter 3, where the temporal frequencies tested were 1.5 and 6 Hz, thresholds were better when spatial frequency was 0.25 rather than 1 cyc/deg, regardless of temporal frequency. An explanation for this difference in results may be that spatial frequency (stripe size) becomes more important in feature tracking at higher ranges of temporal frequencies (above 1 Hz) as sensitivity to second-order motion declines.

The differences that we found between 5-year-olds and adults likely reflect immaturities in the neural mechanisms that process second-order motion, rather than age differences in attention or motivation. In particular, it is difficult to see how differences in attention or motivation could explain why age differences were larger in the 0.75 Hz condition than in the 6 Hz condition. Nor does it seem likely that the observed immaturities on the motion tasks reflect an immaturity of the mechanisms sensitive to form rather than motion. As with the motion tasks, children performed worse than adults on the horizontal/vertical discrimination task. We used spatial frequencies of 0.125 and 2 cyc/deg for the form task; the same spatial frequencies used in Conditions 1 and 4 for the motion tasks. For the form task, children were equally immature at discriminating horizontal from vertical gratings for the two spatial frequencies (see *Figure 2a*). However, for the motion task, children were much more immature when spatial frequency was 0.125 cyc/deg than when it was 2 cyc/deg (see *Figure 2b*).

Although the current results do not test the nature of the second-order motion mechanisms directly, like Seiffert and Cavanagh's (1998) results, they are consistent with the idea that feature tracking is used to process second-order motion, at least under the conditions tested here. Specifically, we found that differences in sensitivity across tasks are evident only when temporal frequency is high, where sensitivity to second-order motion is worse than sensitivity to flicker. This pattern of results was not found for first-order motion (Seiffert & Cavanagh, 1998) where velocity or motion based mechanisms are used to process motion. Regardless of the underlying mechanisms, we found that adults are most sensitive to direction of second-order motion when temporal frequency is relatively low. Likewise, 5-year-olds' sensitivity to second-order stimuli is most immature when temporal frequency is relatively low.

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Table 4.1

Conditions for motion tasks. Each participant was tested on one condition for both the directional and non-directional motion tasks. Temporal Frequency (TF) = Spatial Frequency (SF) multiplied by Velocity (V).

	TF (Hz)	SF (cyc/deg)	V (deg/sec)
Condition 1	0.75	0.125	6
Condition 2	0.75	0.5	1.5
Condition 3	6	1	6
Condition 4	6	2	3

Table 4.2.
Age and gender by group.

	5-year-olds			**Adults**		
	Mean age	SD	% male	Mean age	SD	% male
Condition 1	5.03	0.11	37.5	19.2	1.2	56.2
Condition 2	5.04	0.09	68.8	20.2	2.3	43.8
Condition 3	5.03	0.09	68.8	19.7	1.1	50.0
Condition 4	5.06	0.12	56.2	19.8	1.3	56.2
Form	5.12	0.18	70.0	20.1	2.4	40.0

Table 4.3

Statistics for posthoc t-test. Conditions 1 and 2 have a temporal frequency of 0.75 Hz and Conditions 3 and 4 have a temporal frequency of 6 Hz.

a) Effect of condition on adults thresholds, *df= 30*

Conditions compared	*t*	*p*	**Cohen's d**
1-2	0.1	1.0	0.03
1-3	4.8	< .001	2.0
1-4	5.3	< .001	2.1
2-3	4.7	< .001	1.6
2-4	5.2	< .001	1.6
3-4	0.5	1.0	0.20

b) Effect of age on motion thresholds, *df =30*

Condition	*t*	*p*	**Cohen's d**
1	10.5	< .001	3.7
2	7.1	< .001	2.6
3	5.7	< .001	1.6
4	5.1	< .001	1.7

c) Effect of task type, *df= 31*

Condition	*t*	*p*	**Cohen's d**
1	0.2	0.824	0.02
2	0.05	0.964	0.01
3	5.9	< .001	1.0
4	6.2	< .001	1.1

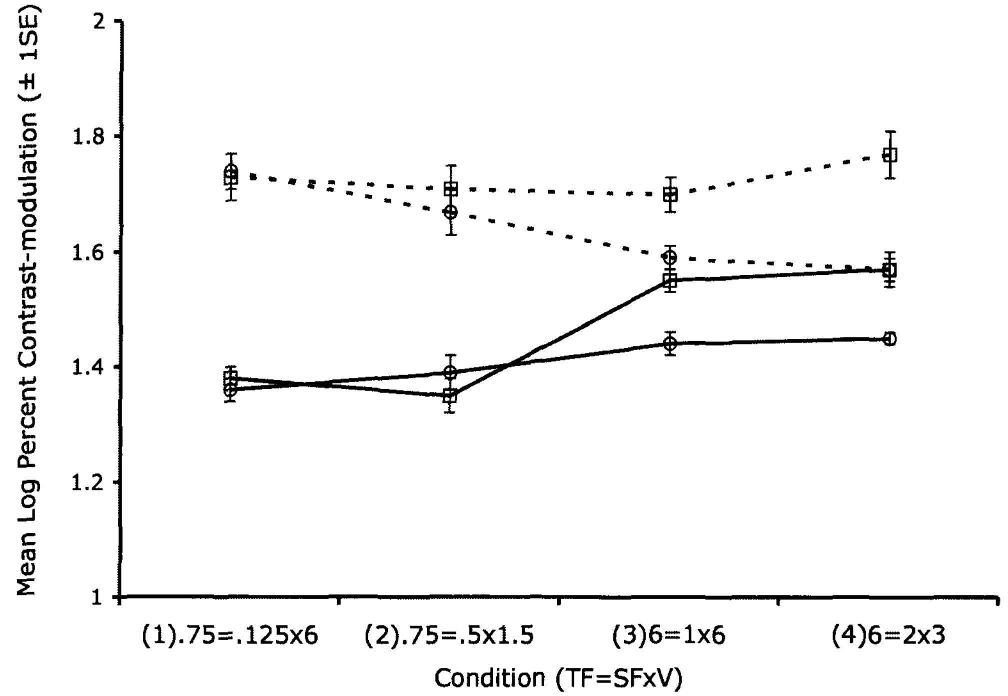
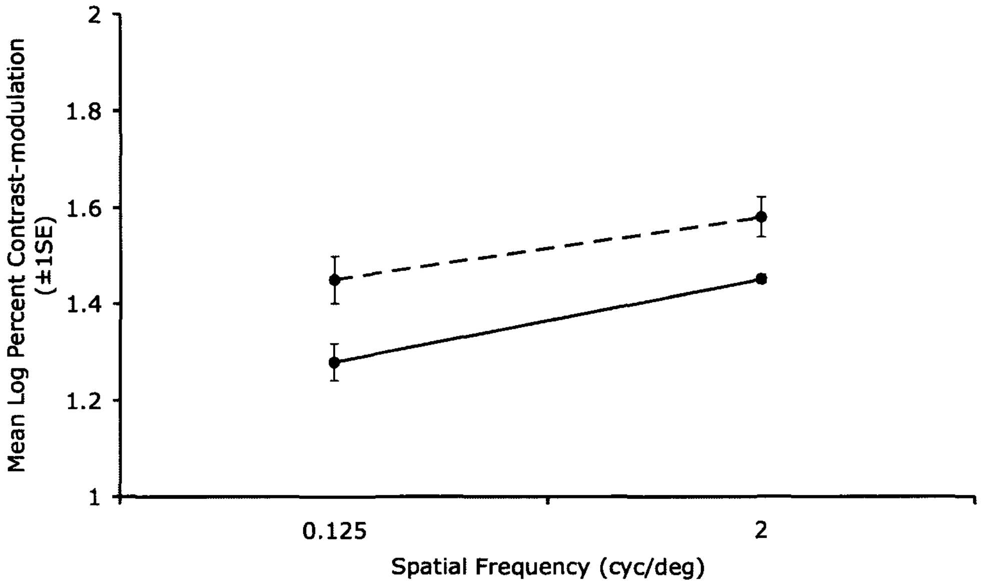


Figure 4.1. Adults' (solid line) and 5-year-olds' (dashed line) mean log thresholds (% contrast modulation ± 1 SEM) for sensitivity to second-order directional (squares) and non-directional (circles) motion for four different temporal frequency (TF), spatial frequency (SF), and velocity (V) combinations.

Panel A: Form



Panel B: motion

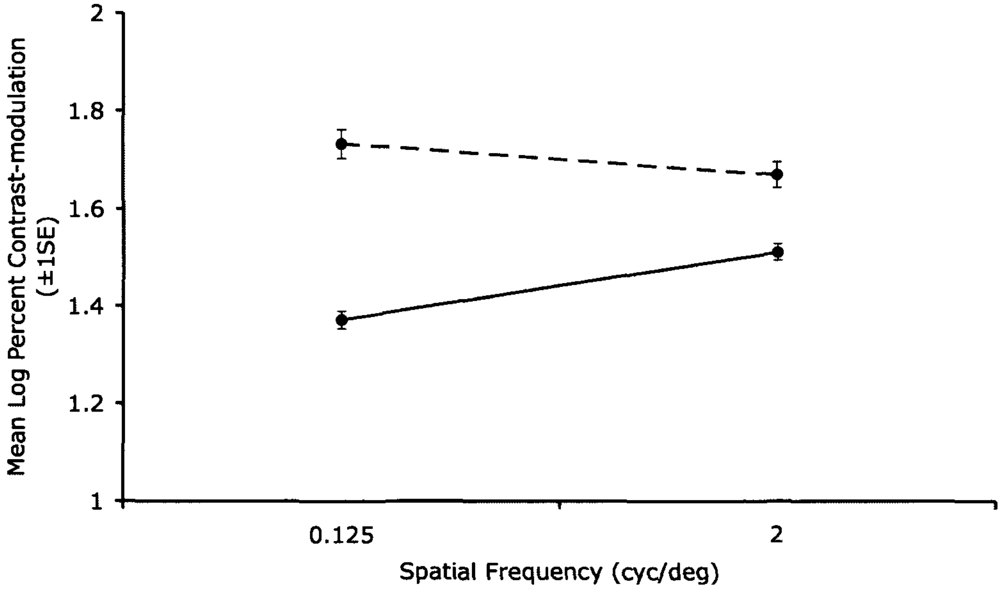


Figure 4.2. Adults' (solid line) and 5-year-olds' (dashed line) mean log thresholds (% contrast modulation ± 1 SEM) for sensitivity to second-order form (Panel A). The motion data shown for comparison (Panel B) are collapsed over task type (directional and non-directional and are for conditions where the spatial frequencies were the same as tested in the form condition.

CHAPTER 5
General Discussion

In this thesis I examined the development of sensitivity to first- and second-order motion during childhood. At 3 and 6 months, infants detect the difference between static and drifting gratings whether they are defined by first- or second-order cues but at 3 months they show no evidence of discriminating the direction of motion (Chapter 2). Sensitivity to the direction of second-order motion becomes adult-like by 7 years of age, while sensitivity to the direction of first-order motion is not adult-like even at 10 years of age (Chapter 3). Furthermore, in both children and adults, sensitivity to first- and second-order motion is limited by different testing parameters. Specifically, thresholds for first-order motion varied with temporal frequency (Chapter 3) while thresholds for second-order motion varied with spatial frequency (Chapter 3) or temporal frequency (Chapter 4), depending upon the range of values tested.

In Chapter 2, sensitivity to first- and second-order motion was examined using forced-choice preferential looking with 3- and 6-month-olds and habituation with 3-month-olds. The forced-choice preferential looking study showed that infants' sensitivity to the difference between first-order static and drifting gratings doubles from 3 to 6 months of age. Sensitivity to the difference between second-order static and drifting gratings also improves, although to a smaller degree. However, at both ages, infants' sensitivity to second-order gratings is more adult-like than their sensitivity to first-order gratings. In contrast to earlier studies of infants' sensitivity to first- and second-order gratings (Thibault, Brosseau-Lachaine, Faubert, & Vital-Durand, 2007), I was able to rule out the possibility that infants' thresholds were based on sensitivity to form by using a control and test stimulus that were identical in form. Furthermore, infants' sensitivity to motion was measured using a method of constant stimuli. Thus, unlike earlier studies (Atkinson, Braddick, & Wattam-Bell, 1993; Braddick, Atkinson, & Hood, 1996), I was able to quantify sensitivity to first- and second-order information in infants. In a subsequent habituation task, 3-month-old infants showed no evidence of sensitivity to direction of motion. Together, the findings from the forced-choice preferential looking and habituation experiments suggest that 3-month-olds are likely sensitive to the flicker of the gratings rather than their direction of motion. These results represent one of the first studies in which infants' sensitivity to both first- and second-order drifting gratings was measured using behavioural methods.

In Chapter 3, sensitivity to the direction of first- and second-order motion was measured over a small range of different temporal frequencies, spatial frequencies, and velocities in children aged 3, 5, 7, and 10 years and in adults. As with infants, children's sensitivity to second-order motion was always more adult-like than their sensitivity to first-order motion. Like Bertone, Hanck, Cornish, and Faubert (2008), I also found that sensitivity to second-order motion reaches adult-like values before sensitivity to first-order motion. Specifically, sensitivity to second-order motion was adult-like at 7 years of age while sensitivity to first-order motion was still not adult-like by age 10. Regardless of age, sensitivity to direction of first-order motion varied with temporal frequency, while sensitivity to second-order motion varied with spatial frequency: first-order thresholds were better when temporal frequency was 6 Hz rather than 1.5 Hz, while second-order thresholds were better when spatial frequency was 0.25 cyc/deg rather than 1 cyc/deg. These results are consistent with the hypothesis that first- and second-order motion are processed by different mechanisms. They fit nicely with the evidence of Seiffert and Cavanagh (1998; 1999) suggesting that first-order motion is processed using a low-level motion-sensitive mechanism, one which should be sensitive to changes in temporal parameters, while second-order motion is processed using a mechanism that operates by tracking the position of features over time, one which should be sensitive to changes in spatial parameters. Further discussion of feature tracking will be presented below.

In Chapter 4, 5-year-olds' and adults' sensitivity to second-order motion was measured using a directional and a non-directional motion task. Unlike Chapter 3, the results from Chapter 4 suggest an important role of temporal frequency in sensitivity to second-order motion. When temporal frequency was relatively high (6 Hz), both adults and children were much more sensitive to non-directional motion, a task in which the observer is required to discriminate drifting from stationary gratings, than directional motion, a task in which the observer is required to discriminate direction of motion. However, when temporal frequency was lower (0.75 Hz), sensitivity to directional and non-directional motion did not differ from each other. Overall, thresholds varied with temporal frequency rather than spatial frequency or velocity. These findings are consistent with previous work reporting that second-order motion mechanisms are most sensitive at lower temporal frequencies (below 1 Hz) and less sensitive as temporal frequency increases beyond 3 Hz (Derrington and Cox, 1998; Seiffert & Cavanagh, 1998). As expected, 5-year-olds' sensitivity to second-order motion was immature in all conditions tested. However, the size of the immaturity was greater when temporal frequency was 0.75 Hz rather than 6 Hz.

Sensitivity to first-order, but not second-order, form was evident at 3 months of age using habituation (Chapter 2). The results of Chapter 3 indicate that sensitivity to form, as measured by a horizontal/vertical discrimination tasks, is adult-like by age 5 when defined by second-order cues, but not until age 10 when defined by first-order cues. Furthermore, sensitivity to this form cue is adult-like before sensitivity to the direction of its motion, regardless of whether the stimuli are first- or second-order. This pattern is consistent with that reported previously for infants. Visual evoked potentials (VEPs) for orientation reversals are evident at a younger age than VEPs for directional reversals, indicating that sensitivity to form emerges before sensitivity to motion, at least as measured by these parameters (Braddick, Birtles, Wattam-Bell, & Atkinson, 2005).

Across all studies, children did not have adult-like sensitivity to first- and second-order stimuli until at least 5 years of age (second-order form) or even past 10 years of age (first-order motion). Age differences in non-visual factors, such as attention or motivation, cannot fully account for these results. In each chapter, the size of the age differences in thresholds varied across conditions. For example, in Chapter 2, 3-month-olds' thresholds were more adult-like when tested with second-order drifting gratings than first-order drifting gratings. However, at the same age, infants showed evidence of sensitivity to changes in first-order form, but not second-order form. In Chapter 3, children reached adult-like thresholds for first- and second-order form and motion at different ages, and for first-order motion, this varied with the temporal frequency of the gratings. Similarly in Chapter 4, the size of 5-year-olds' immaturity to second-order motion varied with temporal frequency. There is no obvious way for non-visual factors to explain these differences across conditions.

Comparisons across chapters allow additional conclusions to be drawn about the development of sensitivity to motion. It is interesting that sensitivity to second-order motion varied with spatial frequency in Chapter 3 and temporal frequency in Chapter 4. An explanation for this difference in findings may lie in the differences in the range of temporal frequencies and spatial frequencies tested. In Chapter 3, temporal frequency was 1.5 or 6 Hz, and spatial frequency was 0.25 or 1 cyc/deg. In Chapter 4, temporal frequency was 0.75 or 6 Hz and spatial frequency was 0.125, 0.5, 1 or 2 cyc/deg. Previous research indicates that direction discrimination for second-order motion is best when temporal frequency is below 1 Hz and quickly declines when temporal frequency reaches 3 Hz (Derrington & Cox, 1998; Seiffert & Cavanagh, 1998). Temporal frequency influenced the results when the comparison included a value below 1Hz (0.75 Hz) with one well above 3 Hz (6Hz) in Chapter 4, but not when the comparison included two values that were both above the 1 Hz cut off in Chapter 3 (1.5 and 6 Hz). Sensitivity to second-order drifting gratings may have increased when temporal frequency was especially low in Chapter 4 (0. 75Hz), above that shown in all other conditions with higher temporal frequencies.

Another, though not mutually exclusive, explanation for the difference in findings across studies is that in both Chapters 3 and 4, spatial frequency exerted a *categorical* rather than a *continuous* effect on sensitivity to second-order motion. Second-order thresholds were worse when spatial frequency was around 1 cyc/deg or higher, than when spatial frequency was below 1 cyc/deg. This is demonstrated with adults' data for the direction discrimination task that was common to both chapters. As shown in *Figure 1,* little to no variation is found in second-order thresholds for spatial frequencies of 1 cyc/deg and above, or among spatial frequencies below 1 cyc/deg. However, thresholds for conditions where spatial frequency is 1 cyc/deg or higher are always higher than thresholds for conditions where spatial frequency is less than 1 cyc/deg.

5.1 Second-Order Motion Mechanisms

One candidate mechanism of second-order motion processing is feature tracking. Feature tracking operates first by extracting features and then by analyzing changes in their location (Derrington, Allen, & Delicato, 2004). The findings that both lower spatial frequencies (Chapter 3) and lower temporal frequencies (Chapter 4) lead to better second-order motion discrimination thresholds are consistent with the notion that feature tracking is used to process second-order motion, at least under the conditions tested here. As spatial frequency decreases, the stripes that compose the grating get larger, making them easier to extract and, thus, track. Similarly, as temporal frequency decreases, the features change location at a slower rate, and therefore, should also be easier to extract and then track (Derrington et al., 2004). This interpretation is consistent with previous evidence from adults that sensitivity to second-order motion drops rapidly when temporal frequency is above 3-4 Hz, while sensitivity to first-order motion remains stable or even improves over the same temporal frequency range, regardless of whether sensitivity is measured using displacement thresholds for motion discrimination tasks (Seiffert & Cavanagh, 1998) or depth modulation thresholds for direction discrimination tasks (Derrington and Cox, 1998).

Together, the results in Chapters 3 and 4 from children and adults are consistent with the hypothesis that, under the conditions tested, first-order motion is processed using a low-level motion sensitive mechanism and second-order motion is processed using a feature tracking mechanism. The low-level motion mechanism operates on the basis of cells tuned to direction of motion and improves with increased rate of change (temporal frequency). The feature tracking mechanism operates by tracking the position of the elements that make up the stimulus across space and time and functions better as those features become easier to track because they are larger or change position more slowly. In Chapter 3, the pattern of results shows that first-order motion thresholds decrease (i.e., improve) as temporal frequency *increased* from 1.5 to 6 deg/sec. This differs from results for second-order motion for both Chapters 3 and 4. In Chapter 3, second-order motion thresholds vary with spatial frequency rather than temporal frequency: thresholds are better for low spatial frequencies. In Chapter 4, second-order motion thresholds decrease (*i.e.*, improve) as temporal frequency *decreased*, the opposite pattern from that found for first-order motion in Chapter 3.

The pattern of results for the motion tasks versus the form task is also consistent with the idea that, under the conditions tested, first-order motion is processed using a low-level motion sensitive mechanism, while second-order motion is processed using a feature tracking mechanism. In Chapter 3, first-order motion thresholds were slightly better than first-order form thresholds (for horizontal/vertical discrimination), while in Chapters 3 and 4, second-order motion thresholds were worse than second-order form thresholds. This relationship implies that the direction of first-order motion could be discriminated at luminance contrasts so low that the grating could not be detected well enough to see its orientation, as would be expected from low-level motion mechanisms based on motion energy detectors (Adelson & Bergen, 1985; Smith & Ledgeway, 2001). On the other hand, second-order motion was discriminated only once the contrast was high enough for the grating and its orientation to be detected. This pattern of results is expected if feature tracking is used to process motion, as the features must be extracted before motion can be tracked.

It must be noted that feature tracking is simply one candidate mechanism for second-order motion processing; feature tracking should be not be considered synonymous with second-order motion mechanisms (Smith & Ledgeway, 2001). In other studies in which the results suggested that second-order motion was processed using a feature tracking mechanism, this was true under some testing conditions but not others. For example, Seiffert and Cavanagh (1998, 1999) found patterns of results suggesting that adults process motion using a feature tracking mechanism for second-order stimuli that are at low contrasts or moving at a lower speed, but a low level motion sensitive mechanism for second-order stimuli that are of higher contrast (greater than 10 times detection threshold) or moving at a higher speed (above 2 Hz; absolute speed of radial grating 5.5-12 deg/sec), as well as for first-order stimuli. Ukkonen and Derrington (2000) found a similar pattern of results using a pedestal test. As described in the Introduction, a pedestal is a static stimulus that is added to a drifting stimulus (e.g. a static grating added to a moving grating). A pedestal is expected to disrupt a feature tracking mechanism because a mismatch between the location of the moving features and the stationary features occurs. However, for a motion energy detector, the net motion signal is unchanged by the stationary pedestal because it ignores static stimuli, and motion processing should remain unaffected, or be immune to the pedestal (Lu & Sperling, 2001). Ukkonen and Derrington (2000) found that the pedestal had a deleterious effect on sensitivity to direction of second-order motion when the grating was low contrast, but no effect on sensitivity to second-order motion when the contrast of the grating was high. Similarly, the pedestal had no effect on first-order motion processing. In sum, second-order motion may be processed using feature tracking under some testing conditions and a low-level motion mechanism under other testing conditions.

Evidence of feature tracking has also been reported for stimuli that are not considered to be second-order. Using luminance-defined random dot kinematograms of various element sizes, Smith and Ledgeway (2001) found results that were consistent with predictions based both on motion energy detectors (a low-level motion mechanism) and on feature tracking mechanisms. They concluded that motion energy mechanisms are most sensitive when element size is small, while feature tracking mechanisms are most sensitive when element size is larger. Furthermore, adults' accuracy showed no clear separation at any specific element size; rather the pattern of results suggested both mechanisms operate simultaneously for some element sizes. Based on these findings, Smith and Ledgway suggested that motion energy and feature tracking mechanisms operate in parallel, with the most sensitive mechanism determining accuracy. Although I found no evidence to suggest that motion energy and feature tracking mechanisms operate in parallel, I did find that increased element or feature size (lower spatial frequency) resulted in higher sensitivity to motion for low-contrast second-order stimuli. As reviewed above, evidence suggests that low contrast second-order motion is processed using a feature tracking, rather than a motion energy mechanism (Seiffert & Cavanagh, 1998; 1999; Ukkonen & Derrington, 2000).

5.2 Development

Further understanding of the developmental trajectory of sensitivity to first- and second-order drifting gratings can be drawn from comparing the results from Chapters 2 and 3. *Figure 2* shows the pattern of children's immaturities to motion (expressed as multiples of adults' thresholds tested under the same conditions) for both Chapters 2 and 3. These comparisons are complicated by the possibility that thresholds are mediated by different mechanisms at different ages and under different testing conditions. Thus, infants' sensitivity to drifting gratings may reflect sensitivity to flicker and/or sensitivity to motion, while the tasks I used assured that older children's sensitivity to first- and second-order gratings reflect sensitivity to direction of motion. In older children and adults, we suspect that the sensitivity we measured for direction of first-order motion is based on low-level motion mechanisms, while the sensitivity we measured for direction of second-order motion is based on feature tracking mechanisms. We don't know if the same is true in younger children.

Nevertheless, 3-month-olds' sensitivity to first-order drifting gratings is many multiples worse that adults'. First-order thresholds improve quickly between 3 months and 7 years of age (*Figure 2*). The slope of improvement levels out between 7 and 10 years of age, although children are still worse than adults, even at 10 years of age. The rate of improvement is more gradual and consistent for second-order gratings between 3 months and 7 years of age, with thresholds reaching adult-like values by age 7. At all ages, children are much closer to adults' mean thresholds for second-order than first-order stimuli. Furthermore, the rate of change is much steeper for the trajectory of development for first-order than second-order stimuli. This pattern of results indicates that the mechanisms involved in processing first-order drifting gratings undergo greater improvements from infancy to adulthood than the mechanisms that process second-order motion.

Results from previous research are mixed with respect to the developmental trajectory of first- versus second-order motion. Thibault et al. (2007) reported that sensitivity to first- and second-order drifting gratings matured at an equal rate in children ranging from just under one year of age until about 7 years of age. However, their method may have measured sensitivity to form or flicker rather than motion. Moreover, individual thresholds for children in the extra-clinical group (typically developing controls) continued to improve after 30 months of age for first-order stimuli, but remained relatively constant over the same age range for second-order stimuli. This suggests that sensitivity to second-order information asymptotes before sensitivity to first-order information. A reanalysis of the data from Ellemberg et al. (2003) indicates that 5-year-olds' sensitivity to first-order motion was more immature than their sensitivity to second-order motion, at least when temporal frequency is relatively low. Similarly, a reanalysis of the data from Bertone et al. (2008) indicates that 5- to 6-year-olds' sensitivity to first-order motion was more immature than their sensitivity to second-order motion, and as they reported, children reach adult-like thresholds for second-order motion by 7-8 years of age, an age at which their first-order thresholds were still not adult-like. Similarly, the results of the current study indicate that sensitivity to second-order motion reaches adult-like levels before first-order motion.

Like the reanalysis of previous studies, one question that arises from the results in this thesis is why sensitivity to first-order motion is so immature during childhood. It is important to remember that typical children, although not as sensitive as adults to first-order motion, can still detect it and its direction over a large range of values (for example, as measured in Chapter 3, 3- and 5-year-olds were accurate at discriminating the direction of first-order motion with luminance modulations ranging from 0.6 to 2 percent, depending upon the stimulus parameters). Furthermore, adults' ability to discriminate first-order motion becomes extremely fine-tuned compared to their relative lack of sensitivity to second-order motion. The late development of adult-like sensitivity may simply reflect the fact that adults eventually become exquisitely sensitive to first-order motion. Such fine-tuning may require years of visual development, possibly sculpted by environmental input.

5.3 Source of Immaturities

The location of the visual immaturities limiting children's sensitivity to motion is beyond the scope of this thesis; however the literature can provide some insight. One set of limiting factors in infants and young children may be the optical and photoreceptor immaturities of the developing eye. For example, infants compared to adults, have smaller and shorter eyes, smaller pupils, and photoreceptors that are less densely packed and that work less efficiently (Banks & Bennett, 1988). However, these front end-immaturities do not account solely for the differences in vision between infants and adults. In a number of studies and on a variety of visual tasks, infants' visual performance is worse than that predicted by ideal observers with the front- end immaturities of an infant (Allen, Bennett, & Banks, 1992; Banks & Bennett, 1988; Candy, Crowell, & Banks, 1998). Thus, post-receptoral mechanisms, discussed in further detail below, must also contribute to the differences observed between infants and adults.

With increasing age, post receptor immaturities likely become the largest or even the sole cause of the observed differences in performance between children and adults. At 4 years of age photoreceptor density and morphology are still not adult-like (Yuodelis & Hendrickson, 1986). This has not been examined in older children. However, based on the finding that monkeys reach adult-like cone packing densities at 15 - 18 months of age (Packer, Hendrickson & Curcio, 1990), Hendrickson (1994) suggested that human cone packing density reaches adult-like levels between 5 - 8 years of age. Furthermore, in humans, other aspects of visual sensitivity, such as grating acuity, reach adult-like values by age 4 - 6 years of age (Mayer & Dobson, 1980; van Hof-van Duin & Mohn, 1986). This implies that vision is no longer impacted by front-end immaturities and suggests that photoreceptors have also become adult-like by the same age. Based on this evidence in monkeys and humans, the differences observed between adults and children at 7 and 10 years of age (Chapter 3) likely reflect immaturities in post-receptoral mechanisms, while the differences observed between adults and infants (Chapter 2), and between adults and 3- and 5-year-olds (Chapter 3) may reflect immaturities in both receptoral and post-receptoral mechanisms.

The source of post-receptoral immaturities in the visual system in infants and children is unlikely to be the retinal ganglion cells or the lateral geniculate cells. In kittens, the functional development of the retinal ganglion cells proceeds rapidly after eye opening. Within 1-2 weeks, retinal ganglion cells become responsive to light, and quickly begin to respond with the regularity and robustness that characterizes adult cells (Tottle, 1993). In monkeys, the transmission of spikes from retinal ganglion cells to cells in the lateral geniculate is as reliable in monkeys at 1 and 4 weeks of age as in adult monkeys (Movshon, Kiorpes, Hawken, &

Cavanaugh, 2005). In the same study, the spatial and temporal resolution and contrast response of cells in the lateral geniculate nucleus showed some improvement between 1 week of age and adulthood. However Movshon et al. demonstrated the change in LGN response properties for tests of spatial resolution and contrast sensitivity were small compared to changes in performance on the same task when measured behaviourally. In a further comparison, Movshon et al. demonstrated that spatial resolution and contrast sensitivity predicted by cone morphology also changed little with development compared to behavioural measures. Therefore, Movshon and colleagues concluded that visual immaturities, as measured using behavioural methods, resulted from immaturities in the visual cortex rather than in the lateral geniculate nucleus or retina.

One source of post-receptoral immaturities is the primary visual cortex (area V1), (Kiorpes & Movshon, 2004). Studies of macaque V1 cells show that their receptive field size decreases and their spatial resolution improves with age (Movshon, Kiorpes, Cavanaugh, & Hawken, 1999; 2000). Furthermore, monkey V1 responses to motion show developmental improvements in response amplitude (spikes/second) and specificity or bias in response to particular directions of motion (Hatta et al., 1998). These measures revealed a great degree of improvement between 1 and 4 weeks of age, though a small degree of change can still be noted between 4 and 8 weeks of age and between 8 weeks of age and adulthood.

Although significant postnatal changes in V1 likely account for much of the changes observed in the development of sensitivity to motion, changes in higher visual areas can be expected to limit performance as well. As demonstrated by Hatta et al. (1998), neural activity measured in macaque single cells in area V1 in response drifting sign wave gratings reaches adult-like levels by about 4 weeks of age. However, macaques' performance on local motion detection and discrimination tasks measured using behavioural methods show significant improvement between 9 and 35 weeks and even between 35 and 58 weeks of age (Hall-Haro & Kiorpes, 2008). These differences in development measured using behavioral and single cell recording in the monkey suggest that areas beyond V1 also undergo significant maturation and are source of post receptoral immaturities.

To date, very few studies have directly investigated developmental changes in MT (Kiopres & Movshon, 2004). The evidence available suggests that are MT develops along the same time course as earlier visual areas, reaching maturity before other extrastriate areas. One technique to provide such evidence was based on immuno-reactive labelling to reveal the neurofilament protein subunits associated with the late phase of neural development. As measured by this technique, MT development in marmosets is synchronous with V1 development, but lags behind the development of area V4, and the medial superior temporal area (MST), which lies upstream of area MT (Bourne & Rosa, 2006). Similarly, macaque V1 and MT show similar age related increases in glucose uptake (a measure of metabolic activity) in response to a moving stimulus (Distler, Bachevalier, Kennedy, Mishkin & Ungerleider, 1996). These results suggest that visual immaturities to motion that are not explained by area V1 may lie upstream of area MT.

Although the areas in the visual stream beyond V1 have not been examined to the same degree as V1, general sources of immaturities that involve the whole cortex include myelination and synaptogenesis, which continue after birth in both monkeys (Rodman, 1994) and humans (Huttenlocher, De Courten, Garey, & Van der Loos, 1982; Yakalev & Lecours, 1967). For example, synaptic density in area 17 in the striate visual cortex increases postnatally to reach a maximum by about 8-12 months of age, after which it declines to adult levels until about 11 years of age (Huttenlocher, 1992). Immature myelination of the visual cortex would cause inefficient transmission of the visual signal throughout the cortex and could account for visual immaturities in both infants and children. In general, myelination progresses in a hierarchical pattern beginning in lower subcortical areas and proceeding later to cortical areas of the brain. For example, in a postmortem study of human myelination, Yakovlev and Lecours (1967) found that myelination of the subcortical sensory areas occurs rapidly and ends during the first post-natal year. Cortical sensory areas have a more protracted time course of myelination that continues until about the end of the first decade of life. Myelination of association areas of the cortex is even more protracted, ending around the end of the second decade of life, and perhaps even later.

5.4 Limitations

There are a number of limitations in the studies described in this thesis. In Chapter 2, the forced-choice preferential looking method may have underestimated infants' sensitivity to drifting gratings. Allen et al. (1992) demonstrated that forced-choice preferential looking measures of infants' grating acuity were worse than those obtained by VEP techniques. However, in their study and in many others (e.g., Aslin & Shea, 1990; Thibault et al., 2007) measures were based on a threshold performance criterion of 75% or higher. In Chapter 2, an above chance preference (50%) was used as the criterion to indicate that infants were sensitive to the difference between the static and drifting grating. This reduced criterion may help to limit any underestimation of infants' sensitivity to drifting gratings introduced by the forced-choice preferential looking method. However, it is still possible that infants could detect the difference at lower depth modulations and that the difference was too weak to induce a looking preference.

In Chapter 3, slightly different methods were used to test 3-year-olds from those used with older subjects; the most notable difference was the lack of practice staircase trials for 3-year-olds. The difference in method was necessary to ensure that all subjects were tested with a method that allowed the *best* estimate of their sensitivity to motion. Pilot testing demonstrated that 3-year-olds were fatigued when a practice staircase was included in the task, subsequently performing worse, while older subjects performed better when a practice staircase was included in the procedure. Because 3-year-olds did not have the added benefit of practice it is likely that their thresholds are underestimated; however, this is a necessary limitation because the effects of practice-related fatigue outweighed any benefits that were gained by practice in the age group. Note also that this underestimation applies to all conditions equally and hence cannot explain the pattern of thresholds across conditions.

Another limitation of the results in this thesis is that the tasks used measured thresholds, while natural images contain above threshold information. The effects of age, spatial frequency, temporal frequency, and speed that I observed on thresholds may not generalize to above threshold stimuli. Although this is true, an understanding of sensitivity to first- and second-order stimuli at threshold levels is also important, as natural visual scenes contain information that is both at the threshold level and at suprathreshold levels. Furthermore, threshold measures serve as a necessary method to quantify age-related differences in sensitivity to first- and second-order information. Studies of the development sensitivity to first- and second-order motion using above threshold stimuli could be carried out using first- and second-order stimuli that are equated for visibility at each age group and by measuring threshold that are not dependent upon contrast, such as displacement thresholds and minimum or maximum velocity thresholds.

5.5 Future Research

There are a number of questions left to be answered. In Chapter 2, we did not test 6-month-olds' sensitivity to direction of motion because this age group is very difficult to test with such simple stimuli in a habituation paradigm. In fact, there are no published studies that have examined sensitivity to the direction of *uniform* motion beyond about 3 months of age. It may be possible to test 4- or 5-month-olds with our current habituation method to see if they show recovery of attention to a novel direction of motion. The habituation task could be made more interesting for 6-month-olds by using a variety of different uniform directional stimuli in both the habituation and test phase. Infants could still be habituated to one direction of motion and be tested for recovery in attention in the opposite direction, as long as the variations across trials in other stimulus properties was interesting enough to maintain their attention. In the habituation phase the patterns could include gratings, dots, and checks, all presented sequentially, and all moving in one direction of motion (e.g., rightwards). Once habituated, infants would then be presented the opposite direction of motion (e.g., leftward) using the same pattern that created the motion in the last trial of the habituation phase. This would avoid a confound between a change in direction of motion and the pattern of the stimulus. This procedure has been used successfully in the past to determine if infants can discriminate male from female faces after being habituated to a variety of faces of the same sex (Quin, Yahr, Kuhn, Slater, & Pascalis, 2002) and to determine if infants can discriminate colours after being habituated to various shades of grey (Adams, Maurer, & Davis, 1986).

In addition to using stimuli that capture older infants' attention, eye movements could be monitored using eye tracking equipment and/or recorded and later analyzed off line. This may make the shorter fixations and faster saccades of older infants easier to measure for habituation tests. The only drawback of off-line analysis is that it would require fixed-trial rather than infant-controlled habituation procedures. Fixed-trail procedures limit the duration of stimulus presentation to a predetermined display time rather than basing the end of the trial on a change in the infant's behaviour. Unlike the infant-controlled procedure, the fixed-trials technique has been criticized as it does not account for individual differences in the time required for each infant to become habituated to a stimulus (Bornstein, 1985).

In Chapter 3, we did not determine the age at which children reach adult-like thresholds for first-order motion. Although there is evidence that 10-year-olds were adult-like for one condition, they were immature for the other conditions. Older children should be tested to determine when sensitivity to first-order motion becomes adult-like for all conditions. Based on the findings that 10-year-olds' thresholds were only slightly worse than adults when tested on sensitivity to form and motion (see Chapter 3), it is likely that children reach adult-like thresholds shortly after 10 years of age.

Further research on the effect of temporal frequency, spatial frequency and velocity is also warranted. In Chapters 3 and 4, the effect of spatial and temporal frequency on sensitivity to motion was examined, and their effects on sensitivity to second-order motion were found to differ across the two chapters. The effects of both parameters seemed to be the strongest when spatial frequency was below 1 cyc/deg and temporal frequency was below 1 Hz. Pairing low spatial frequencies with a range of high and low temporal frequencies and low temporal frequencies with a range of high and low spatial frequencies would help to disambiguate the influence of spatial and temporal frequency on sensitivity to second-order motion. This could be done easily in adults, either in a between- or within-subjects design; however, the number of conditions may require too many groups of children to make any examination of the development of sensitivity to motion over such values feasible. Ideally, test conditions would include a minimum of two to three spatial frequencies each paired with at least three different temporal frequencies, resulting in at least six to nine conditions. As children cannot be tested reliably on all of these conditions in a within-subjects design during a single session, one possibility would be to test children in each age group on all conditions over multiple testing sessions. Although feasible, a high participant drop out rate would be expected, as children (and their parents) may quickly lose interest in completing multiple sessions. Another possibility would be to use a between-subjects design in which each condition would require at least 10 children, resulting in a minimum requirement of 60 - 90 children in each age group to be tested.

Comparisons of neuroimaging results in adults in children may also help identify the source of the immaturity in first- versus second-order motion. However, because fMRI studies in adults have shown mixed results, considerable work is likely needed on BOLD responses to first- versus second-order motion in adults before this is feasible. Some studies have shown little difference in pattern of activity in response to first- versus second-order motion (e.g. Nishida, Sasaki, Murakami, Watanabe, & Tootell, 2003; Seiffert, Somers, Dale, & Tootell, 2003). However, with certain approaches, different patterns of activation have been found for first versus second-order motion. Using gabor micropatterns that contained both first- and second-order structure, Dumoulin and colleagues (Dumoulin, Baker, Hess & Evans, 2003) ensured that both first- and second-order conditions contained first- and second-order structure, a condition that was not met by some previous studies. They were able to equate performance levels and force direction discrimination by either first- or second-order mechanism by varying the lifetime, coherence, and carrier phase of the stimulus. This was possible because the correct net direction of motion could be determined based on one type of motion cue, first-order or second-order. After identifying the region that was activated by *any* aspect of the stimulus (using stimulus versus blank control) Dumoulin and colleagues compared the pattern of relative activation for first- versus second-order motion conditions. This comparison revealed that activation in area V1 and V2 was stronger for first-order stimuli, while higher visual areas showed stronger activation for second-order motion, specifically the lateral occipital cortex near human MT complex.

Adaptation experiments reveal another solution in determining if cortical activity is selective for first- versus second-order motion. Because fMRI resolution is rather coarse, activation in a particular voxel could represent more than one process or mechanism, and the pattern of activation may not be distinguishable for one stimulus versus another (Ashida, Lingnau, Wall & Smith, 2007). By using a direction selective adaptation paradigm, previously shown to produce no cross adaptation between first- and second-order stimuli (Nishida, Ledgeway, & Edwards, 1997), Ashida and colleagues examined human MT complex for direction-selective adaptation effects. Specifically, they compared how the BOLD signal decreased when the same direction of motion was repeated versus varied on sequential trials. A decrease in BOLD signal on repeated trials indicates that neurons in the voxel are involved in processing the repeated parameter. They used this method as it allows for comparison of the pattern activation resulting from different sets of neurons in the same neural area being activated by different stimuli. They found direction selective-adaptation in both fMRI activity and detection thresholds when the adaptation and test stimuli were of the same type (i.e., both first-order or both second-order). However when the adaptation and test stimulus were of the opposite type, no direction-selective adaptation occurred. The same pattern of adaptation was found for area V3a and for MST and MT when analyzed separately. However, it could not be determined where adaptation actually occurred, because the adaptation measured in MT+ and V3a could have resulted from adapted input signals in earlier processing levels and the stimuli were not optimized for measuring cortical adaptation in these earlier visual areas. The response of these areas could be more readily determined by using stimuli that produced an optimal response for each area of interest and scanning procedures intended to locate each area of interest separately. (Ashida et al., 2007)

In Chapter 3 and 4, five-year-olds' sensitivity to motion was considerably worse than that of adults. Although imaging studies are difficult to conduct with young children, previous studies have shown that fMRI can be carried out successfully with children 5 years of age or even younger (e.g., Byars et al., 2002; Schapiro et al., 2004). fMRI studies in children could be used to determine if relative patterns of activation show significant differences from those in adults measured by Dumoulin and colleagues (2004). Similarly, once the areas responsible for direction selective adaptation measured by Ashida and colleagues (2006) are established in adults, comparisons between children and adults could be made. At the very least, these comparisons may reveal if differences between children and adults occur early or late in the visual stream and how these differences change with age.

Also of importance with imaging studies is to test second-order motion under different conditions. Here we measured contrast thresholds, a method that seems to favour feature tracking mechanisms as opposed to low-level motion mechanisms. Conditions that favour feature tracking mechanisms likely tap different neural mechanism than conditions that favour low level motion mechanisms. This could result in different patterns of neural activation. Imaging and behavioural studies undertaken to understand the immaturities reported in Chapters 2 and 3 with second-order stimuli could be contrasted with imaging and behavioural results based on tasks where a low-level motion sensitive mechanism is likely responsible for sensitivity to motion, such as high contrast or speed conditions (Seiffert & Cavanagh,1998; 1999, Derrington et al., 2004).

5.6 Summary

In summary, I have shown that, under the conditions tested in this thesis, sensitivity to first- and second-order drifting gratings develops at different rates. Between 3 months and 5 years of age, sensitivity to second-order drifting gratings is more adult-like than sensitivity to first-order drifting gratings. Furthermore, at 7 years of age, sensitivity to the direction of second-order motion reaches adult-like levels, while sensitivity to the direction of first-order motion is not adult-like even at 10 years of age. In both children and adults, sensitivity to the direction of first-order motion is best when temporal frequency is high, while sensitivity to the direction of second-order motion is best when spatial frequency is low (Chapter 3) or when temporal frequency is low (Chapter 4). The different results for the developmental trajectories and the different effect of parameters on sensitivity to first- versus second-order motion support the idea that first- and second-order motion are processed by different mechanisms. These results are also consistent with the idea that low contrast first-order motion is processed using motion sensitive mechanisms, while low contrast second-order motion is processed using feature tracking mechanisms and that these differences have emerged by 3 years of age.

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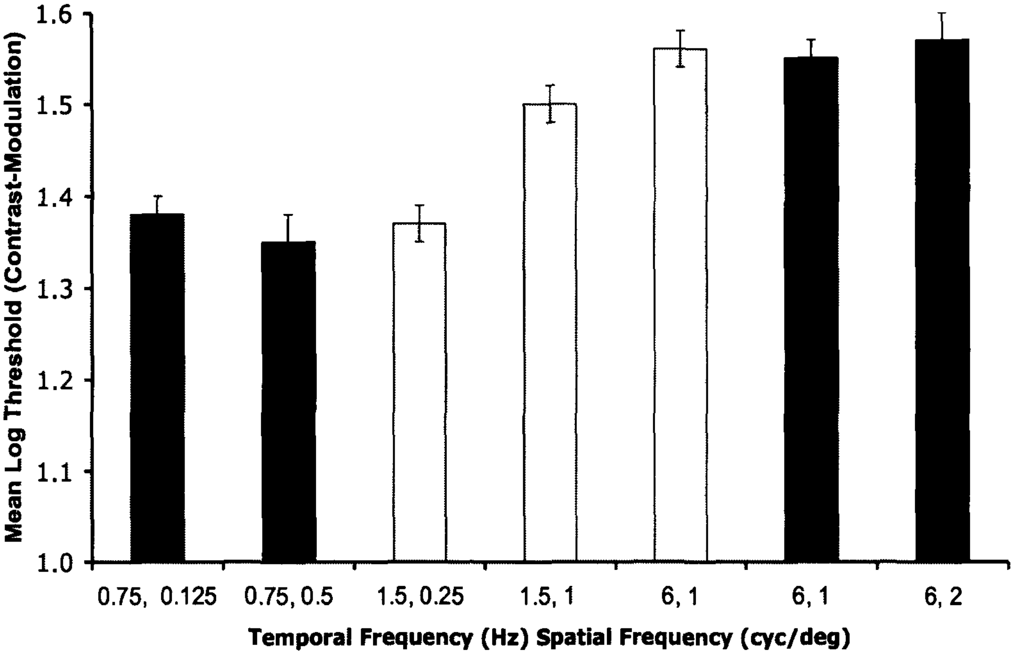

Figure 5.1. Adults' thresholds for second-order direction discrimination measured in Chapters 3 (light grey) and 4 (dark grey) plotted in relation to the spatial frequency of the conditions tested. Error bars represent standard error of the mean.

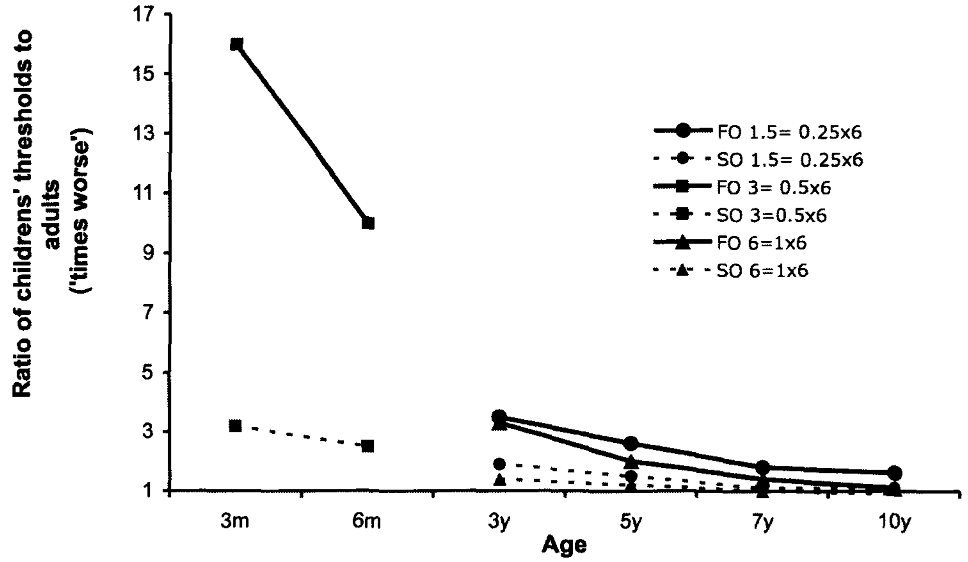

Figure 5.2. Ratio of thresholds for infants and children compared to adults for first-order (solid-lines) and second-order (dashed-lines) drifting gratings. At 3 and 6 months of age, the ratio is estimated from group results on a forced-choice preferential looking task (Chapter 2). The estimate, at least at 3-months of age, likely reflects sensitivity to flicker rather than direction of motion. At 3-years of age and older, ratios reflect sensitivity to direction (Chapter 3). The legend shows conditions for different temporal frequencies, spatial frequencies, and velocities (TF = SF * V). The two conditions plotted from Chapter 3 are the ones that most closely match the temporal frequency, spatial frequency, and velocity of the stimuli used to test infants in Chapter 2.