

RESOLVING INCONSISTENCIES IN THE MATURATION OF  
HUMAN GLOBAL MOTION PERCEPTION

by

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## Abstract

The typical development of motion perception is commonly assessed with tests of global motion integration using random dot kinematograms (RDKs). There are discrepancies, however, with respect to when typically-developing children reach adult-like performance on this task, ranging from as early as 3 years to as late as 12 years. While much research characterizes performance in terms of dot speed, there is evidence that different spatial and temporal components can impact performance on this task in adults and in children. Other studies suggest that the distance that dots are displaced each animation frame ( $\Delta x$ ), rather than frame duration ( $\Delta t$ ) or dot speed ( $\Delta x/\Delta t$ ) per se, determines performance in developing macaques. No studies have directly investigated whether psychophysical performance follows this pattern in children. The current studies measured motion coherence thresholds in adults and children in two experiments. Experiment 1 examined differences in adult performance in two studies with similar RDK parameters except for the  $\Delta x$  and  $\Delta t$  used to make up similar speeds. This experiment tested four  $\Delta x/\Delta t$  pairs yielding a speed of 1 deg/s, and held the number of presented frames constant, or the duration of the stimulus constant. These factors had no effect on the thresholds of adults. Experiment 2 was designed to replicate the results of macaque studies in human children, and compare their thresholds to adults. Two  $\Delta t$  values were used in combination with seven  $\Delta x$  values, for a range of speeds (0.3-38 deg/s). Adult thresholds followed a u-shape as a function of  $\Delta x$ , with lower coherence thresholds for larger  $\Delta t$  when  $\Delta x$  was small. Child thresholds followed a rough u-shape as a function of  $\Delta x$ , regardless of  $\Delta t$ . Developmental comparisons showed children performed as well as adults for larger  $\Delta x$ , and were immature for smaller  $\Delta x$ . When parameters were expressed as speed, there was a range of intermediate speeds (4-12 deg/s) for

which maturity was dependent on the values of  $\Delta x$  and  $\Delta t$  tested. These results resolve previous discrepancies by showing that motion sensitivity to a given speed may be mature, or not, depending on the underlying spatial and temporal properties of the motion stimulus.

## **Preface**

All research described in this report was conducted through the Department of Psychology at the University of British Columbia under the supervision of Dr. Deborah Giaschi. I was responsible for programming the stimuli and experimental procedures in MATLAB, for conducting or supervising data collection, for conducting all data analysis, and for writing this manuscript.

Data from Chapter 3 were presented at the Department of Ophthalmology and Visual Sciences' Ophthalmology Research Day 2013; at PsychFest 2013; and at the Child Vision Research Society's 2013 Annual Meeting.

This research ("Brain Mechanisms Underlying Human Motion Perception") was approved by the UBC and Children & Women's Research Ethics Boards, H01-80499 and CW01-0127 (Chapter 2); H12-03331 and CW12-0344 (Chapter 3).

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## **1. Introduction**

### **1.1. Maturational Trajectories of Visual Development in Humans**

While much of the human visual system develops in utero, many components continue to mature into childhood. For example, the visual acuity of infants improves rapidly in the first 6 months of life (Mayer et al., 1995), but has a critical sensitive period for damage as late as age 10 (Lewis & Maurer, 2005; Veagan & Taylor, 1979), and does not improve to adult-like levels, depending on the aspect of acuity measured, until at least age 11 (Fern & Manny, 1986; Kothe & Regan, 1990). Sensitivity for texture-defined borders emerges sometime around 4-9 months (Atkinson & Braddick, 1992; Norcia et al., 2005; Sireteanu & Rieth, 1992), but the ability to identify texture-defined shapes is not mature until about age 11 (Parrish, Giaschi, Boden, & Dougherty, 2005) and the ability to integrate spatially-separated contours into a form is still developing at age 14 (Hadad, Maurer, & Lewis, 2010; Kovács, Kozma, Fehér, & Benedek, 1999). Stereopsis—that is, sensitivity to depth information from retinal disparities—emerges around 4 months after birth (Birch & Petrig, 1996; Fox, Aslin, Shea, & Dumais, 1980; Takai, Sato, Tan & Hirai, 2005) but stereoacuity is not adult-like until at least age 6 (Heron, Dholakia, Collins, & McLaughlan, 1985; Leat, St. Pierre, Hasan-Abadi & Faubert, 2001), and stereopsis for fine disparities is not mature even by age 14 (Giaschi, Narasimhan, Solski, Harrison & Wilcox, 2013).

Crudely, motion perception involves detecting a visual feature that has moved in time and in space. However, there are many aspects of motion perception that can be studied—for example, biological motion, motion-defined form, optic flow, and motion in depth—and many methods for studying them. Psychophysical thresholds can be measured for the detection of motion, or the discrimination of a feature of motion (e.g., motion direction). We can vary a number of stimulus

properties to obtain thresholds, like the coherence or contrast of elements in a stimulus, or the duration for which the stimulus is presented. Stimuli can include dots, stripes, plaids, or complex patterns. First-order motion is motion of objects defined by luminance differences, while second-order motion is the motion of objects defined by other features like textures, colours, or patterns.

Sensitivity to directional motion information emerges extremely early in life. Newborns make automatic, reflexive eye movements to drifting black and white bars (optokinetic nystagmus response; Kremenitzer, Vaughn, Kurtzberg, & Dowling, 1979), indicating directionally-sensitive subcortical mechanisms exist at birth. However, perceptual sensitivity to motion direction likely requires visually-driven experience. Behaviorally, babies do not show sensitivity to motion direction until around 6-8 weeks as measured with preferential looking techniques when viewing a pattern of coherently-moving dots (Wattam-Bell, 1992; Wattam-Bell, 1996a), and direction selectivity can also be measured at this age in infant VEP responses (Wattam-Bell, 1991; Braddick, Birtles, Wattam-Bell, & Atkinson, 2005). Direction sensitivity to moderate motion speeds develops first, and the range of speeds to which infants are sensitive widens quickly with age. Minimum speeds decrease from 9 deg/s at 1.5 months to 3 deg/s at 3 months when measured with moving bars (Aslin & Shea, 1990) and from 3.5 deg/s at 3 months to 1.2 deg/s at 5 months when measured with shearing motion created by moving dots (Bertenthal & Bradbury, 1992). Maximum speeds increase from 12 deg/s at 2 months to 33 deg/s at 3.5 months when measured with coherent dot patterns (Wattam-Bell, 1990). Maturity on direction-discrimination tasks with dot patterns has been shown to occur as late as age 12 (Hadad, Maurer, & Lewis, 2011).

The perception of biological motion is typically studied using point-light walkers, animated figures comprised of dots depicting a human body completing an action like walking.

Using a preferential looking technique, Simion, Regolin, and Bulf (2008) showed that newborns gazed longer at upright than inverted animations of human biological motion. The ability to accurately categorize point-light animations of humans and other moving animals is not mature until age 5 (Pavlova, Krägeloh-Mann, Sokolov & Birbaumer, 2001). When figures are embedded in noise dots in a biological motion detection task, maturity is not reached on until age 12 (Hadad et al., 2011).

A third commonly-studied aspect of motion processing is motion-defined form, the ability to perceive shapes with edges that are defined kinetically with no luminance, contrast, or chromatic cues. The ability to detect edges or boundaries defined by motion emerges sometime around 3 months of age (Johnson & Aslin, 1998; Johnson & Mason, 2002; Kaufmann-Hayoz, Kaufmann, & Stucki, 1986; Wattam-Bell, 1996b). Motion-defined form perception is mature sometime around age 7 (Giaschi & Regan, 1997; Parrish et al., 2005), age 10 (Gunn et al., 2002), or age 15 (Schrauf, Wist, & Ehrenstein, 1999), depending on the stimulus used. Children as young as 4 years are mature on motion-defined form tasks using motion speeds of 5 deg/s, but not at slower speeds of 0.9 or 0.1 deg/s (Hayward, Truong, Partanen, & Giaschi, 2011).

We use motion information to inform the representation of our bodies in space, and the ability to integrate this information also appears to have a long maturational trajectory. Optic flow—associated with the motion of the environment on the retina—is often studied with large-field expanding or contracting dots that have slow velocities at a point of focus (heading) with increasing velocities towards the periphery. Children are not mature on heading estimation tasks by age 12 (Baumberger & Fluckiger, 2004), and compared to adults, children age 7-12 rely more on visual cues than somatosensory information when they conflict on a postural sway task (Sparto et al., 2006). Motion in depth—that is, the impression that an object is moving toward or

away from one's body—shows a similar late maturation: children aged 6-11 years are worse than adults at looming detection tasks with cars as stimuli, especially when the cars travel at faster speeds (Wann, Poulter, & Purcell, 2011).

The focus of this thesis is on the maturation of global motion perception. As with the other forms of motion perception identified above, global motion perception may also have long trajectory for development.

## **1.2. Global Motion Perception**

While there are debates over the exact computational mechanisms by which it is accomplished (for review, see Braddick & Qian, 2001; Derrington, Allen, & Delicato, 2004; Snowden & Verstraten, 1999), the perception of global motion is generally considered to consist of two stages: a computation of motion vectors at local positions on the retina, and integration of these local vectors for an overall, global percept. The first stage involves direction-selective neurons in early visual area V1 (Albright, 1984). These neurons have relatively small receptive fields, and in macaques, they can detect maximum displacements of 1.28 degrees of visual angle (Mikami, Newsome, & Wurtz, 1986). Here, local movement over a small area of the visual field is computed. The second stage involves area MT, where most neurons are directionally-selective (Zeki, 1974) and have receptive fields about 10 times larger than those in V1 (Gattass & Gross, 1981; Mikami et al., 1986). MT neurons receive inputs primarily from V1 or areas that have inputs from V1 (Felleman & van Essen, 1991), and many cells have reinforcing surrounds (Born & Tootell, 1992). Here, local signals are integrated for a global percept of motion direction, likely reflected in a population of neuron responses rather than any one cell alone (e.g., Priebe & Lisberger, 2004). MT also has reciprocal connections with higher areas MST and VIP (Maunsell

& van Essen, 1983), which are involved in more complex functions like optic flow and self-motion (Duffy & Wurtz, 1991) or multisensory integration of motion information (Duhamel, Colby, & Goldberg, 1998), respectively.

While most studies of physiology and neural response properties, including those cited above, have been conducted with macaques, we have solid evidence indicating macaque models of motion perception are good descriptors of motion processing in humans from human lesion studies (e.g., Regan, Giaschi, Sharpe, & Hong, 1992; Shipp, Dejong, Zihl, Frackowiak, & Zeki, 1994; Schenk & Zihl, 1997; Vaina, Lemay, Bienfang, Choi, & Nakayama, 1990; Zihl, Voncramon, Mai, & Schmid, 1991) and functional magnetic resonance imaging studies (e.g., Dumoulin et al., 2003; Smith, Greenlee, Singh, Kraemer, & Henning, 1998; Sunaert et al., 1999; Tootell et al., 1995). It has also been possible to make direct comparisons between human and macaque brain function: for example, Orban et al. (2003) used functional neuroimaging in humans and monkeys to compare activation patterns and concluded that early visual areas and MT in macaques are appropriate functional homologues to human areas for global motion stimuli. It is important to note, however, that the human ‘MT+’ typically studied in humans represents a complex of at least three macaque areas (MT, FST, and MST, which has at least two subdivisions), which can respond to different types of motion (e.g., Orban et al., 2003; Orban, van Essen, Vanduffel, 2004). Huk, Dougherty, and Heeger (2002) were able to use functional magnetic resonance imaging to subdivide human MT+ into areas MT and MST, and found they had similar relative positions in humans as they do in macaques.

### **1.3. The Random Dot Kinematogram**

A commonly-used stimulus for assessing global motion perception is the random dot

kinematogram (RDK), an animation consisting of an array of moving dots. Early studies with random dot stimuli would use a random dot pattern that is displaced in time and space to study phi motion, the perception of movement between two still images (Anstis, 1970; Lee, 1972); and the maximum spatial displacement thresholds that lead to the perception of a coherently-moving pattern rather than two patterns presented in quick succession (e.g., Braddick, 1974).

The current paper is concerned with the RDKs introduced by Morgan and Ward (1980), and popularized by Newsome and Paré (1988). In this stimulus, some dots ('signal' dots) are moving together in the same direction, while other dots ('noise' dots) are moving in random directions.<sup>1</sup> A participant's task is to indicate the direction of the coherently-moving dots, typically in a two-alternative forced-choice paradigm. The proportion of dots moving coherently is reduced using a psychophysical method to obtain motion coherence thresholds. Lower thresholds are taken as better performance. This task has been extensively used in the context of single-unit recording and electro-stimulation studies looking at the response properties of neurons in area MT of macaques. Monkeys with MT lesions have elevated motion coherence thresholds (Newsome & Paré, 1988). The pattern of cell firing in this area varies with the coherence level of a stimulus (Britten, Shadlen, Newsome, & Movshon, 1993) and can predict a monkey's psychometric function (Britten, Shadlen, Newsome, & Movshon, 1992; Britten, Newsome, Shadlen, Celebrini, & Movshon, 1996). Stimulating direction-selective cells in this area will cause monkeys to indicate they perceived the stimulated rather than actual direction of signal motion (Salzman, Murasugi, Britten, & Newsome, 1992). This task has been adopted for use in other contexts with humans, including cross-sectional studies that compare performance of

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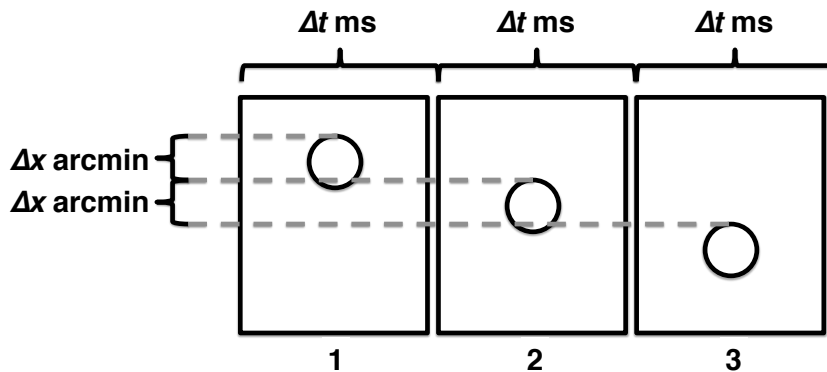
<sup>1</sup> A similar type of stimulus varies the range of directions in which all dots move rather than introducing noise dots (e.g., Williams & Sekuler, 1984). At 100% coherence, all dots move in the same direction. A bandwidth of motion directions in which the dots can move is incrementally increased until the overall average direction of motion can no longer be identified.



children or the elderly to healthy young adult controls in order to study the development of global motion perception; and in clinical studies that compare the performance of patient populations (e.g., autism, preterm children, dementia) to healthy age-matched controls.

### 1.3.1. Characteristics of an RDK Stimulus

Importantly, RDK animations are *apparent* motion stimuli, like the motion we perceive in movies. This means that a series of still frames is presented to participants quickly enough that they perceive motion rather than a sequence of stationary images. Figure 1.1 demonstrates this concept. The amount of time a single frame remains on the screen before the next frame is presented is often termed  $\Delta t$ , temporal offset, or temporal displacement, equivalent to the stimulus onset asynchrony. Stimuli with small values of  $\Delta t$  contain frames that are rapidly presented, while stimuli with large values of  $\Delta t$  contain frames that are presented at a slower rate. Animations with a frame rate of 60 Hz, for example, will display 60 frames in 1 second and have a  $\Delta t$  of 17 ms (from  $1/60$  s); while animations with a frame rate of 20 Hz will display 20 frames

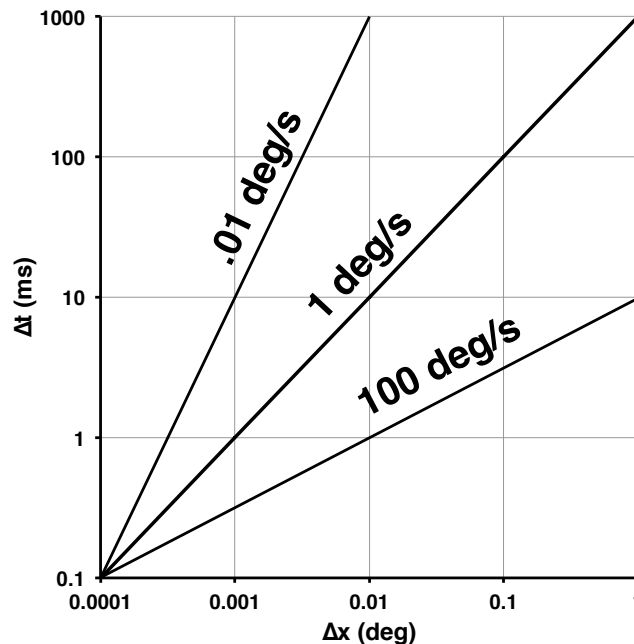


**Figure 1.1: A representation of  $\Delta x$  and  $\Delta t$  in apparent motion animations.** Frames are presented in rapid succession to participants. In this demonstration, three frames of a stimulus, labeled 1 through 3, are presented. A frame remains on the screen for  $\Delta t$  ms, after which a new frame is presented. To create the impression of motion, the animation frames presented to participants contain an object that is displaced in space from frame-to-frame. In this demonstration, a dot is displaced in the downward direction on each subsequent frame. The dot is displaced a constant distance of  $\Delta x$  arcmin between frames. Dashed lines are for illustration and are not present in the animation.

in 1 second and have a  $\Delta t$  of 50 ms (from 1/20 s). Note that the value of  $\Delta t$  will be limited by the refresh rate of the monitor displaying the stimulus such that it will be a multiple of the duration of a single monitor refresh. The total duration of a stimulus can be calculated as  $\Delta t \times (\text{total number of frames})$ .

To create the impression of motion, stimuli must also be moving in space. The distance that an onscreen object is displaced between frames is often termed  $\Delta x$ , spatial offset, or spatial displacement. Stimuli with larger values of  $\Delta x$  will contain images that have larger spatial displacements from frame-to-frame. We will refer to values of  $\Delta x$  according to retinal, rather than physical, measures; either in degrees, or in minutes of arc (60 arcmin = 1 deg).

The speed an object is moving depends on the ratio  $\Delta x/\Delta t$ , which represents the distance an object will travel over a given time. As demonstrated in Figure 1.2, a single ratio can arise from a range of  $\Delta x$  values (or a range of  $\Delta t$  values). Faster speeds can be created by holding  $\Delta x$



**Figure 1.2: A representation of speed as the ratio  $\Delta x/\Delta t$ .** In the example above, the solid lines represents  $\Delta x/\Delta t$  values that comprise the same speed. For example, objects that move 0.01 deg every 10 ms travel at 1 deg/s, the same speed as stimuli that move 1 deg every 1000 ms. Combinations of  $\Delta x$  and  $\Delta t$  that fall above the line are moving slower than 1 deg/s, and those that fall below the line are moving faster than 1 deg/s.

constant and decreasing the value of  $\Delta t$ , or holding  $\Delta t$  constant and increasing the value of  $\Delta x$ .

The following subsections comprise an incomplete list of additional parameters one must consider when creating RDK stimuli, and the effect of varying these parameters on performance.

### **1.3.1.1. Signal Dot Directions**

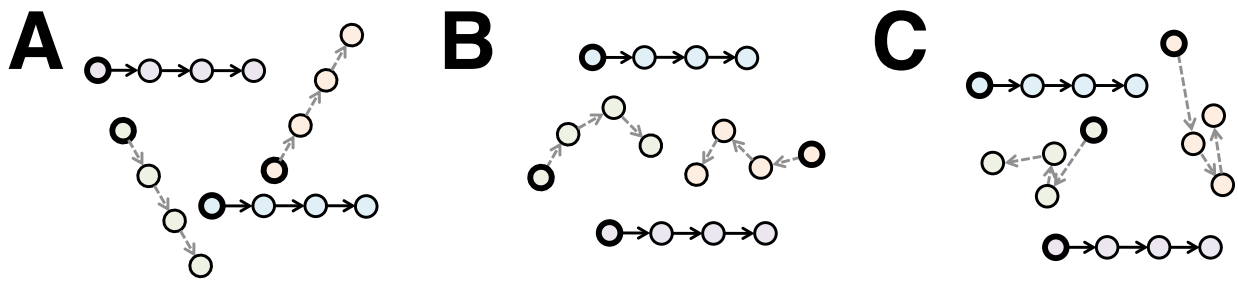
Typically, RDK stimuli are used in two-alternative forced-choice tasks that require participants to respond whether they saw coherent motion in a left or right direction, or to respond whether they saw coherent motion in an up or down direction. No consistent differences have been demonstrated between tasks that implement left/right or up/down directions, and it is assumed that motion coherence thresholds obtained under either condition are comparable. In support of this notion, studies have demonstrated an oblique effect (e.g., Greenwood & Edwards, 2007; Gros, Blake, & Hiris 1998; Matthews & Qian 1999) such that humans are more sensitive to motion in the cardinal (up, left, down, right) directions than motion in other, diagonal directions. In coherent motion *detection* tasks, however, it has been demonstrated that small directional anisotropies exist such that participants are more sensitive to left/right than to up/down coherent motion at the fovea (Raymond, 1994) and that this anisotropy is magnified at retinal eccentricities along the vertical meridian (van de Grind, Koenderink, van Doorn, Milders, & Voerman, 1993). Pilot studies I have conducted in my lab have indicated elevated thresholds for up/down compared to left/right discrimination tasks, but only for small ( $\sim 9 \text{ deg}^2$ ) stimuli with signal dots moving at moderately fast (10-18 deg/s) speeds, with no difference between coherence thresholds in stimuli with larger areas or slower speeds. Additional pilot data from my lab indicates no differences in coherence thresholds for children tested on up/down versus left/right direction discrimination tasks.

### 1.3.1.2. Dot Movement Algorithms

While signal dots are displaced in the signal direction on each frame of an RDK, noise dots are displaced in random directions. Practically, however, there are a number of algorithms that can govern how dots move. First is what dictates which dots are signal dots. Dots that are labeled 'signal' and 'noise' can hold on to these labels throughout the entire animation.

Alternately, these labels can be probabilistically reassigned on each frame such that each dot has a probability equal to the coherence level of the trial of being a signal dot. For example, at a coherence level of 0.60, 60% of the dots are selected at random to move in the signal direction, and 40% to move randomly. Scase, Braddick, and Raymond (1996) demonstrated that RDKs with probabilistic labels led to slightly higher coherence thresholds.

A second dot movement parameter to consider in RDKs is the algorithm used to displace noise dots. While signal dots are always displaced in a fixed distance in the signal direction, noise dots can be displaced in a fixed distance in a fixed direction each frame ('direction' or 'transparent' noise, Figure 1.3A); in a fixed distance in a random direction each frame ('walk' or 'brownian' noise, Figure 1.3B); or in a random distance in a random direction each frame ('white' or 'position' noise, Figure 1.3C). Scase et al. (1996) showed that the effect of noise type on motion coherence thresholds can interact with other parameters like signal dot speed or signal/noise label reassignment rule; in general, though, thresholds for stimuli using random walk noise were higher than the other two types of noise. Schütz, Braun, Movshon, and Gegenfertner (2010) demonstrated that when subjects are asked to track the motion of these three types of noise, the gain of smooth pursuit eye movements and perceived speed both decrease with decreases in coherence levels for walk and white noise, but not transparent motion.



**Figure 1.3: Examples of dot behaviour across four frames of animation under different noise algorithms.** The dark border indicates where a dot is located on the first frame, and arrows indicate where a dot is moving on subsequent frames. In each schematic, there are two signal dots moving to the right (black solid arrows) and two noise dots moving at random (grey dashed arrows). These are represented with signal and noise labels preserved throughout the entirety of the animation; signal labels can also be assigned to dots on each frame with a probability equal to that of the coherence level, such that a dot can be a signal or a noise dot at different points in the animation. A: Direction noise (also known as transparent noise). Noise dots move in a fixed distance in a fixed direction each frame. This tends to give the impression of many surfaces sliding over each other. B: Walk noise (also known as brownian noise). Noise dots move in a fixed distance in a random direction each frame. This tends to give the impression of wiggling dots. C: White noise (also known as position noise). Noise dots move in a random direction in a random distance each frame. This tends to give the impression of twinkling dots, like television snow. Figure inspired by Scase, Braddick, and Raymond (1996).

A final dot movement parameter to consider is the lifetime of dots. If dots exist on the screen and are moved along their same trajectory throughout the animation, they have unlimited lifetimes. Alternately, a dot can follow its trajectory for a limited number of frames before being replotted in a new, random start location. Lifetimes apply to both signal and noise dots. To the best of my knowledge, there is no systematic investigation of how dot lifetime impacts motion coherence thresholds. It is often argued that limiting the lifetime of the dots prevents participants from following any single dot to discern the correction motion direction. Anecdotally, it is difficult to follow the movement of single dots, especially when dots are small and RDKs are presented with short durations. Pilot studies I have conducted in my lab indicate that using limited lifetime dots leads to approximately equal coherence thresholds across the three noise

types; while unlimited lifetime stimuli yields highest coherence thresholds for random direction noise, and lowest coherence thresholds for random walk noise.

### **1.3.1.3. Stimulus Density**

The density of an RDK can be measured and reported in three ways: dots/deg<sup>2</sup>, reflecting density for a single frame of the stimulus; dots/deg<sup>2</sup>/sec, reflecting density for multiple frames of the stimulus; or as a percentage calculated from (dot area/total stimulus area), reflecting the proportion of stimulus area dots make up on a single frame. The first two measures are independent of dot size and are calculated on the basis of total number of dots, while the last measure is reliant on both. The calculation of dots/deg<sup>2</sup>/sec requires knowledge of  $\Delta t$ . Most studies report only one measure, though the other two are usually calculable from other information given.

Increasing density as a function of total number of dots has been shown to impact maximum  $\Delta x$  displacement thresholds under some conditions (e.g., Baker & Braddick, 1982; Eagle & Rogers, 1996; 1997) and it has been suggested that higher-level feature matching mechanisms become involved with increases in density or dot size (Sato, 1998; Smith & Ledgeway, 2001). In direction-discrimination RDKs, changes in total number of dots have not been shown to impact adult thresholds from a range of 1 to 30 dots/deg<sup>2</sup>, though 5- to 6-year-olds have lower motion coherence thresholds for dense stimuli (Narasimhan & Giaschi, 2012). Talcott, Hansen, Assoku, and Stein (2000) also showed that thresholds for adult controls were not impacted by changes in density from 1.5 to 12.2 dots/deg<sup>2</sup>, and adults with dyslexia also performed better with more dense displays.

#### 1.3.1.4. Stimulus Duration

The duration of a stimulus is  $\Delta t$ \*(total frames). However, the number of frames in a presented RDK may be a more appropriate quantifier than stimulus duration itself, such that increasing the number of displacements a participant sees can facilitate sensitivity to motion. This phenomenon has been termed *sequential recruitment* after McKee and Welch (1986), who found that performance on a velocity discrimination task improves with increased total frames to an asymptote of about 8-10 frames. Sequential recruitment has shown to increase the maximum  $\Delta x$  displacement that is perceived as motion (e.g., Snowden & Braddick, 1989). Nakayama and Silverman (1984) demonstrated that sequential recruitment also increases with increases in stimulus area, and suggest that this mechanism operates by providing the motion system more information for solving the correspondence problem. To my knowledge, no one has investigated the relationship between duration and total frames in a direction discrimination task, but coherence thresholds have been shown to decrease with increasing durations (Downing & Movshon, 1989), possibly to a limit of about 900 ms or 18 frames (Talcott et al., 2000). This long integration time suggests that sequential recruitment is not the result of a low-level retinal process (e.g., Bloch's law<sup>2</sup>).

#### 1.3.1.5. Stimulus Area

As noted above, increasing the area of a stimulus is associated with increases in maximum  $\Delta x$  displacement thresholds (Baker & Braddick, 1982; Nakayama & Silverman, 1984). Tadin, Lappin, Gilroy, and Blake (2003) demonstrated that increases in stimulus area can be accompanied by increases in duration thresholds (i.e., worse performance) for direction

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<sup>2</sup> Bloch's Law: Response = Intensity\*Time. For cones, this holds up to 50 ms; for rods, 100 ms.

discrimination, likely due to antagonistic centre-surround mechanisms, but this appears only to hold for very small stimulus areas ( $< 4$  deg) presented foveally. For larger stimuli, increased stimulus areas yield lower thresholds (Watamaniuk & Sekuler, 1992). Work by Downing and Movshon (1989) suggests that this effect plateaus, for adults at least, at an area of about  $25 \text{ deg}^2$ . In support of this, pilot studies I conducted using  $60$  and  $400 \text{ deg}^2$  show no difference in thresholds as a function of area for a speed of  $1 \text{ deg/s}$  for adults. This area is near the maximum area governed by Piper's law<sup>3</sup>, and so benefits to motion coherence thresholds as a function of area might be due to similar low-level processes.

#### **1.4. Inconsistencies in the Maturation of Human Global Motion Perception**

As noted in section 1.3, the RDK has been used to study the developmental trajectory of global motion perception in humans. However, the conclusions drawn from these studies have been inconsistent. Parrish et al. (2005) compared motion coherence thresholds in children aged 3-12 and adults, and found no significant differences between thresholds, indicating global motion perception is mature by age 3. Consistent with this, in clinical studies that included control groups of children and adults, no difference between control groups of 6-year-old children and adults were found by Ellemberg, Lewis, Maurer, Brar, and Brent (2002) or Reiss, Hoffman, and Landau (2005). In contrast, Narasimhan and Giaschi (2012) found that 5- to 6-year-old children had immature global motion perception, and a study by Hadad et al. (2011) testing children aged 6-14 found that maturation did not occur until age 12. Studies using random Gabor kinematograms, which are similar to RDKs but with Gabor patches rather than dots, have also found significant differences in global motion perception between 5-year-olds and adults

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<sup>3</sup> Piper's Law:  $\text{Response} = \text{Intensity} * \sqrt{\text{Area}}$ . This law holds for areas between  $10$  arcmin and  $24$  deg beside the fovea.



(Elleberg et al., 2004; 2010).

Why have studies come to different conclusions about the maturation of global motion perception? Because each lab must create its own stimulus, it is likely that different stimulus parameters are driving performance differences in children and adults. However, most stimulus differences do not predict which studies found early maturation and which did not. For example, Parrish et al. (2005) and Elleberg et al. (2002) used up/down direction discrimination and found early maturation, but so did Hadad et al. (2011), who found quite late maturation. Both Reiss et al. (2005) and Narasimhan and Giaschi (2012) used left/right discrimination, and also came to different conclusions about 5- to 6-year-olds. Studies also differ in the type of noise algorithm used (direction noise: Hadad et al.; Elleberg et al.; walk noise: Parrish et al.; Narasimhan & Giaschi; white noise: Reiss et al.), and in the dot size and density used (small dots, dense stimulus: Parrish et al.; small dots, varying densities: Narasimhan & Giaschi; large dots, sparse stimulus: Elleberg et al., Reiss et al., Hadad et al.). Studies used a range of durations, but studies using short (400 ms; Narasimhan & Giaschi) and long (2000 ms; Hadad et al.) durations came to similar conclusions about development.

The studies also overlap in the speeds they tested, ranging from 1 to 18 deg/s. Mature performance was found for 1.3 deg/s (Parrish et al., 2005), 2.5 deg/s (Reiss et al., 2005), and 18 deg/s (Elleberg et al., 2002); and immature performance was found for 1 and 4 deg/s (Narasimhan & Giaschi, 2012), and 4 and 18 deg/s (Hadad et al., 2011). However, I will argue that the underlying distance and time parameters used to create a speed (e.g., the  $\Delta x$  and  $\Delta t$  values of Figure 1.2) matter more than simply their ratio; and that this may account for some conflicting conclusions on when global motion perception is adult-like.

## 1.5. Speed and Motion Coherence Thresholds

Generally, sensitivity to speed follows a u-shaped function in adults. Downing and Movshon (1989) measured direction discrimination thresholds for speeds between 0.9 to 26.7 deg/s and found a peak of best performance around 3-5 deg/s. Similarly, van de Grind, van Doorn, and Koenderink (1983) found peak motion detection thresholds at speeds between 1-10 deg/s. Adults in Narasimhan and Giaschi (2012) showed no difference in thresholds for speeds of 1 and 4 deg/s.

A number of studies suggest that sensitivity to fast motion matures sooner in life than sensitivity to slow motion. For example, Narasimhan and Giaschi (2012) found children's global motion direction discrimination thresholds were more immature at a speed of 1 deg/s than at 4 deg/s. Using random Gabor kinematograms, ElleMBERG et al. (2004) found children aged 5 were very immature at stimuli with speeds of 1.5 deg/s, and less so at 6 and 9 deg/s. Speed discrimination thresholds in 5-year-old children are immature, but more so for reference speeds of 1.5 deg/s than for 6 deg/s (Ahmed, Lewis, ElleMBERG, & Maurer, 2005). Children do not show adult-like thresholds in speed discrimination tasks until age 11 for reference speeds of 6 deg/s, and thresholds for speeds of 1.5 deg/s are still immature at this age (Manning, Aagten-Murphy, & Pellicano, 2012). In motion-defined form tasks, children aged 4-6 show adult-like coherence thresholds for stimuli moving at 5 deg/s, but are immature at 0.9 deg/s and even more so at 0.1 deg/s (Hayward et al., 2011). Some early developmental disorders have been shown to disrupt performance on motion tasks at slow speeds only, indicating a protracted sensitive period for damage. For example, Hayward et al. found that children with amblyopia had elevated thresholds for the motion-defined form task in the affected and unaffected eyes at 0.1 deg/s, but not at 0.9 or 5 deg/s, and Edwards et al. (2004) found elevated global motion direction discrimination

thresholds in children with dyslexia for speeds of 0.24 and 1.2 deg/s, but not 7.3 deg/s.

Few studies have examined coherence thresholds as a function of  $\Delta x$  and  $\Delta t$  rather than speed during development, but evidence from developing macaques suggest these parameters matter. A longitudinal study by Kiorpes and Movshon (2004) demonstrated that macaque coherence thresholds for a given speed would vary, depending on underlying values of  $\Delta x$  and  $\Delta t$ . For example, a 40-week old macaque could best discriminate speeds from 1-4 deg/s when  $\Delta t$  was 19ms, speeds from 3-6 deg/s when  $\Delta t$  was 37ms, and speeds from 7-11 deg/s when  $\Delta t$  was 56ms. Given their values of  $\Delta t$ , however, these three optimal speeds have  $\Delta x$  in common: about 7-12 arcmin. In other words, psychophysical tuning curves obtained from developing macaques have the same peak when plotted as a function of  $\Delta x$ , but not when plotted as a function of the  $\Delta x/\Delta t$  ratio, speed. While overall coherence thresholds decreased from 3 weeks to 3 years of age, optimal  $\Delta x$  values also decreased, from 15-40 arcmin around 3 weeks to 6-8 arcmin at about 3 years (approximately equivalent to ages from 3 months to 12 years in human development; Boothe, Dobson, & Teller, 1985). Even at 3 years, thresholds were best expressed as a function of  $\Delta x$  rather than speed. A similar pattern was found in macaques studied by Kiorpes, Price, Hall-Haro, and Movshon (2012). This suggests a potential mechanism for why sensitivity to slow speeds takes longer to develop in human children: smaller distances of  $\Delta x$  will yield slower speeds. These results also suggest that the coherence values measured in two studies that use the same signal dot speeds may vary widely, depending on the value of  $\Delta x$  used in the RDK stimulus.

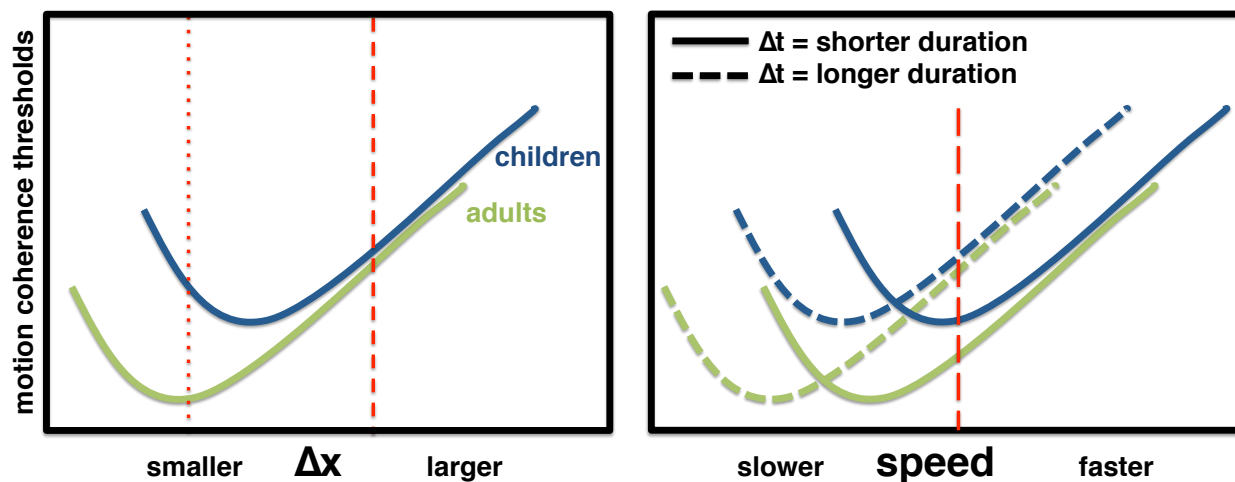
There is also evidence these parameters matter in humans, which is a good indicator that we should expect to see the same developmental pattern in humans as macaques. In three direction-discrimination experiments with adults, Arena, Hutchison, and Shimozaki (2012) held

$\Delta x$ ,  $\Delta t$ , or speed constant while varying the other two parameters. When  $\Delta t$  was held constant at 107ms and  $\Delta x$  was varied from 4 to 64 arcmin, they found thresholds were increased for distances greater than about 18 arcmin. When  $\Delta x$  was held constant at 37.5 arcmin and  $\Delta t$  varied from 27 to 427 ms, thresholds were slightly increased for times greater than 250 ms. When speed was held constant at 2.5 deg/s, participants had increased coherence thresholds for larger values of  $\Delta x$  and  $\Delta t$  (32 arcmin / 213 ms) than smaller ones (16 arcmin / 107 ms and below). These results suggest that a stimulus made with larger values of  $\Delta x$  and  $\Delta t$  will yield higher thresholds than one with lower values of  $\Delta x$  and  $\Delta t$ , even when they travel at the same speed. Consistent with this, Elleberg et al. (2010) investigated thresholds in 5-year-old children and adults with random Gabor kinematograms, holding speed constant at 1.5 deg/s, and testing  $\Delta x/\Delta t$  values of 6 arcmin / 66 ms, 30 arcmin / 333 ms, and 60 arcmin / 666 ms. Children were immature at all displacements, and in general, as displacements increased, thresholds increased in both groups.

### **1.6. A Framework for Understanding Thresholds as a Function of $\Delta x$ and $\Delta t$**

Taken together, these results suggest a framework for resolving previous inconsistencies in results on the maturation of human global motion perception. This framework is illustrated in Figure 1.4. The left panel shows a hypothetical relationship between coherence thresholds and values of  $\Delta x$  for children and adults obtained at some fixed value of  $\Delta t$ . The evidence from macaque development described above suggests that with age, the psychometric function is shifted down, reflecting an overall decrease in motion coherence thresholds; and to the left, reflecting a shift in optimal  $\Delta x$  values from larger to smaller distances. Motion coherence thresholds obtained at smaller values of  $\Delta x$  will show significant immaturities between children and adults that will not be shown at larger values of  $\Delta x$ . This is consistent with findings from the

human developmental studies outlined above (e.g., Ellemberg et al., 2010, Narasimhan & Giaschi, 2012), as smaller values of  $\Delta x$  represent slower speeds. Consider what happens when thresholds are obtained for two values of  $\Delta t$ , and plotted as a function of speed. This is depicted in the right panel of Figure 1.4. If optimal  $\Delta x$  values remain constant, functions describing coherence thresholds for longer  $\Delta t$  values will be shifted to the left. For very slow speeds, we would expect children to always have elevated motion coherence thresholds compared to adults. For very fast speeds, we would expect children to have mature motion coherence thresholds. But when sampling some intermediate speeds, children may or may not be considered mature, depending on the precise values of  $\Delta x/\Delta t$ . For the speed identified in the right panel of Figure 1.4, larger values of  $\Delta x$  and  $\Delta t$  would lead to the conclusion that children perform like adults at



**Figure 1.4: Theoretical framework for understanding the relationship between speed and motion coherence thresholds during development.** *Left:* If motion coherence thresholds as a function of  $\Delta x$  are shifted down and to the left for adults (light green) compared to children (dark blue), children may be considered immature if tested at small values of  $\Delta x$  (red dotted line) but not at large values (red dashed line). *Right:* If thresholds depend on  $\Delta x$  but not  $\Delta t$ , thresholds for two values of  $\Delta t$  as a function of speed will be shifted such that the curve describing the longer  $\Delta t$  will move to the left. If tested at an intermediate speed (red dashed line), children may be adult-like (larger  $\Delta x$  distance and longer  $\Delta t$  duration) or not (smaller  $\Delta x$  distance and shorter  $\Delta t$  duration). See in-text description for more details. Note that for simplicity, functions are shown with identical shapes; but it is not necessarily the case that the shape is identical between children and adults, or even between one age group at different  $\Delta t$  values.

this speed, while smaller values of  $\Delta x$  and  $\Delta t$  would lead to the conclusion that children are immature at this speed.

The goal of this thesis is to unify previous conflicting results under such a framework by manipulating distance and time parameters to get a better understanding of how changes in  $\Delta x$  and  $\Delta t$  impact motion coherence thresholds. In Experiment 1, I focus on resolving the conflicting results of Parrish et al. (2005) and Narasimhan and Giaschi (2012) by measuring coherence thresholds in adults for four different  $\Delta x/\Delta t$  values that yield the same speed ratio. I predicted that, as the green curves illustrated in Figure 1.4 (right) demonstrate, larger values of  $\Delta x$  and  $\Delta t$  would produce higher motion coherence thresholds in adults. In Experiment 2, I tested a range of  $\Delta x$  and  $\Delta t$  values in both adults and children to plot out functions similar to those in Figure 1.4. I predicted that children would show mature performance for larger values of  $\Delta x$  regardless of  $\Delta t$ , and that for an intermediate speed, children may or may not be mature, depending on the underlying  $\Delta x/\Delta t$  parameters.

## **2. Experiment 1, The Effect of Holding $\Delta x$ and $\Delta t$ Constant at 1 deg/s on Adult Thresholds**

### **2.1. Introduction**

The aim of this experiment was to investigate the conflicting results of Parrish et al. (2005) and Narasimhan and Giaschi (2012). Because these studies were both run out of the same lab, stimulus parameters were quite similar. They showed different developmental trajectories, however. Parrish et al. found no significant differences in motion coherence thresholds for children aged 3-12 years and adults using a dense stimulus (32 dots/deg<sup>2</sup>) with signal dots traveling at approximately 1.3 deg/s. In contrast, Narasimhan and Giaschi varied density of the dot field (1, 15, or 30 dots/deg<sup>2</sup>) and dot speed (1 or 4 deg/s) and found that children aged 5-6 years performed worse than adults at all conditions. Children did best in the dense, 30 dots/deg<sup>2</sup> condition, which explains in part why children in Parrish et al., which also used dense stimuli, were performing so well. Curiously, though, adults performed a lot worse in Parrish et al.: here, adult coherence thresholds were around 0.20, but adults in Narasimhan and Giaschi's study had thresholds of around 0.08 across all conditions. This is another reason why young children appeared adult-like in Parrish et al.: the adult comparison group had quite high thresholds. If adults in Narasimhan and Giaschi had obtained thresholds around 0.20, children's thresholds would be elevated around 1.9x those of adults, instead of the reported 4.6x in the slow, dense condition.

That adults had lower motion coherence thresholds in Narasimhan and Giaschi (2012) than in Parrish et al. (2005) was especially surprising, since many parameters were similar. These studies used similar motion speeds (1 and 1.3 deg/s); similar algorithms for moving noise dots (no signal/noise label reassignment, random walk noise, similar lifetimes; see section 1.3.1.2); and they used similar methods for calculating motion coherence thresholds (the

psychometric function-fitting method used in this paper; see section 2.2.5). Differences between the stimuli were few, and most would predict lower motion coherence thresholds in Parrish et al.: stimulus duration (section 1.3.1.4) was longer in the Parrish et al. study (853ms vs. 400ms); and stimulus area (section 1.3.1.5) was larger in the Parrish et al study ( $123 \text{ deg}^2$  vs.  $44 \text{ deg}^2$ ). Parrish et al. used up/down direction discrimination, while Narasimhan and Giaschi used left/right; it is possible, though not expected, that up/down discrimination would lead to elevated thresholds in adults (section 1.3.1.1).

There are two key differences between the two studies that are investigated in the current experiment. First, though both studies use similar signal motion speeds, the underlying values of  $\Delta x$  and  $\Delta t$  used to obtain this speed were different. Narasimhan and Giaschi (2012) used 2.4 arcmin / 40 ms, while Parrish et al. used 8.5 arcmin / 107 ms. As discussed in sections 1.5-1.6, there is evidence to suggest that these values may impact motion coherence thresholds both in adults and children. While Arena et al. (2012) tested  $\Delta x/\Delta t$  values at a speed of 2.5 deg/s and found higher thresholds when these values were large, it is not clear if this would hold for a speed as slow as 1 deg/s. Elleberg et al. (2010) tested  $\Delta x/\Delta t$  values at a speed of 1.5 deg/s using a random Gabor kinematogram and also found higher thresholds when these values were large, but used  $\Delta x$  values of 6, 30, and 60 arcmin. It is unclear from these data how smaller changes between 2.4 and 8.5 arcmin would impact thresholds. The current study seeks to extend these previous findings to a speed of 1 deg/s with a tighter range of displacements.

Second, while the total duration of the stimulus in Parrish et al. (2005) was longer, this stimulus contained fewer total frames (8 vs. 10). While it seems unlikely that a two-frame difference between the studies could account for such a difference in thresholds, it is possible that sequential recruitment (section 1.3.1.4) led to lower motion coherence thresholds in adults



participating in Narasimhan and Giaschi's (2012) study. It is essential to investigate whether the total number of frames can impact motion coherence thresholds because the relationship between  $\Delta t$ , total frames, and total duration may have led to a confound in the results of Arena et al. (2012) and Elleberg et al. (2010). Both studies found higher thresholds with increased  $\Delta t$  values, but both studies held the total duration of the stimulus constant. This has the consequence of presenting fewer total frames to participants when  $\Delta t$  is at its longest (4 frames in Arena et al., 2012; and 2 or 3 frames in Elleberg et al., 2010). It may be, then, that the fewer number of frames led to these higher motion coherence thresholds rather than the actual  $\Delta x/\Delta t$  values themselves.

To investigate, I tested four paired values of  $\Delta x$  and  $\Delta t$  that would yield a speed of 1 deg/s. Like previous research, to compare motion coherence thresholds across these pairs, I exposed participants to stimuli with equal durations (such that total number of frames decreased as the  $\Delta t$  of the condition increased). To explore whether the total number of animation frames was important, I included a second condition in which participants were exposed to stimuli with equal total number of animation frames (such that the total duration increased as the  $\Delta t$  of the condition increased). I hypothesized I would find performance has a relationship with  $\Delta x/\Delta t$  values such that as they get larger, performance is worse; generalizing results from previous experiments to RDKs at slower speeds with a finer range of displacements. However, this may hold only for comparisons made across stimuli of equal durations. If the effect also appears when comparing across stimuli of equal frame totals, we can be confident that the effect is truly due to the underlying values of  $\Delta x$  and  $\Delta t$ . On the other hand, if the effect does not hold when comparing across stimuli of equal frame totals, it may be that increased coherence thresholds for stimuli with larger  $\Delta t$  found in previous studies could be due to the decreased number of

animation frames to which participants are exposed.

## **2.2. Methods**

### **2.2.1. Participants**

Participants were adults recruited through the community via postings at BC Children's Hospital and Craigslist, and remunerated \$10 for their participation. A total of 25 participants were recruited (19 female;  $M$  age = 23.7,  $SD$  = 3.9, range 18.1-31.0). Potential participants were screened (through self-report) for the presence of any visual, neural, developmental, or cognitive disorders that might impact performance or interfere with binocular vision. Before the experiment, stereoacuity was measured with the Randot Preschool Stereoacuity Test (Stereo Optical Co., Inc.); only participants with the best score possible (40 arcsec, considered typical for adults: Birch et al., 2008) were included in analysis, as brain mechanisms responsible for motion and depth perception are, in part, shared (Born & Bradley, 2005). Visual acuity was assessed with the Regan high-contrast letter chart (Regan, 1988) at a distance of 6 m. To be included in the analysis, participants needed to obtain a visual acuity of at least 0.10 LogMAR (20/25 Snellen acuity; 0 LogMAR is equivalent to a Snellen acuity of 20/20, and lower values mean better acuity). Participants with a difference in left and right eye visual acuity greater than 0.20 LogMAR (2 lines on a standard clinical eye chart) were excluded for being at risk for amblyopia, which may affect motion processing (Ho & Giaschi, 2006).

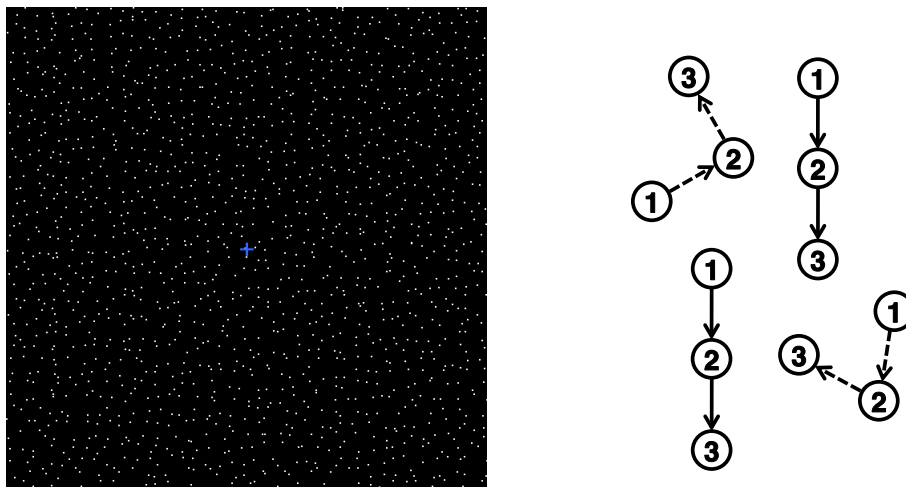
Four participants were excluded from analysis: one for a red-green colour vision deficiency, one for poor stereoacuity, one for being at risk for amblyopia, and one for perceiving motion in the opposite direction at 100% coherence. In total, 21 participants were included in the analysis.

### 2.2.2. Apparatus

Stimulus presentation was controlled by a Quad-Core Intel Xeon Macintosh computer running MATLAB R2007a (The MathWorks, Inc.) with the Psychophysics Toolbox extension version 3.0.8 (Brainard, 1997; Pelli, 1997; Kleiner, Brainard, & Pelli, 2007). Stimuli were presented on a BenQ XL2420T LED-backlit LCD monitor at a resolution of 1920 x 1080 and a refresh rate of 120 Hz. Participants were seated 1.9 m from the monitor in a dimly-lit room. Responses were collected with a Logitech gamepad.

### 2.2.3. Stimuli and Experimental Conditions

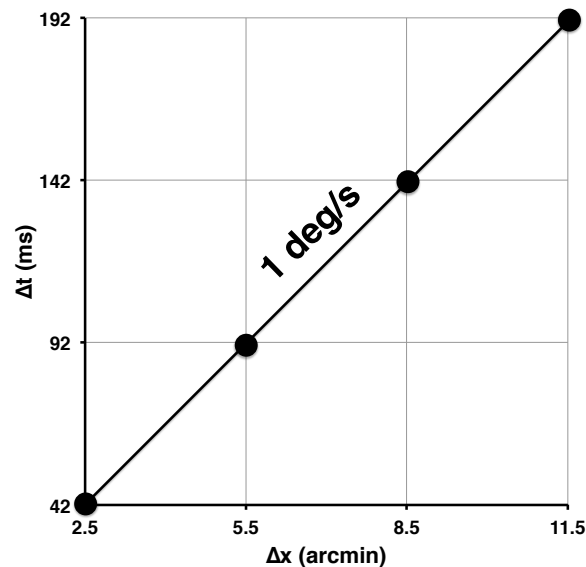
The stimuli and conditions used in this experiment are represented in Figure 2.1. The parameters of the RDK stimulus used in this study were selected to best match those used by Parrish et al. (2005) and Narasimhan and Giaschi (2012). White dots (1 arcmin in diameter; 270 cd/m<sup>2</sup>) were presented on a black (0.7 cd/m<sup>2</sup>) background. An array of 1936 dots per frame



**Figure 2.1: The RDK used in Experiment 1.** *Left:* a single frame of the RDK stimulus used in Experiment 1. *Right:* a schematic of dot behaviour on three subsequent frames of the RDK. Dots are numbered for the frame in which they appear. Two signal dots (solid arrows) are moving down. Two noise dots (dashed arrows) are moving according to the random walk noise algorithm: they move the same distance each frame as signal dots, but in a new random direction every frame. Dots retained their signal/noise assignment through the full animation.

subtended a square of 8 x 8 deg (in contrast to the smaller 7.7 x 5.7 deg rectangle used by Narasimhan & Giaschi, and the larger 12.8 x 9.6 deg rectangle used by Parrish et al.) for a dot density of 30 dots/deg<sup>2</sup>. Signal dots moved either up or down (as in Parrish et al.; Narasimhan & Giaschi used left and right directions). Noise dots were governed by the random walk algorithm, wherein noise dots move the same distance as signal dots but in a new direction randomly selected from 360° on each frame. All dots had an unlimited lifetime (i.e., they moved continuously without being replotted during the animation).

This experiment crossed two factors in a fully-within design, for a total of eight conditions. The first factor was the size of the  $\Delta x/\Delta t$  values used to create apparent motion. Four conditions were created by linearly increasing the  $\Delta x$  distance by 3 arcmin (6 pixels) increments from 2.5 arcmin to 11.5 arcmin, and the  $\Delta t$  time was adjusted accordingly so that each distance/time ratio yielded a speed of 1 deg/s (see Figure 2.2). For comparison, Narasimhan and Giaschi used 2.4 arcmin / 40 ms, and Parrish et al. used 8.5 arcmin / 107 ms. The time each frame remained on the screen was controlled by varying the total number of monitor refreshes



**Figure 2.2: The four pairs of  $\Delta x$  (distance) and  $\Delta t$  (time) values tested in Experiment 1. All four pairings yield a speed of 1 deg/s.**

(8.33 ms per refresh on a 120 Hz screen) per animation frame from 5 (for the shortest  $\Delta t$  value of 42 ms) to 23 (for the longest  $\Delta t$  value of 192 ms).

The second factor tested in this experiment was the exposure length of the motion animation. Exposure length was examined in two conditions: total frames held constant, or total duration held constant. In the first condition, the total number of presented frames was held constant at 8. In the second condition, duration was held constant at around 600 ms. Note that the time parameter used in a given distance/time condition dictates the total duration of a stimulus (when frames are held constant) or the total number of frames of a stimulus (when duration is held constant). Because the total duration of a stimulus must be a multiple of a single frame duration, stimuli cannot be identical durations when durations are held constant. Specific exposure parameters are outlined in Table 2.1.

Table 2.1

*Parameters for the Distance/Time (4 levels) and Exposure (2 levels) Conditions of Experiment 1.*

| Exposure Condition     | Distance ( $\Delta x$ ) / Time ( $\Delta t$ ) Condition |                       |                        |                         |
|------------------------|---|-----------------------|------------------------|-------------------------|
|                        | 2.5 arcmin /<br>42 ms                                   | 5.5 arcmin /<br>92 ms | 8.5 arcmin /<br>142 ms | 11.5 arcmin /<br>192 ms |
| Frames held constant   |   |                       |                        |                         |
| total frames           | 8   | 8                     | 8                      | 8                       |
| total duration         | 333 ms  | 733 ms                | 1133 ms                | 1533 ms                 |
| Duration held constant |   |                       |                        |                         |
| total frames           | 14  | 6                     | 4                      | 3                       |
| total duration         | 583 ms  | 550 ms                | 567 ms                 | 575 ms                  |

#### 2.2.4. Procedure

The participant's task was to decide whether the pattern was moving up or down. At the beginning of a trial, participants saw a fixation cross, followed by the motion stimulus, followed by a question mark. Once a response was input via the gamepad, feedback (the words "Good

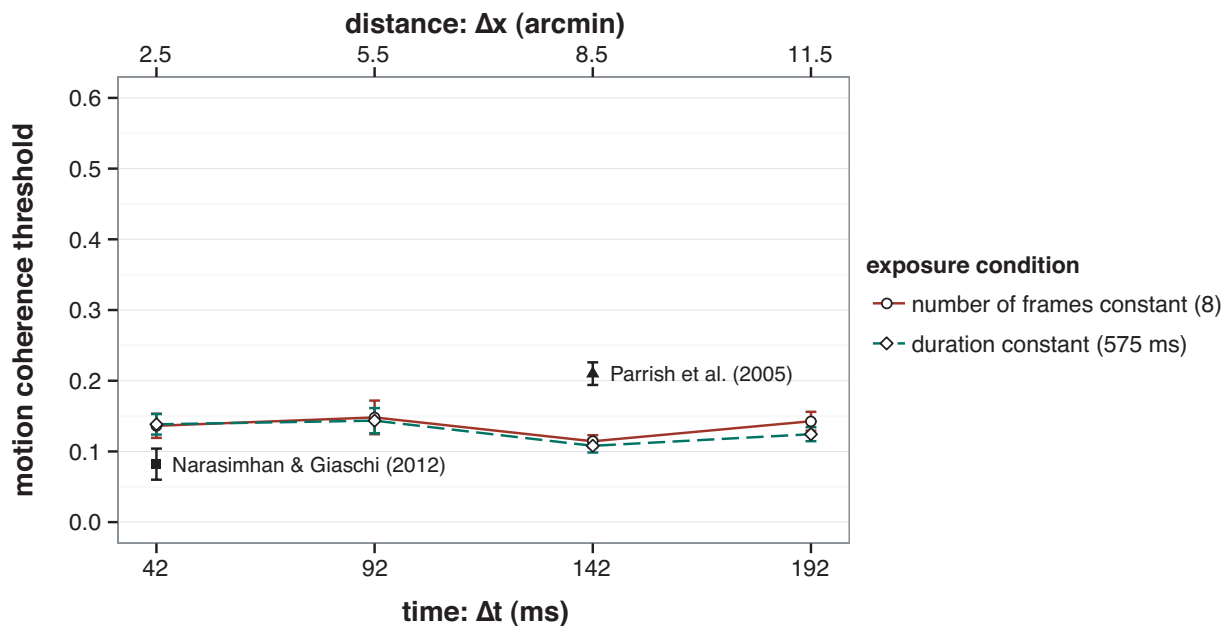
job!” or “Oops!”) appeared on the screen for 750ms. The next trial began upon button-press. The first RDK of a staircase was always presented with 100% coherence. Trial-by-trial coherence was adjusted according to a two-down, one-up staircase procedure, meaning that the coherence value of the next trial was decreased (i.e., made harder) if the participant got two correct trials in a row, or increased (i.e., made easier) if the participant got one trial incorrect. A response reversal occurs when the participant’s response changes from correct to incorrect and the staircase changes from descending coherence values to ascending ones, or vice versa. Coherence was adjusted in steps of 10% until three response reversals occurred, after which step-size halved at each reversal until a minimum step size of 1% was reached. Staircases terminated after 50 trials or 10 response reversals, whichever occurred first. Each participant completed one staircase for each of the eight conditions. All testing was conducted monocularly, using the eye with the best visual acuity (or, when the eyes had the same visual acuity, a randomly-selected eye).

### **2.2.5. Analysis**

A motion coherence threshold was obtained for each staircase run by fitting a Weibull function to responses using a maximum-likelihood minimization bootstrap procedure (Watson, 1979) and verifying the function fit with a chi-square test. Coherence thresholds are expressed as a proportion, and so can take on a value from 0 (completely random dot motion) to 1 (completely coherent dot motion). The coherence level at the slope of maximum inflection on the Weibull curve, which is at 82% correct for a two-alternative forced-choice task (Strasburger, 2001), was taken as the motion coherence threshold for that run.

### 2.3. Results

Motion coherence thresholds (see Figure 2.3) were analyzed with a 4 x 2 within-subjects ANOVA using factors distance/time pair (four levels as described above) and exposure condition (frames held constant, duration held constant). Degrees of freedom were corrected with Greenhouse-Geisser estimates where the assumption of sphericity was violated. There was no significant main effect of distance/time pair,  $F(2.12, 42.31) = 2.29, p = .11$ ; no significant main effect of exposure condition,  $F(1, 20) = 1.04, p = .32$ ; and no significant interaction between the two,  $F(1.67, 33.38) = 0.19, p = .79$ .



**Figure 2.3: Mean motion coherence thresholds (expressed as a proportion) obtained in Experiment 1.** Error bars reflect standard error. Mean motion coherence thresholds and standard errors are also plotted for results obtained by Narasimhan & Giaschi, 2012 (square) and Parrish et al., 2005 (triangle), with the x-axis representing the condition to which these studies most closely correspond.

## 2.4. Discussion

Contrary to my prediction, Experiment 1 found no significant differences in thresholds for a speed of 1 deg/s when  $\Delta x$  values of 2.5 to 11.5 arcmin and  $\Delta t$  values of 42 ms to 192 ms were used. This was the case whether the total number of frames was held constant at 8 and total duration of the stimulus ranged from 333 ms to 1533 ms, or the total duration of a stimulus was held constant at around 600 ms and total frames ranged from 14 to 3.

These data do not help to elucidate differences between Parrish et al. (2005) and Narasimhan and Giaschi (2012), and I did expect to find significant differences in thresholds in these conditions based on previous research. This study may be underpowered for detecting a small effect, but an initial power calculation suggested a sample size of 12 was sufficient based on effect sizes estimated from Parrish et al. and Narasimhan and Giaschi. Moreover, the obtained pattern of mean differences is essentially flat, and does not imply that simply collecting additional subjects would produce practically significant results. Ultimately, I must conclude that slower speeds (around 1 deg/s) do not produce the same effects as the higher speed (2.5 deg/s) tested by Arena et al. (2012), at least in the range of  $\Delta x$  and  $\Delta t$  values tested in this study. It is likely that if I had selected a wider range of displacements to test, as in Ellemberg et al. (2010) (6 arcmin / 66 ms, 30 arcmin / 333 ms, and 60 arcmin / 666 ms), an effect would have been present. In the range of values tested in this study, coherence thresholds were about 0.13 regardless of condition.

The differences between adults' thresholds in Parrish et al. (2005) and Narasimhan and Giaschi (2012) remain to be explained. It may be that up/down direction discrimination tasks, as Parrish et al. used, yield larger thresholds than left/right discrimination tasks, as Narasimhan and Giaschi used. Motion detection thresholds have shown some anisotropies such that up/down



coherence thresholds are higher than left/right coherence thresholds, though this has not been demonstrated for direction discrimination tasks (section 1.3.1.1). Parrish et al. and Narasimhan and Giaschi used horizontally-oriented rectangles as stimulus areas, which means signal dots in Parrish et al. moved up/down along the smaller ‘height’ of the rectangle, while signal dots in Narasimhan and Giaschi moved along the larger ‘width’ of the rectangle. Although the actual sizes of these edges follow the same pattern as their stimulus areas—for Parrish et al., the height of the rectangle subtended 9.6 deg, which is larger than the width of the rectangle used by Narasimhan and Giaschi, 7.65 deg—it is possible this may have afforded an advantage to participants in the Narasimhan and Giaschi study. van Doorn and Koenderink (1984) found that for a given fixed area, thresholds for motion detection decrease as the ratio of rectangle width:height increases in favor of the direction of motion. The ratio of Parrish et al.’s stimulus was 0.75, while the ratio of Narasimhan and Giaschi’s stimulus was 1.33. It is unclear how this relationship might play out when comparing two areas of different size in a direction discrimination task, but van Doorn and Koenderink’s data suggest that the ratio of 0.75 in Parrish et al.’s study could lead to higher motion coherence thresholds than the ratio of 1.33 of Narasimhan and Giaschi’s study. This key difference between the two studies remains to be investigated.

### **3. Experiment 2, The Effect of Varying $\Delta x$ and $\Delta t$ on Coherence Thresholds in Adults and Children**

#### **3.1. Introduction**

In Experiment 1, I selected a single speed and varied the values of  $\Delta x$  and  $\Delta t$  that went into the speed ratio. I found no difference between coherence thresholds for a range of values from 2.5 arcmin / 42ms to 11.5 arcmin / 192ms. In Experiment 2, I varied speed by sampling a range of  $\Delta x$  and  $\Delta t$  values, with the goal of obtaining psychophysical tuning curves to test out the hypotheses suggested by section 1.6, figure 1.4. I hypothesized that adults would have similar coherence thresholds for values of  $\Delta x$  regardless of  $\Delta t$ ; that children would show this same pattern; and that, when characterized by speed, children would be immature at slow speeds, mature at fast speed, and maturity would depend on  $\Delta x$  and  $\Delta t$  values for a range of intermediate speeds such that maturity would be found with larger  $\Delta x$  and longer  $\Delta t$  values.

The values selected in this experiment were chosen to closely match those used by Kiorpes and Movshon (2004), who tested an approximately logarithmic progression of  $\Delta x$  values from 1 to 60 arcmin, and  $\Delta t$  values of 19 ms, 37 ms, and 56 ms. In pilot studies with adults it was determined that some people have difficulties seeing motion from  $\Delta x$  displacements greater than 40 arcmin at longer values of  $\Delta t$ , so a range from 1 to 38 arcmin was used. I selected two  $\Delta t$  values similar to the shortest and longest tested by Kiorpes and Movshon, 17ms and 50ms.

#### **3.2. Methods**

##### **3.2.1. Participants**

Children and adults were recruited through the community via postings at BC Children's Hospital and Craigslist. Adults were also recruited through the Psychology Department at the

University of British Columbia. Participants were remunerated \$10 for their participation, with Psychology students having the option to receive course credit in lieu of money. Parents of child participants were given \$4 to cover transportation costs. As assessed through self- or parental-report, all participants were free of any visual, neural, developmental, or cognitive disorders that might impact performance or interfere with binocular vision.

A total of 42 adults were recruited (20 female;  $M$  age = 21.9 years,  $SD$  = 3.1, range 18.3-29.5). As in Experiment 1, adults were excluded from analysis if they failed to achieve stereoacuity scores of 40 arcseconds on the Randot Preschool Stereoacuity Test, or visual acuity scores of 0.10 logMAR or better as measured on the Regan high-contrast letter chart at a distance of 6 m (equivalent to a Snellen fraction of 20/25). Participants were also excluded if they were at risk for amblyopia (difference in left and right eye visual acuity greater than 0.20 LogMAR, or 2 lines on a standard clinical eye chart). Five adults were excluded for poor stereoacuity, five were excluded for poor visual acuity, and one was excluded for failing to achieve at least 5/8 correct on a series of preliminary practice trials (described below). This left 31 adults total for analysis.

A total of 33 children were recruited (22 female;  $M$  age = 5.6 years;  $SD$  = 0.9, range 4.0-7.0). Children were excluded from analysis if they did not have stereoacuity scores within the expected range for their age on the Randot Preschool Stereoacuity Test (200 arcseconds for children 4-5 years old, 100 arcseconds for children 6 years old; Birch et al., 2008). Children were also excluded from analysis if they failed to obtain visual acuity scores at least as good as the lower limit of normal for their age range (0.38 LogMAR for children 4-5 years old, 0.30 LogMAR for children 6 years old; Dobson, Clifford-Donaldson, Green, Miller, & Harvey, 2009) on the Regan high-contrast letter chart or, for three children who could not reliably recognize letters, the PattiPics Symbol Chart (Precision Vision), at a distance of 6 m. Finally, children were

also excluded if they were found to be at risk of amblyopia. In all, two children were excluded for difficulties attending to the task, two children were excluded for failing to achieve at least 5/8 correct on a series of preliminary practice trials; and one child was excluded for being at risk for amblyopia.

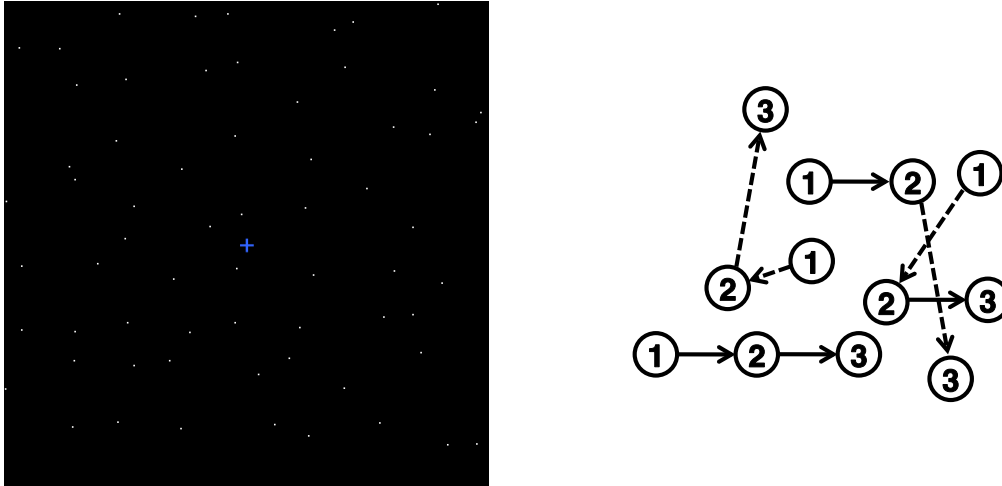
### **3.2.2. Apparatus**

Stimulus presentation was controlled by an Intel Core i7 Macintosh Macbook Pro running MATLAB R2008b with the Psychophysics Toolbox extension version 3.0.10. Stimuli were presented on a BenQ XL2420T LED-backlit LCD monitor at a resolution of 1920 x 1080 and a refresh rate of 60 Hz. Participants were seated 1 m from the monitor in a dimly-lit room. Responses were collected with a Logitech gamepad.

### **3.2.3. Stimuli and Experimental Conditions**

The parameters of the RDK stimulus used in this study were selected to closely match those used by Kiorpes and Movshon (2004). White dots (1 arcmin in diameter; 270 cd/m<sup>2</sup>) were presented on a black (0.7 cd/m<sup>2</sup>) background. An array of 64 dots subtended a 7.7 x 7.7 deg square area, for a density of 1.1 dots/deg<sup>2</sup>. The total duration of an animation was 600 ms. In contrast to Experiment 1, signal dots moved either to the left or to the right, and a white noise algorithm was used to control the movement of dots (see Figure 3.1).

This experiment crossed two factors: time ( $\Delta t$ ), the duration of a single animation; and distance ( $\Delta x$ ), the distance a signal dot was displaced between frames. Two times were tested: 17 ms and 50 ms. In the 17 ms condition, animation frames were replaced at a rate equal to the refresh rate of the monitor (60 Hz). To achieve the total duration of 600 ms, this stimulus



**Figure 3.1: The RDK used in Experiment 2.** *Left:* a single frame of the RDK stimulus used in Experiment 2. *Right:* a schematic of dot behaviour on three subsequent frames of the RDK. Dot movement is governed by a white noise algorithm with signal and noise labels assigned probabilistically, such that on every animation frame, dots are selected to be a signal dot with a probability equal to the coherence value. In this four-dot example, coherence is 0.50; on each frame, two dots are selected at random to be signal dots, and the remaining two are noise dots. Signal dots move in the signal direction (in this example, right) at a fixed distance. Noise dots move in a randomly-selected direction at a randomly-selected distance.

consisted of 36 frames total. In the 50 ms condition, animation frames were replaced at a rate of 20 Hz (every three monitor refreshes), for a total of 12 frames. Seven distances were tested, ranging from 1 to 38 arcmin. The combination of these parameters created motion speeds ranging from 1 to 38 deg/s in the 17 ms condition, and from 0.3 to 13 deg/s in the 50 ms condition (see Table 3.1). Adults participated in all possible conditions of the experiment, and children were randomly assigned to either the 17 ms or 50 ms time conditions.

Table 3.1

*Parameters for the Time (2 levels) and Distance (7 levels) Conditions of Experiment 2.*

| Time Condition ( $\Delta t$ ) | Distance Condition ( $\Delta x$ ) |             |             |              |              |              |              |
|-------------------------------|-----------------------------------|-------------|-------------|--------------|--------------|--------------|--------------|
|                               | 1<br>arcmin                       | 3<br>arcmin | 5<br>arcmin | 11<br>arcmin | 23<br>arcmin | 30<br>arcmin | 38<br>arcmin |
| 17 ms                         |                                   |             |             |              |              |              |              |
| speed (deg/s)                 | 1                                 | 3           | 6           | 11           | 23           | 30           | 38           |
| 50 ms                         |                                   |             |             |              |              |              |              |
| speed (deg/s)                 | 0.3                               | 1           | 2           | 4            | 8            | 10           | 12           |

### **3.2.4. Procedure**

The general procedure was similar to that of Experiment 1. The task was made child-friendly by introducing a Toy Story themed backstory to provide instructions and frame the psychophysical task as a computer game in which the child had to save characters from being hit by moving stars. The participant's task was to indicate whether they perceived coherent motion to the left or to the right after viewing each RDK. A Toy Story character was placed on each side of the screen, and children were asked to indicate which character the stars were moving towards. Coherence was adjusted according to the same staircase procedure used in Experiment 1. Feedback was provided by presenting a cartoon character along with an auditory chime for correct responses, and a different cartoon character presented with no sound for incorrect responses. At the beginning of the session, participants conducted eight trials of a practice staircase using a distance of 15 arcmin. For adults, the time parameter used in practice was determined randomly. Each adult completed 14 staircases total, one for each time by distance crossing. Each child completed up to seven staircases within one time condition. Children were encouraged to complete all seven staircases, but were not kept longer than one hour; thus, data were included only for children who could complete at least three conditions during the experimental session. Condition order was determined by a Latin square. All testing was conducted monocularly, using the eye with the best visual acuity (or, when the eyes had the same visual acuity, a randomly-selected eye).

### **3.2.5. Analysis**

As before, responses were fit with a Weibull function to measure the 82% correct motion coherence threshold. A marginal linear model (also known as a *population-averaged model*;

West, Welch, & Galecki, 2007) was used to test main effects and interactions in these analyses. Like the general linear model (GLM), this procedure models parameters as a linear combination of terms (e.g.,  $x_{ijk} = \mu + \alpha_j + \beta_k + \alpha\beta_{jk} + \varepsilon_i$ ), but rather than using least squares methods, maximum-likelihood (ML) techniques are employed to estimate variance components. The marginal model procedure can account for the assumption violations that often render traditional GLM methods unreliable by directly modeling variance-covariance structures rather than making assumptions about their form (e.g., sphericity for within-subjects designs, or homogeneity of variance for between-subjects designs). Additionally, ML estimation can account for missing data on a repeated measurement, unlike the GLM, where a subject's entire set of data must be removed from analysis when at least one cell is missing. Finally, the ML technique does not lead to biased estimates when sample sizes are disproportionate. These advantages motivated the selection of the marginal model analysis rather than the traditional analysis of variance method. Marginal models can be considered a special case of the linear mixed model, which also accounts for random effects in nested or hierarchical designs.

In all analyses below, parameters were estimated with restricted maximum-likelihood estimation (SPSS 21, IBM Corp.). All analyses modeled an unstructured variance-covariance matrix, as no assumptions were made about the form of these matrices. Follow-up procedures (simple main effects and mean difference comparisons) were performed using the same ML framework, and all were Bonferroni-corrected for a family-wise error rate of  $\alpha = .05$ .

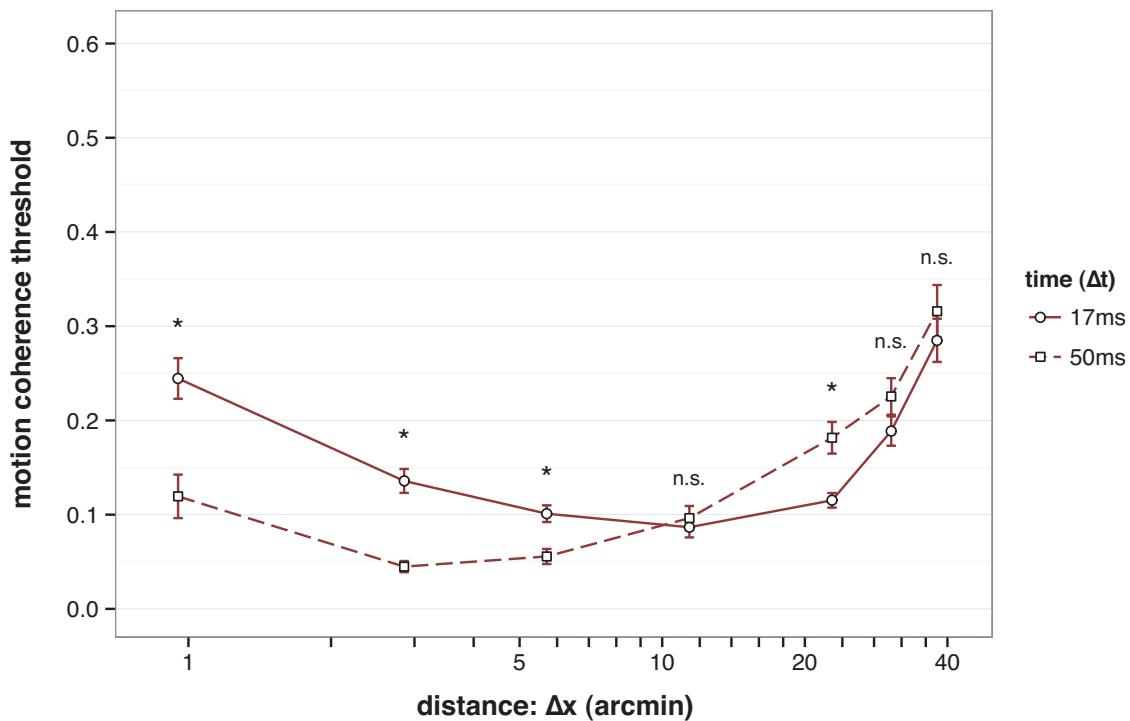
### **3.3. Results**

First, the adult and child data were each analyzed separately to describe differences in performance that depend on parameters within each of these age groups. Next, developmental

differences in performance were investigated in the 17 ms condition, and the 50 ms condition.

### 3.3.1. Adults

Data for 31 adults (see Figure 3.2) were analyzed as a completely within-subjects design, with factors Time (2 levels: 17 ms, 50 ms) and Distance (7 levels, as described above). Because there were no missing data, this analysis can be conducted with a conventional repeated-measures ANOVA; however, due to significant and extreme violations of the assumption of sphericity (for Distance,  $\chi^2(20) = 120.72, p < .0001$ ; for Time by Distance,  $\chi^2(20) = 55.24, p <$

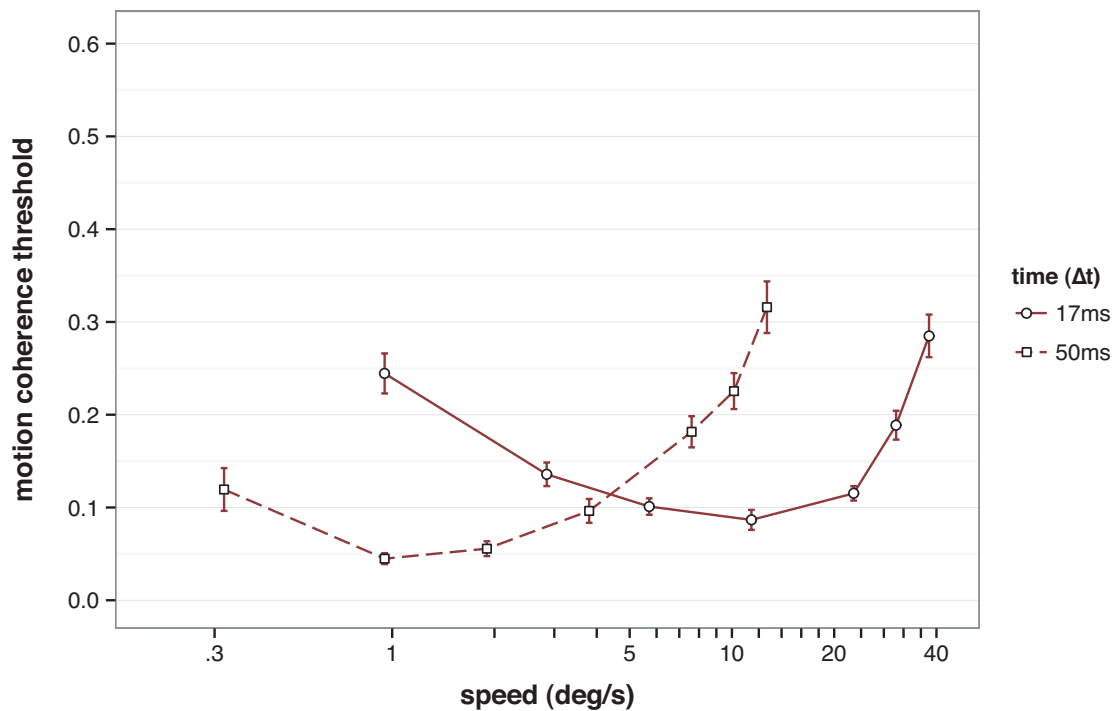


**Figure 3.2. Motion coherence thresholds (expressed as a proportion) for adults obtained in Experiment 2.** Lower thresholds mean better performance. Error bars reflect standard error. Significant differences between the 17 ms and 50 ms conditions are indicated with asterisks (Bonferroni family-wise error rate of  $\alpha = .05$ ); n.s. indicates no significant differences.



.0001), and for consistency with subsequent analyses, data were analyzed under the marginal model framework described above (total number of estimated parameters = 119). There was a significant main effect of Time,  $F(1, 30) = 4.25, p = .048$ ; a significant main effect of Distance,  $F(6, 30) = 26.48, p < .0001$ ; qualified by a significant Time by Distance interaction,  $F(6, 30) = 9.47, p < .0001$ . A simple main effects analysis examining the effect of Time at each Distance found significantly higher thresholds in the 17 ms than 50 ms condition at 1 arcmin ( $F(1, 30) = 39.28, p < .0001$ ), 3 arcmin ( $F(1, 30) = 50.29, p < .0001$ ), and 6 arcmin ( $F(1, 30) = 22.35, p = .00035$ ) distances; significantly higher thresholds in the 50 ms than 17 ms condition at 23 arcmin ( $F(1, 30) = 14.28, p = .0049$ ) distances; and no significant differences between the 17 ms and 50 ms conditions at 11 arcmin ( $F(1, 30) = 0.47, p > .99$ ), 30 arcmin ( $F(1, 30) = 2.49, p = .87$ ), or 38 arcmin ( $F(1, 30) = 1.18, p > .99$ ) distances. Analyses performed with the conventional least squares method lead to the same conclusions.

Inspection of Figure 3.2 suggests that optimal distance values (and thus, motion speeds) depend on time. In other words, peak motion sensitivity varies as a function of the time parameter used in the stimulus. Optimal performance lies near distances of about 11 arcmin for the 17 ms condition, and about 3 arcmin for the 50 ms condition. These points correspond to drastically different speeds: 11 deg/s and 1 deg/s, respectively. In fact, plotting thresholds as a function of speed rather than distance (Figure 3.3) reveals that, except for speeds within the range of 3-6 deg/s, thresholds for a given speed rely heavily on the distance/time pair used to create that speed. For example, adult thresholds in the 17 ms condition are about 5x higher than those in the 50 ms condition at 1 deg/s, but are only about a third as high as thresholds in the 50 ms condition at around 11 deg/s.

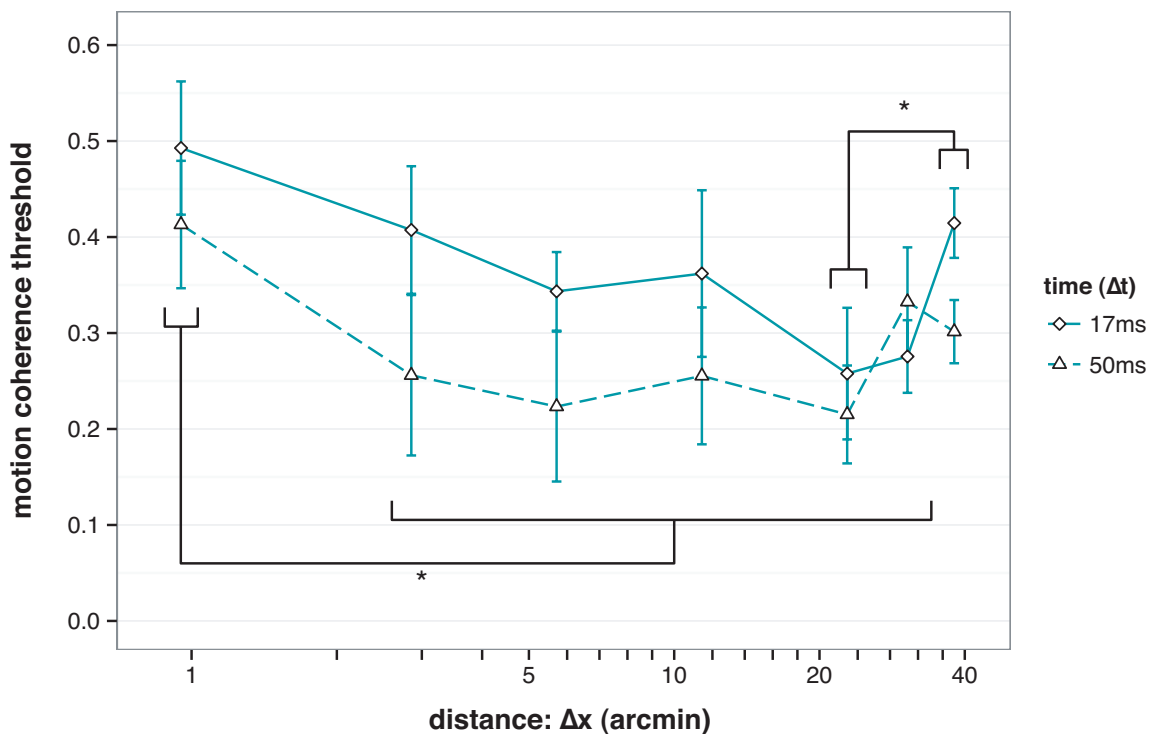


**Figure 3.3. Motion coherence thresholds of adults plotted as a function of speed.** Error bars reflect standard error.

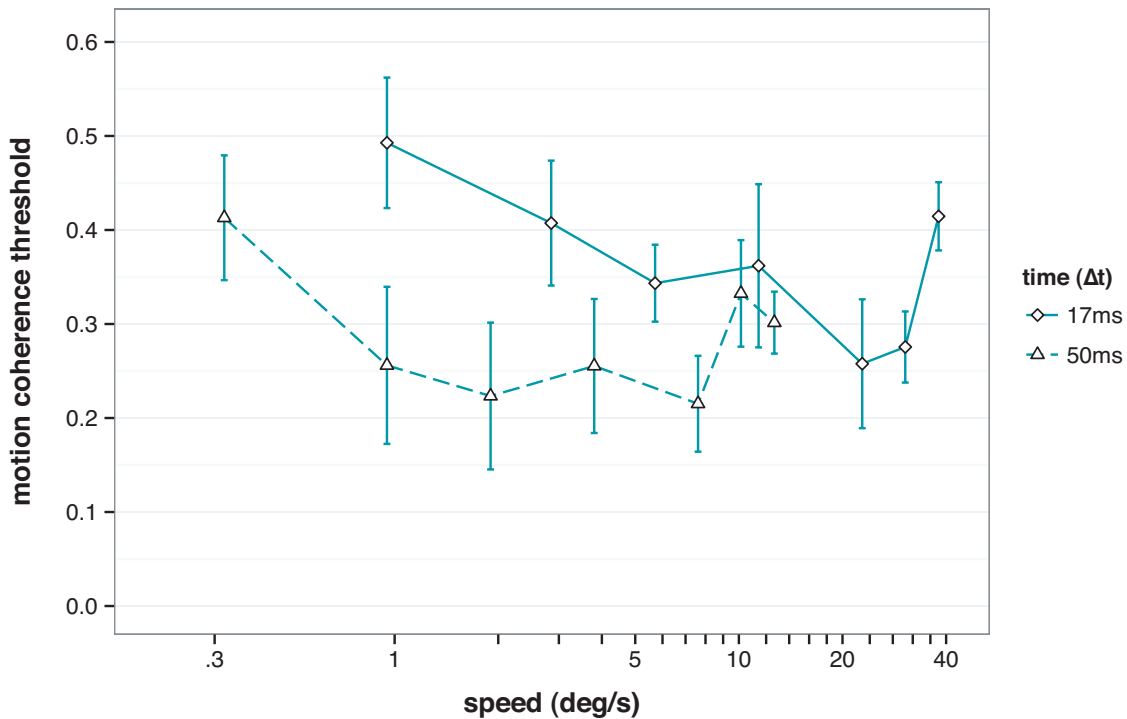
### 3.3.2. Children

Data for 28 children (see Figure 3.4) were analyzed with the between-subjects factor Time, and the within-subjects factor Distance (total number of estimated parameters = 42). Fourteen children (10 female) were in each Time condition, and there were no significant differences in age ( $t(26) = 0.26, p = .80$ ), visual acuity ( $t(26) = 0.31, p = .76$ ), or stereoacuity ( $t(26) = 1.34, p = .19$ ) between conditions. For the 17 ms condition, 7 of 14 children had at least 1 and no more than 4 cells of missing data. For the 50 ms condition, 6 of 14 children had at least 1 and no more than 3 cells of missing data. No more than 3 cells of data were missing from each Time by Distance condition. Because missing data arose primarily from children who were unable to complete all seven staircases during a one-hour session, data were considered missing

completely at random. There was no significant main effect of Time,  $F(1, 23.78) = 0.65, p = .42$ , a significant main effect of Distance,  $F(6, 17.77) = 23.56, p < .0001$ , and no significant interaction between the two,  $F(6, 17.77) = 1.10, p = .40$ . Follow-up comparisons indicated that thresholds in the 1 arcmin condition were significantly higher than all other conditions except the 38 arcmin condition; and that the 38 arcmin condition was significantly higher than the 23 arcmin condition. In the 1 arcmin condition, these elevated thresholds were correlated with age,  $r(21) = -.57, p = .0049$ , uncorrected. Controlling for age, there was no correlation between visual acuity and thresholds at 1 arcmin distances:  $r(20) = -0.01, p = .96$ .



**Figure 3.4. Motion coherence thresholds for children obtained in Experiment 2.** Error bars reflect standard error. Significant mean differences between distances, collapsed across time, are indicated with asterisks (Bonferroni family-wise error rate of  $\alpha = .05$ ).



**Figure 3.5. Motion coherence thresholds of children plotted as a function of speed rather than distance.** Error bars reflect standard error.

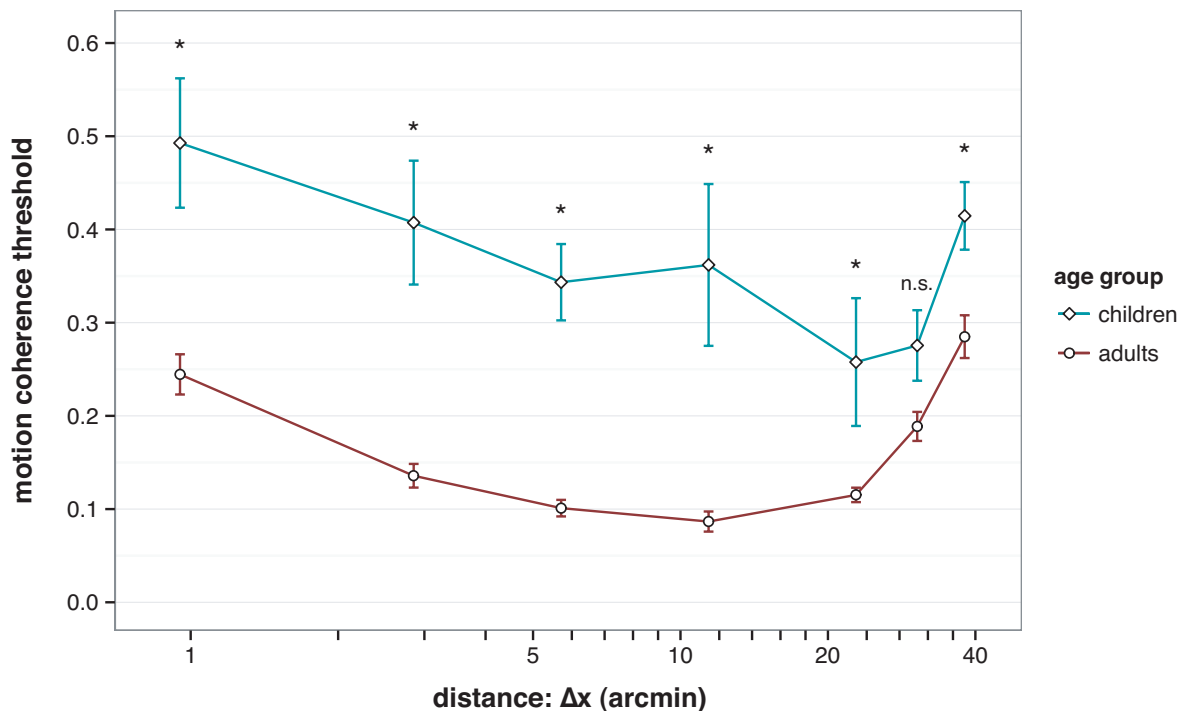
Figure 3.5 shows the child data plotted as a function of speed. It is clear that motion coherence thresholds at slower speeds, like 1 deg/s, follow the same pattern as those of adults—thresholds are higher for the 17 ms condition than for the 50 ms condition. However, children do not appear to show the same reversal that adults do at faster speeds like 10 deg/s. Instead, it appears that coherence thresholds for children are about the same regardless of time condition.

### 3.3.3. Developmental Differences

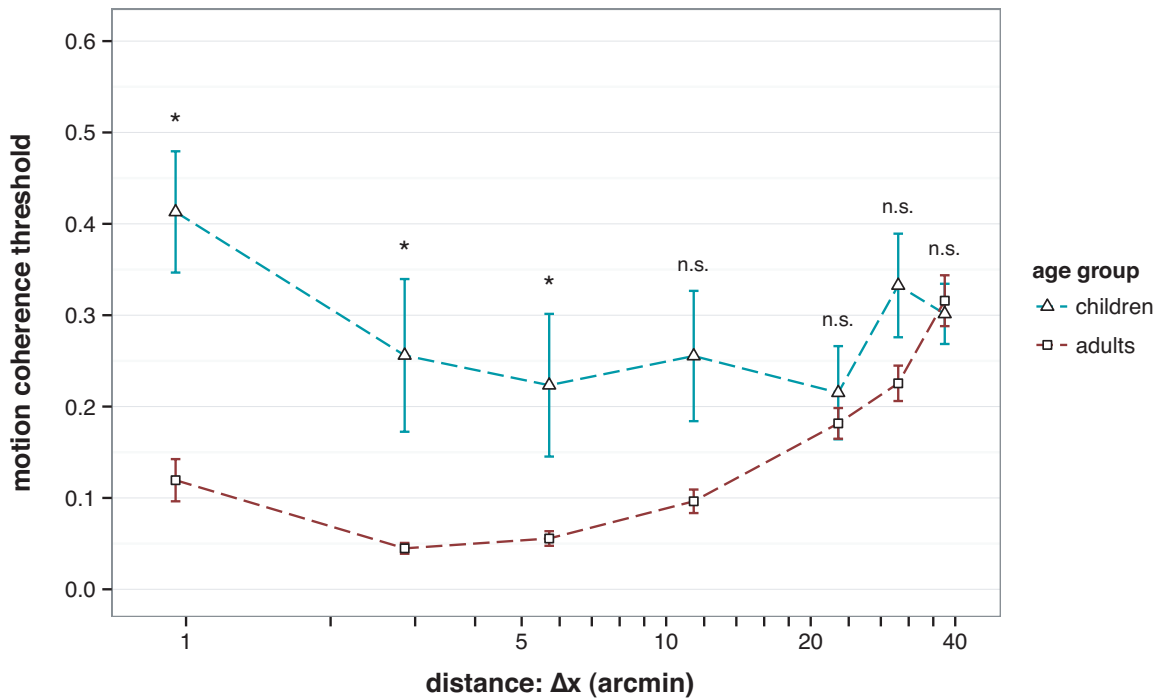
Developmental differences in coherence thresholds were examined with the between-subjects factor Age Group (2 levels: Child,  $n = 14$ ; and Adult,  $n = 31$ ) and within-subjects factor Distance (7 levels). Two analyses were conducted separately, one for the 17 ms condition, and another for the 50 ms condition (total number of estimated parameters in each = 42).

For the 17 ms condition (Figure 3.6), there was a significant main effect of Age Group,  $F(1,37.17) = 53.02, p < .0001$  and a significant main effect of Distance,  $F(6, 35.06) = 19.23, p < .0001$ , qualified by a significant Age Group by Distance interaction,  $F(6, 35.06) = 3.72, p = .0058$ . Simple main effects analysis examining the effect of Age Group at each Distance indicated that adults had significantly lower thresholds than children in all Distance conditions, 1 arcmin:  $F(1, 40) = 20.77, p < .0004$ , 3 arcmin:  $F(1, 42) = 33.83, p < .0001$ , 6 arcmin:  $F(1, 45) = 74.03, p < .0001$ , 11 arcmin:  $F(1, 47) = 22.71, p < .0002$ , 23 arcmin:  $F(1, 45) = 11.52, p = .011$ , 38 arcmin:  $F(1, 45) = 8.59, p = .039$ ; except for 30 arcmin,  $F(1,46) = 6.36, p = .10$ .

In the 50 ms condition (Figure 3.7), there was a significant main effect of Age Group,  $F(1, 39) = 11.81, p = .0014$ , a significant main effect of Distance,  $F(6, 39.33) = 20.33, p < .0001$ ,



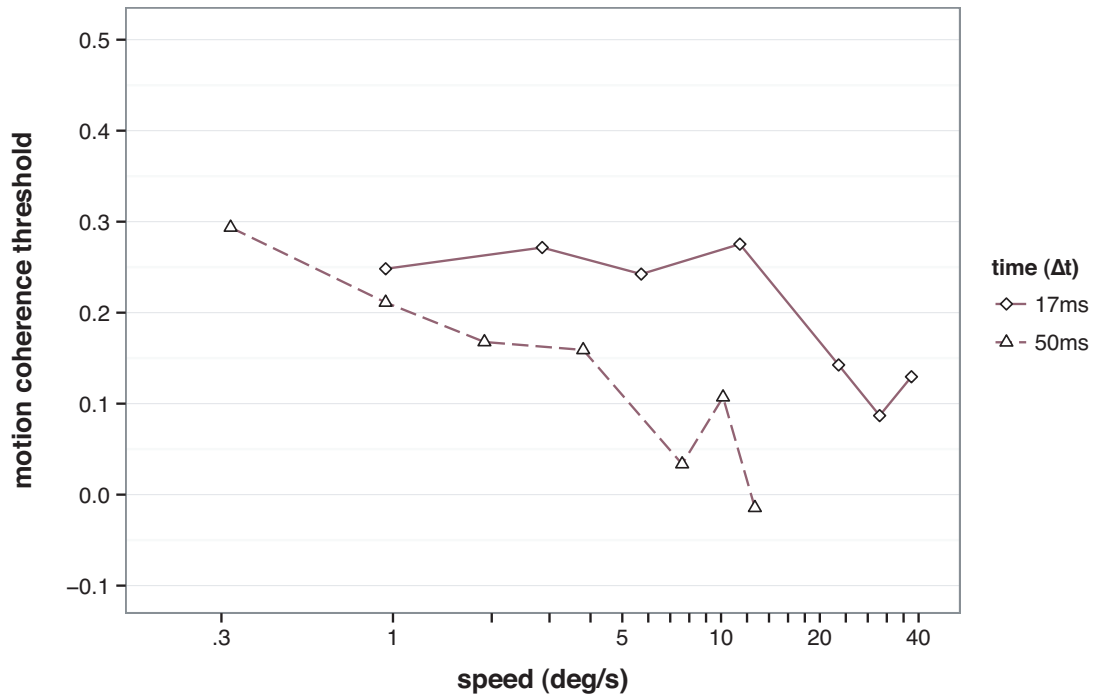
**Figure 3.6. Motion coherence for children and adults obtained for the 17 ms time condition in Experiment 2.** Error bars reflect standard error. Significant differences between children and adults are indicated with asterisks (Bonferroni family-wise error rate of  $\alpha = .05$ ); n.s. indicates no significant differences.



**Figure 3.7. Motion coherence thresholds for children and adults obtained for the 50 ms time condition in Experiment 2.** Error bars reflect standard error. Significant differences between children and adults are indicated with asterisks (Bonferroni family-wise error rate of  $\alpha = .05$ ); n.s. indicates no significant differences.

and a significant Age Group by Distance interaction,  $F(6, 39.33) = 8.73, p < .0001$ . Simple main effects analysis revealed adults had significantly lower thresholds than children in the 1 arcmin ( $F(1, 41) = 18.78, p < .0001$ ), 3 arcmin ( $F(1, 41) = 13.05, p = .0070$ ), 6 arcmin ( $F(1, 41) = 11.54, p = .014$ ) conditions, but thresholds were not significantly different between adults and children in the 11 arcmin ( $F(1, 41) = 7.44, p = .063$ ), 23 arcmin ( $F(1, 42) = 0.13, p > .99$ ), 30 arcmin ( $F(1, 43) = 5.89, p = .14$ ), and 38 arcmin ( $F(1, 41) = 0.11, p > .99$ ) conditions.

To facilitate comparisons between adults and children as a function of speed, Figure 3.8 presents the child and adult data from Figures 3.3 and 3.5 on one graph, plotted as the difference (child – adult).



**Figure 3.8. Motion coherence thresholds obtained in Experiment 2 plotted as a difference (children – adults) as a function of speed.**

### 3.4. Discussion

#### 3.4.1. Adult Performance

These results provide a framework for understanding the relationship between speed and motion coherence thresholds. First, these results suggest that at smaller distances (1-6 arcmin), shorter times (and thus, faster speeds) lead to increased thresholds in adults (Figure 3.2). To my knowledge, no studies have investigated coherence thresholds by varying time and holding distance constant at distance values this low. However, these results are consistent with the observation by Fredericksen, Verstraten, and van de Grind (1993) that minimum  $\Delta x$  displacement thresholds in a left-right motion discrimination task decrease as  $\Delta t$  is increased from 11 ms to 66-100 ms. A very small distance displacement is much closer to threshold under the 17 ms condition than the 50 ms condition, and so performance in this condition is worse.

Second, these results suggest that the  $\Delta t$  of a stimulus dictates the speed at which lowest motion coherence thresholds will be obtained in adults, with shorter times showing best performance at faster speeds (10 deg/s and above), and longer times showing best performance at slower speeds (1 deg/s and below) (Figure 3.3). This is consistent with previous research outlined above for monkeys. Mikami, Newsome, and Wurtz (1986) measured the maximum  $\Delta x$  and  $\Delta t$  values to which direction-selective cells in V1 and MT could respond, and found they never occur together, with maximum  $\Delta x$  values occurring for much smaller values of  $\Delta t$ . This implies that larger  $\Delta x$  displacements are more likely to be detected at smaller values of  $\Delta t$ , so I would predict the peak motion sensitivity of these psychophysical tuning curves to shift to the right (toward larger  $\Delta x$  values) as  $\Delta t$  decreases.

We can see support for this shift in curvilinear functions by comparing the current results to previous studies that measure motion coherence thresholds at different speeds. For example, Narasimhan and Giaschi (2012) used a  $\Delta t$  of 40 ms and tested adults at  $\Delta x$  distances of 2.4 and 9.6 arcmin, respectively, to create speeds of 1 and 4 deg/s. Consulting Figure 3.2, I would predict very similar thresholds for both distances tested, which is what they found. If they had tested faster speeds by holding time constant and using larger values of  $\Delta x$ , I predict that they would have found higher coherence thresholds. In support of this, Downing and Movhson (1989) used a time of 45 ms and found that coherence thresholds increased for speeds greater than 5 deg/s, testing distances up to 80 arcmin.

In contrast to Downing and Movhson's (1989) findings, Hadad et al. (2011) tested speeds of 4 and 18 deg/s and found *lower* thresholds in adults for the 18 deg/s condition. However, inspection of Figure 3.2 would predict this difference: Hadad et al. used a  $\Delta t$  of 13 ms, and  $\Delta x$  distances of 4 and 14.4 arcmin, respectively. For a  $\Delta t$  of 17 ms, we expect peak sensitivity to be



around  $\Delta x$  of 11 arcmin, and perhaps an even larger distance for a time of 13 ms.

Three pieces of evidence from adult performance have potentially conflicting results with this framework. The first comes from Arena et al. (2012), who found that when speed was held constant at 2.5 deg/s, participants had increased coherence thresholds for values of  $\Delta x$  and  $\Delta t$  larger than 16 arcmin / 107 ms. The second comes from Knox, Ledgeway, and Simmers (2013), who found at a speed of 1.5 deg/s, values of  $\Delta x$  and  $\Delta t$  (14.4 arcmin / 160 ms) yielded a mean threshold of 0.21, significantly higher than the mean threshold of 0.10 obtained with smaller values of  $\Delta x$  and  $\Delta t$  (2.4 arcmin / 27 ms). The third comes from comparison of two papers that used similar stimuli and speeds: Parrish et al. (2005) also found thresholds of 0.21 with values of 8.5 arcmin / 107 ms, while Narasimhan and Giaschi (2012) found thresholds of 0.08 with smaller values, 2.4 arcmin / 40 ms. These results are opposite of those predicted by Figure 3.3, which suggests that, for a given speed, larger pairings are associated with *decreased* thresholds. However, the “large” pair depicted at 1 deg/s (3 arcmin / 50 ms) corresponds to smaller pairs tested by Arena et al., Knox et al., and Narasimhan and Giaschi. Just as coherence thresholds show a u-shaped pattern as a function of distance, where motion sensitivity peaks around 3-11 arcmin, we should expect thresholds to show a u-shaped pattern as a function of time. Fredericksen et al. (1993) found a similar u-shaped function in the minimum  $\Delta x$  displacement thresholds referred to above: they increased again for times longer than 100 ms. It is possible, then, that thresholds for a given  $\Delta x$  value as a function of  $\Delta t$  have peak sensitivities around values between 40 and 100 ms.

### **3.4.2. Child Performance**

The current results predict that children’s motion coherence thresholds depend on the

distance value,  $\Delta x$ , rather than the time value,  $\Delta t$ , with the smallest distance yielding the largest motion coherence thresholds (Figure 3.4). This is not likely due to poor visual acuity in children, as no association between acuity and performance was found. Kiorpes and Movshon (2004) found that although contrast sensitivity (a measure related to, though not the same as, visual acuity) and motion developed with similar patterns, such that larger spatial frequencies develop first followed by a fine-tuning of high spatial frequencies, sensitivity to motion developed beyond the age at which the contrast sensitivity function was adult-like.

Narasimhan and Giaschi (2012) found children had significantly higher thresholds at  $\Delta x$  values of 2.4 arcmin compared to 9.6 arcmin. From Figure 3.4 we would predict 1 arcmin distances, but not 3 arcmin distances, to have significantly higher thresholds than a distance of 9.6 arcmin. While it is not possible to make a clear prediction for differences involving 2.4 arcmin, Narasimhan and Giaschi's finding is not surprising in light of the current study. Hadad et al. (2011) found children had significantly higher thresholds for 4 arcmin than for 14.4 arcmin. While visual inspection of Figure 3.4 suggests we would find such a trend, this prediction is not supported statistically in the current data. It should be noted that elevated thresholds for the 4 arcmin condition in the Hadad et al. study may be driven by a higher proportion of children obtaining ceiling thresholds of 1.0 in the 4 than in the 14 arcmin condition. Alternately, the large number of  $\Delta x$  values tested coupled with highly variable data may have led to poor power to detect an effect between these  $\Delta x$  values in the current study. Finally, it is likely that coherence thresholds, and maturity, depend on additional differences between the two studies (dot size, area, or noise type, for example). Further conclusions cannot be made without a more targeted experiment.

Finally, inspection of Figure 3.5 underscores the importance of taking caution when

comparing children's thresholds between two tasks that report the same speeds, but use different  $\Delta x$  and  $\Delta t$  values, particularly for slow speeds. At 1 deg/s, thresholds in the 17 ms condition are twice those of the 50 ms condition. Knowing the speed of the stimulus alone will not predict this difference.

### **3.4.3. Developmental Differences**

The current study found that for a  $\Delta t$  of 17 ms, all but one  $\Delta x$  value tested (30 arcmin) showed significant differences between children and adults. For a  $\Delta t$  of 50 ms, children had significantly higher motion coherence thresholds than adults at distances of 6 arcmin and below (corresponding to speeds of 2 deg/s and slower). However, there were no significant differences between children and adults for distances of 11 arcmin and above (corresponding to speeds of 4 deg/s and faster). This suggests two things: first, children are more mature as values of  $\Delta x$  increase. Second, it may also be that children are more mature as values of  $\Delta t$  decrease. While these are both consistent with previous findings that sensitivity for fast speeds matures earlier than for slow speeds (section 1.5), Figure 3.8 shows that knowing the speed of the stimulus alone is not enough to predict maturity on this task.

Taking into account the significant differences between age groups outlined in section 3.3.3, a qualitative comparison of Figure 3.8 with Figure 1.4 provides some support for the framework proposed in section 1.6. First, for a given  $\Delta t$ , children are indeed significantly immature at slow speeds. Second, children are not significantly different than adults at most fast speeds (though this is true only for one speed—30 deg/s—in the 17 ms condition). Finally, there are some intermediate speeds (4-12 deg/s) for which we find that children are performing like adults in the longer 50 ms condition, but not in the shorter 17 ms condition.

This framework can resolve some of the inconsistencies identified in section 1.4, because it predicts the pattern of maturity observed in previous experiments. For example, we would predict that the children in the study by Narasimhan and Giaschi (2012) using a  $\Delta t$  value of 40 ms, which is between the two values tested in this study, would be immature for speeds of 1 deg/s, and closer to maturity at speeds of 4 deg/s. We would also predict that children tested in the study by Hadad et al. (2011) using a  $\Delta t$  value of 13 ms, shorter than the shortest value tested here, would be immature at speeds of 4 and 18 deg/s. Parrish et al. used larger  $\Delta x$  and  $\Delta t$  values, 8.5 arcmin and 107 ms, and found children had mature motion coherence thresholds. While a speed of 1 deg/s is below the intermediate range of speeds (4-12 deg/s) identified above, the  $\Delta t$  value used in that study was twice that of the largest value used here. The pattern of results demonstrated in this study is consistent with the notion that the minimum speed at which children can be considered mature decreases as  $\Delta t$  increases.

The additional studies that demonstrated mature performance in 6-year-olds require some consideration. First, Reiss et al. (2005) found that children were mature in a task using a  $\Delta t$  of 50 ms, allowing for direct comparison to the current study. Reiss et al. tested a speed of 2.51 deg/s, using a distance of 7.5 arcmin. This is between the two distances that were found to be immature (6 arcmin) and mature (11 arcmin) in the current study for a  $\Delta t$  of 50 ms. Other stimulus properties may have pushed performance in Reiss et al.'s study towards maturity. While the same algorithm for dot movement was used in both that study and the current study, children in Reiss et al.'s study may have benefitted from an extended stimulus duration (6150 ms or 123 total frames; compared to 600 ms or 12 frames in the current study).

Second, Ellemberg et al. (2002) demonstrated mature performance in 6 year olds with stimulus parameters reported to be the same as those used in Hadad et al. (2011). However, some

of the authors of the Ellemberg et al. paper have since reported that signal dots had unlimited lifetimes (Hadad et al., 2011) and noise dots may have had limited lifetimes, which would likely have made the task easier for children.

It should be noted that children may not necessarily appear more adult-like as distance increases beyond the distances tested here. For example, we know that for an 8-frame, 107 ms per frame stimulus, the maximum  $\Delta x$  that is perceived as motion is about 58 arcmin for children 5-6 years old, and about 73 arcmin for adults (Parrish et al., 2005). As distances reach and exceed children's maximum  $\Delta x$  displacement thresholds, they are expected to perform worse than adults. At a distance of 65 arcmin, young children may not even perceive motion at 100% coherence, while adults will.

Two studies using random Gabor kinematogram stimuli in 5-year-old children appear to have conflicting results with this study. Ellemberg et al. (2004) tested three motion speeds by holding  $\Delta x$  constant at 14.4 arcmin, and varying  $\Delta t$  for speeds of 1.5 deg/s ( $\Delta t$  of 160 ms), 6 deg/s ( $\Delta t$  of 40 ms), and 9 deg/s ( $\Delta t$  of 27 ms). They found that children's performance at a  $\Delta t$  of 160 ms was far *more* immature than of 40 and 27 ms. Similarly, Ellemberg et al. (2010) held speed constant at 1.5 deg/s and tested  $\Delta x/\Delta t$  pairs of 6 arcmin / 66 ms, 30 arcmin / 333 ms, and 60 arcmin / 666 ms. Here, children's performance was most mature at the smallest values of  $\Delta x$  and  $\Delta t$ . These findings are inconsistent with the current study's predictions that longer  $\Delta x$  and  $\Delta t$  values at speeds around 1 deg/s should lead to more mature performance, as demonstrated by the comparison between immature and mature performance found in Narasimhan and Giaschi (2012) and Parrish et al. (2005), respectively.

Two factors may account for these discrepancies. First, because stimulus duration was held constant at 1500 ms in these studies, the total number of frames presented to participants (9

in Elleberg et al., 2004; 3 in Elleberg et al., 2010) was fewest in the conditions in which children were found least mature. The reduced number of frames may account for these immaturities. Second, as noted above, children have smaller maximum  $\Delta x$  displacement thresholds than adults (Parrish et al., 2005), and the immature performance found in Elleberg et al.'s (2010) 60 arcmin condition may be due to the fact that this displacement is near thresholds for children. It is also likely children have shorter maximum  $\Delta t$  thresholds than adults, though this has yet to be tested. If so, this may explain why children in Elleberg et al. (2004) at 160 ms were considered immature, while the children in Parrish et al. at 107 ms were not: 160 ms, but not 107 ms, may be close to children's maximum  $\Delta t$  threshold, while adults have a threshold much larger than this (e.g., Mather & Tunley, 1995).

It should be noted that the current study also controlled for stimulus duration, and not number of frames. As described in the methods, the 17 ms condition presented 36 total frames, and the 50 ms condition presented 12 total frames. If 12 frames were not enough for children to perform well, we might expect to see lower coherence thresholds for children in the 17 ms condition, or for children in the 17 ms condition to appear more mature than children in the 50 ms. This does not appear to be the case, and children's performance is slightly better, if not the same, in the 50 ms condition.

## 4. Conclusions

### 4.1. General Discussion

This thesis sought to resolve inconsistencies in previous studies on the maturation of human global motion perception by studying the impact of  $\Delta x$  and  $\Delta t$  in RDKs on motion coherence thresholds. I proposed a theoretical framework (section 1.6) for understanding the relationship between these factors and performance, and how they may lead to discrepant findings if only their ratio or speed, is considered. I investigated this possibility in two experiments. In Experiment 1, I measured adults' motion coherence thresholds while holding speed constant at 1 deg/s and varying the parameters  $\Delta x$  (from 2.5 arcmin to 11.5 arcmin) and  $\Delta t$  (from 42 ms to 192 ms). Experiment 1 found no effect of  $\Delta x$  and  $\Delta t$  on motion coherence thresholds in adults. In Experiment 2, I measured motion coherence thresholds in adults and children for a range of speeds (from 0.3 to 38 deg/s) while varying the parameters  $\Delta x$  (from 1 arcmin to 38 arcmin) and  $\Delta t$  (at 17 ms or 50 ms). Here, I found that for  $\Delta x$  values below 6 arcmin, a shorter  $\Delta t$  (17ms) led to higher thresholds than a longer  $\Delta t$  (50ms) in adults, and that children's performance can be described as a function of  $\Delta x$  regardless of  $\Delta t$ . I also found that children demonstrated mature performance when  $\Delta x$  values were large, though the exact  $\Delta x$  values at which they were mature depended on  $\Delta t$ . Finally, I found that motion coherence thresholds for some speeds depended on the values of  $\Delta x$  and  $\Delta t$  used to create that speed; and that children tested at intermediate speeds (4-12 deg/s) may be considered mature or not, depending on the  $\Delta t$  of the RDK stimulus.

The null results of Experiment 1, where I held speed constant at 1 deg/s and varied  $\Delta x$  and  $\Delta t$ , are especially surprising in light of the results of Experiment 2. Inspecting Figure 3.3, I would predict that varying the  $\Delta x$  and  $\Delta t$  values used should cause differences in performance for

speeds of 1 deg/s and below, and 10 deg/s and above. If I had tested a speed between these two extremes in Experiment 1, a null result may have been expected. There are two things that may account for this, though they cannot explain the performance differences found between the adults in Narasimhan and Giaschi (2012) and Parrish et al. (2005). It could be that performance saturates at a  $\Delta t$  around 50 ms, and this is why a speed of 1 deg/s does not show these effects for  $\Delta t$  values of 42 ms and above. On the other hand, it is important to note that a number of other stimulus parameters differed between the two experiments—both were designed to match parameters of previous studies as close as possible. It is possible, then, these parameters had an impact on the shape or the position of the functions displayed in Figure 3.3. For example, Experiment 1 used up/down discrimination, signal and noise labels preserved with random noise, and dots had no limited lifetimes. Experiment 2, on the other hand, used left/right discrimination, probabilistic signal and noise labels, and white noise, which effectively gave dots limited lifetimes, especially at lower coherence values. The RDK in Experiment 1 was very dense, while in Experiment 2, very sparse. The evidence outlined in section 1.3 makes no consistent predictions about thresholds in Experiment 1 (e.g., up/down discrimination might yield higher thresholds; unlimited random walk dots might yield lower thresholds; the density differences should not impact performance), and there are no studies investigating how these parameters might change the shape or position of a psychophysical tuning curve like the one pictured in Figure 3.3. It would be appropriate to conduct follow-up experiments using parameters identical to those used in Experiment 2 (see section 4.3, Future Directions).

## **4.2. Speed-Tuning in the Brain with Development**

Some accounts suggest a single system comprised of speed-tuned mechanisms can



represent a range of speeds (e.g., Perrone & Thiele, 2002; van Boxtel & Erkelens, 2006). As reviewed in the Introduction, these mechanisms may lie in the interactions between V1 and MT. Liu and Newsome (2003) demonstrated that MT neurons in macaques are clustered according to preferred speed. Nover, Anderson, and DeAngelis (2005) found that the distribution of MT neurons' speed sensitivity reflects a normal distribution in logarithmic space, such that nearly half of all neurons measured were responsive to speeds below 7 deg/s. These studies held  $\Delta t$  at a short constant and varied  $\Delta x$  to sample different speeds, so these preferences may reflect preferred displacements rather than speed per se. However, Priebe, Lisberger, and Movshon (2006) demonstrated that while simple cells in V1 have separable preferred spatial and temporal frequency tuning, many V1 complex cells and MT cells are specifically speed-tuned, such that they will respond maximally to a preferred speed rather than to a preferred spatial or temporal frequency. There is some evidence that newborn macaques have adult levels of direction-selectivity in V1 neurons (Movshon, Kiorpes, Cavanaugh, & Hawken, 1999; Kiorpes & Movshon, 2003) and that spatial-frequency responses of V1 neurons mature rapidly to near-adult levels in one month (Chino, Smith, Hatta, & Cheng, 1997). V1 neurons appear to have adult-like output projections (Kiorpes, Doron, & Movshon, 2003). While MT neurons are also directionally-selective at birth, their dynamics are sluggish at infancy and show maturation by 4 months (Movshon, Rust, Kohn, Kiorpes, & Hawken, 2003; 2004). Maturation at 4 months is still too early in life to explain the behavioural developmental patterns of macaques until 3 years (Kiorpes & Movshon, 2004; Kiorpes et al., 2012), however. Immaturities are likely to lie in the computational mechanisms that integrate motion information, which may need experience to undergo a coarse-to-fine refinement.

Functional neuroimaging studies in human adults have shown that global motion tasks

activate MT and area V3a (Braddick et al., 2001). Activation in MT increases linearly as a function of the coherence of the stimulus (Rees, Friston, & Koch, 2000), though activation has also been shown to be higher for near-threshold than suprathreshold coherence levels during a discrimination task (Giaschi, Zwicker, Au Young, & Bjornson, 2007), which may be because this relationship can be influenced by attention (Stoppel et al, 2011). Activity in MT also has a curvilinear relationship with speed, with greatest responses in the range of 4-8 deg/s, and V3a shows a similar pattern of activation (Chawla, Phillips, Buechel, Edwards, & Friston, 1998; Chawla et al., 1999). Speed discrimination tasks have been found to activate MT but also other areas including V3, V3a, and V4 (Sunaert, van Hecke, Marchal, & Orban, 2000). Thus, it is unlikely that global motion integration stimuli like the RDKs studied here exclusively recruit V1 and MT, and more likely that a network of areas is involved.

Mounting evidence suggests there may be separate systems for perceiving slow (below 3 deg/s) and fast motion, with considerable overlap at intermediate speeds (e.g., Burr, Fiorentini, & Morrone, 1998; Edwards, Badcock, & Smith, 1998; Gorea, Papathomas, & Kovacs, 1993; Heinrich, van der Smagt, Bach, & Hoffmann, 2004; Khuu & Badcock, 2002; Thompson, Brooks, & Hammett, 2006; van der Smagt, Verstraten, & Van de Grind, 1999). Based on psychophysical evidence, some authors argue slow motion information may be carried by the parvocellular or ventral stream, whereas fast motion information is carried by the magnocellular or dorsal stream (Verstraten, van der Smagt, & van de Grind, 1998; van de Grind, van Hof, van der Smagt, & Verstraten, 2001). For example, Gegenfurtner and Hawken (1996) have suggested that a pathway through V1 to V3 and V4 may carry slow motion information. Neuroimaging evidence is beginning to support a cortical basis for ventrally-carried slow speed information. For example, using electroencephalography, Lorteije, van Wezel, and van der Smagt (2008) found ventral

areas activated for stimuli moving at slow speeds (3.5 deg/s) and dorsal areas activated for both slow and fast speeds (32 deg/s). The results from Experiment 2 suggest that if slow speeds are carried by different brain areas than fast speeds, it may be because of the smaller  $\Delta x$  distances used in the stimuli presented.

If slow speed is carried ventrally, this might account for the prolonged development of slow motion sensitivity—if ventral areas do indeed take longer to mature. Evidence on which processing stream matures first is inconsistent. Mitchell and Neville (2004) measured ERP components in 6- to 10-year-olds and adults to isoluminant colour stripes (a “ventral” stimulus) and moving gratings (a “dorsal” stimulus) and found ERPs for the dorsal stimulus displayed more immaturities. Langrová, Kuba, Kremláčček, Kubová, and Vít (2006) measured pattern-reversal and motion-onset visual evoked potentials and came to similar conclusions. In contrast, Dekker, Mareschal, Sereno, and Johnson (2011) studied the same age group by using functional magnetic resonance imaging to measure responses to animal faces in ventral areas and tools in dorsal areas, and found activations in dorsal areas were adult-like, but activations in ventral areas were not. Studies of the structural neurological pathways in developing macaques suggest dorsal motion and parietal pathways mature earlier than the ventral temporal pathways involved in form and object perception (Distler, Bachevalier, Kennedy, Mishkin, & Ungerleider, 1996). Of course, development is likely nuanced throughout the brain: areas within a single processing stream may mature at different rates.

### **4.3. Future Directions**

The current study has sampled only a slice of the spatiotemporal surface. A number of investigations with other  $\Delta x$  and  $\Delta t$  parameters would answer some outstanding questions that

have been raised throughout this paper.

First, to follow-up Experiment 1 with an investigation into the differences between motion coherence thresholds in Narasimhan and Giaschi (2012) and Parrish et al., (2005), an experiment should be conducted to measure thresholds as a function of motion discrimination direction and stimulus shape. The higher thresholds in Parrish et al. may be because up/down discrimination tasks yield higher thresholds than left/right tasks. Or, the higher thresholds may be due to the fact that Parrish et al. measured thresholds for up/down discrimination along the short axis of a horizontally-oriented rectangle. As discussed, van Doorn and Koenderink (1984) found that motion detection thresholds varied as function of the rectangle width:height ratio in the axis of motion direction. However, Parrish et al. used a larger stimulus than Narasimhan and Giaschi, so it is unclear how thresholds would compare. An experiment testing the factors direction (up/down, left/right), stimulus rectangle orientation (horizontal, vertical), and stimulus area (small, large) would answer this question.

A number of questions raised by Experiment 2 could be answered by obtaining psychophysical tuning curves for values of  $\Delta t$  as a function of  $\Delta x$ , rather than vice versa as done here. This would clarify the relationship between the current study—which found for a given speed, smaller values of  $\Delta x$  and  $\Delta t$  yield higher coherence thresholds in adults—and the studies of Arena et al. (2012), Knox et al. (2013), Narasimhan and Giaschi (2012), and Parrish et al. (2005), which suggest that larger values of  $\Delta x$  and  $\Delta t$  yield higher coherence thresholds. Given that the largest value of the current study was around the smallest value used in those studies, I would predict to see u-shaped functions for  $\Delta t$  with a value around 50 ms at best performance. From Experiment 1, it is unclear if larger values of  $\Delta t$  would also create maximal differences at speeds below 1 deg/s and above 10 deg/s (see Figure 3.3), but based on the results of Experiment

2, I would begin by testing these speeds. This would also clarify the relationship between the current study and other developmental studies that used  $\Delta t$  values larger than those tested here. It would allow comparison of the current study with Elleberg et al. (2004), who tested  $\Delta t$  values of 27 ms, 40 ms, and 160 ms, and found greater immaturities at larger values of  $\Delta t$ . I predict we would find a u-shaped function for performance at a given intermediate speed when  $\Delta x$  and  $\Delta t$  are varied: children will appear mature at intermediate values of  $\Delta x$  and  $\Delta t$ , but immature at very small ones (like in the 17 ms condition tested in this experiment) and very large ones (like in the 160 ms condition tested in Elleberg et al., 2004). Moreover, this would allow us to investigate whether the minimum speed considered mature decreases as  $\Delta t$  increases, which is suggested in the data collected here, and would be consistent with the comparison between Parrish et al. and Narasimhan and Giaschi's findings.

An investigation into additional parameters that impact children's performance to clarify when children appear mature would be relevant. This study demonstrated that  $\Delta x$ ,  $\Delta t$ , and speed are all important things to consider. Narasimhan and Giaschi (2012) demonstrated that the density of the stimulus impacted children's performance such that they did better with denser displays, but density had no impact on adults. This may be because adult performance saturates at a low density, while the higher densities provide additional information to the developing motion system of children. There may be other similar factors (e.g., increasing dot size, stimulus area, or stimulus duration or number of frames) that decrease children's coherence thresholds, but have no impact on adult thresholds.

Future work can target the cortical basis of speed-tuned differences in development by using functional neuroimaging to investigate whether fast and slow motion are activated by the same cortical areas in adults, and whether these patterns of activation appear mature in children.

This would allow us to learn more about the neural correlates of our psychophysical tasks. Being able to relate these tasks to different brain areas or processing streams will allow us to make fewer speculations and more conclusive contributions to current debates on which areas of the brain carry motion information of different speeds, as well as which areas involved in these tasks are still developing.

Finally, because speed-tuned deficits have been identified in children with amblyopia (Hayward et al., 2011), it would be worth investigating whether these deficits follow the same pattern of dependence on  $\Delta x$  and  $\Delta t$  for a given speed. If stimuli can be developed to optimally detect global motion deficits, we can begin to use them to track patients through treatment (e.g., patching or binocular input therapy) or probe visual function of children with other developmental disorders affecting vision that also have discrepant results with respect to whether or not deficits exist (e.g., autism: Milne et al., 2002; Jones et al., 2011; or Williams Syndrome: Atkinson et al., 1997, Reiss, et al., 2005).

#### **4.4. Conclusion**

In section 1.6, I outlined a framework for understanding motion coherence thresholds as a function of  $\Delta x$  and  $\Delta t$ . Experiment 1 found thresholds in adults were the same regardless of  $\Delta x$  and  $\Delta t$ , which did not support this framework. However, in Experiment 2, I found that thresholds in adults and children were better described as a function of  $\Delta x$  rather than of speed. I demonstrated that children can be considered immature at slow speeds and mature at fast speeds, but whether they were mature at intermediate speeds (4-12 deg/s) depended on the values of  $\Delta x$  and  $\Delta t$  in the speed ratio. This has resolved previous inconsistencies in research on the maturation of global motion perception by providing a framework in which to place comparisons

between child and adult performance. These results caution experimenters to carefully report the parameters they use to study global motion maturation.

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