

Deficits in the processing of local and global motion in very low birthweight children

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Abstract

This study evaluated the impact of premature birth on the development of local and global motion processing in a group of very low birthweight (<1500 g), 5- to 8-year-old children. Sensitivity to first- and second-order local motion stimuli and coherence thresholds for global motion in random dot kinematograms were measured. Relative to full-term controls, premature children showed deficits on all three aspects of motion processing. These problems could not be accounted for by stereo deficits, amblyopia, or attentional problems. A history of mild retinopathy of prematurity and/or intraventricular hemorrhage increased risk, but deficits were observed in some children with no apparent ocular or cerebral pathology. It is important to note that, despite the observed group differences, individual profiles of performance did vary; the results suggest that these three forms of motion processing may involve separate neural mechanisms. These findings serve to increase our understanding of the organization and functional development of motion-processing subsystems in humans, and of the impact of prematurity and associated complications on visual development.

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Over the past decade, advances in obstetric and neonatal care have increased markedly the survival rate of children born very prematurely. Although many of these infants go on to score within the normal range on tests of intelligence in later childhood (e.g., Downie, Frisk, & Jakobson, submitted for publication; Forslund & Bjerre, 1990; Ornstein, Ohlsson, Edmonds, & Asztalos, 1991), a substantial proportion exhibit “minor” developmental disabilities that nonetheless have a significant impact on functioning in multiple domains (e.g., Aylward, 2002; Ross, Evelyn, & Auld, 1996; Taylor, Klein, Minich, & Hack, 2000). It is important to understand the bases of these difficulties in order to design interventions aimed at optimizing long-term outcomes in this high-risk population.

One area of active research focuses on visual outcomes in children born at very low birthweight (<1500 g). These

children are at high risk for a variety of central visual processing difficulties, with problems in visuomotor control, in particular, being cited frequently (e.g., Forslund & Bjerre, 1990; Frisk, Whyte, & Barnes, 1997; Jakobson, Frisk, Knight, Downie, & Whyte, 2001; Ross, Lipper, & Auld, 1991). Unfortunately, however, much of the research in this area is characterized by complex research designs and confounded variables that make interpretation of findings difficult. For example, clinical samples are often heterogeneous and include premature children with a variety of medical and neurological complications. In addition, most investigators rely on tests used in clinical practice that are quite complex and require a number of subskills. Without a fine-grained assessment of basic sensory, perceptual, or neurocognitive abilities, it can be difficult to determine the reasons why children may be experiencing problems with these tasks. This, in turn, makes it difficult to develop and implement effective therapies.

Accurate processing of motion is critical for many aspects of visuomotor planning and control. Consider, for example,

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what is involved in grasping a moving object. One must not only extrapolate the object's trajectory, but also guide the moving limb to the correct location, and coordinate the timing of hand closure with the motions of the object and limb. The success of these actions depends on accurate processing of dynamic cues (e.g., Schenk, Mai, Ditterich, & Zihl, 2000). This fact led Jakobson, Frisk, Downie, and Whyte (2003) to propose that some of the visuomotor difficulties that very low birthweight children experience could stem from a basic deficit in motion processing.

The computations underlying motion processing occur in a series of steps. The first stage, local motion processing, involves the perception of motion discerned from a small region. If the motion is defined by a change in luminance over time (e.g., a black dot moving across a white background), the motion is called first-order local motion and cells responsive to it are found in the primary visual cortex, but not lower levels of the visual pathway (Smith, Greenlee, Singh, Kraemer, & Hennig, 1998). If the motion is defined by spatiotemporal variation in image characteristics other than luminance, such as contrast, depth, or texture (e.g., a region of high contrast moving across a background of lower contrast but of the same mean luminance), the motion is called second-order local motion and additional cortical processing is required. Cells representing second-order local motion are first encountered in higher cortical areas, namely areas V3 and VP (Smith et al., 1998). At the next stage of motion processing, global motion is extracted through perceptual grouping of several local motion signals. It is generally agreed that detection of global motion coherence involves the MT complex—a visual association area that, in humans, lies close to the junction of the inferior temporal sulcus and the ascending limb of the inferior temporal sulcus, at the intersection of the ventral and dorsal streams (Dumoulin et al., 2000). Smith et al. (1998) suggest that first- and second-order local motion signals are integrated in MT and, perhaps, in other near-by areas in the lateral occipital cortex (V3A and V3B). One of these latter areas (V3B, also known as the kinetic occipital area; Van Oostende, Sunaert, Van Hecke, Marchal, & Orban, 1997) is believed to be involved in another form of global motion processing—that underlying our ability to see objects defined by differential movement (motion-defined forms) (Dupont et al., 1997; Van Oostende et al., 1997; but see Zeki, Perry, & Bartels, 2003).

Recently, Jakobson and colleagues examined premature children's ability to detect and recognize motion-defined forms (Downie, Jakobson, Frisk, & Ushycky, 2003; Jakobson et al., 2003). In one report, extremely low-birthweight (<1000 g) children tested at a mean age of 11 years showed a marked impairment on the task, with 71% of the preterm sample performing at a level three standard deviations or more below full-term controls (Downie et al., 2003). This result was replicated recently in a younger sample of extremely low birthweight children, and it was shown that the degree of difficulty individual preterm children had with the recognition of motion-defined forms was related to their performance on

tasks assessing visuomotor skill, visual attention, and depth perception (Jakobson et al., 2003).

Given that performance on the motion-defined form task used in the studies described above depends on the extraction of global motion in a region that probably integrates first- and second-order local motion signals (Smith et al., 1998), poor performance on the task could reflect difficulties arising at earlier stages of motion processing. To date, no one has assessed more basic forms of motion processing in premature children. The purpose of the research reported here was to examine this issue by measuring sensitivity to first- and second-order local motion and coherence thresholds for global motion in a group of very low birthweight children.

We suspected that very low birthweight children might demonstrate reduced sensitivity to all three types of motion studied, for two reasons. First, a large percentage of these children experience an ocular disease known as retinopathy of prematurity (ROP; Palmer et al., 1991), and/or damage to the periventricular region of the brain (Volpe, 1995). A history of one or both of these disorders substantially elevates risk for problems with motion-defined form recognition in extremely low birthweight children (Jakobson et al., 2003). That more basic forms of motion processing might also be affected is supported by several recent findings. Fulton, Hansen, Petersen, and Vanderveen (2001) have shown that even mild ROP that has undergone spontaneous regression is associated with rod photoreceptor dysfunction. This is significant as there is some evidence from electrophysiological (Gouras & Link, 1966; Lee, Pokorny, Smith, Martin, & Valberg, 1990; Lee, Smith, Pokorny, & Kremers, 1997; Purpura, Kaplan, & Shapley, 1988; Virsu & Lee, 1983; Virsu, Lee, & Creutzfeld, 1987; Wiesel & Hubel, 1966) and psychophysical (D'Zmura & Lennie, 1986; Sun, Pokorny, & Smith, 2001) studies suggesting a significant rod input to the subcortical magnocellular pathway (although the strength of this input remains controversial, see Lennie, 1993). This pathway provides a major input to cells in primary visual cortex involved in local motion processing (Hawken, Parker, & Lund, 1988), and to the MT complex (Tootell et al., 1995) which is involved in detecting coherent global motion (Newsome & Paré, 1988). In addition, it has been argued elsewhere (Downie et al., 2003; Jakobson et al., 2001) that periventricular brain damage may also frequently compromise the magnocellular pathway and/or its cortical targets. Given this, one might expect that, when present, either ROP or periventricular brain damage could interfere with the normal development and functioning of systems that analyze both local and global motion.

A second reason why we suspected that even basic motion processing would be impaired in very low birthweight children is that, even if they escape ROP or periventricular brain damage, these children invariably experience abnormally early visual stimulation as a result of their premature births. Other research suggests that this early visual experience may, in itself, interfere with normal visual development (Dowdeswell, Slater, Broomball, & Tripp, 1995). Although motion processing was not specifically examined by

Dowdeswell and colleagues, another form of atypical early visual experience (specifically, the early visual *deprivation* produced by congenital cataracts) has been shown to be associated with abnormal development of sensitivity to both local (Ellemberg et al., *in press*) and global motion (Ellemberg, Lewis, Maurer, Brar, & Brent, 2002).

In summary, the goal of the present study was to assess the impact of premature birth on the development of sensitivity to first- and second-order local motion, and on the ability to detect coherent motion. It was hypothesized that very low birthweight children would be at increased risk, relative to typically developing peers born at term, for functional impairment in all three forms of motion processing tested. In order to evaluate the contribution of general cognitive delay and of other visual deficits to any impairment, children were also administered a test of verbal IQ and a visual screening battery.

1. Method

1.1. Participants

A group of 19, very low birthweight children were recruited to participate through the Newborn Follow-up Program at Children's Hospital in Winnipeg, Manitoba. These children had a mean age of 6 years, 10 months (S.D. 11.7 months) at the time of testing. All had been born at an appropriate weight for their gestational age, and had been found to be free of significant developmental delays and major neurological abnormalities (i.e., mental retardation, blindness, deafness, cerebral palsy) when assessed at 18–24 months corrected age. Eight of the children had no history of ROP or periventricular brain damage, four had experienced mild (stage 1 or 2) ROP that had undergone spontaneous regression (see staging criteria outlined in *Committee for the Classification of Retinopathy of Prematurity, 1984*), six had an ultrasound diagnosis of mild periventricular brain damage (grade 1 or 2 intraventricular hemorrhage; Papile, Burstein, & Koffler, 1978), and one had a history of both mild ROP and mild periventricular brain damage. The children had a

mean gestational age of 29 weeks (S.D. = 1.8 weeks), and a mean birthweight of 1198 g (S.D. = 245 g). Only four of the children had birthweights below 1000 g (see *Table 1*).

A control group of 19 children, born at term without medical complication or developmental problems, was recruited through local schools and day-care centres. The mean age of the control children was 6 years, 10 months (S.D. = 15.4 months). All participating families were asked to supply information regarding maternal and paternal educational attainment and family income (see *Table 1*). The experimental protocol was approved by the Human Research Ethics Board of the University of Manitoba. Informed consent for participation was obtained from parents of all children.

1.2. Materials

1.2.1. Intellectual screening

Although all preterm participants had been found to be free of significant developmental delays at 18–24 months corrected age, we administered the Peabody Picture Vocabulary Test—Third Edition (PPVT-III; Dunn & Dunn, 1997) to obtain a recent estimate of their Verbal IQ. This general measure of “outcome” was selected over tests of Performance IQ as these latter tests tend to place heavy demands on visuomotor skills which, like motion-processing skills, are dependent on the functional integrity of visual areas such as MT that provide key inputs to the dorsal stream (e.g., Schenk et al., 2000). Given this co-dependence, we might well expect an association between problems with motion processing and lowered Performance IQ (indeed, see Downie et al., 2003; Jakobson et al., 2003). Our goal in the present study was to ensure that any difficulties we observed with motion processing in our preterm sample could not be attributed to the presence of a general cognitive delay that would also affect verbal functioning.

1.2.2. Visual screening

The visual screening battery included two tests of linear acuity: the Good-Lite Acuity Chart (Good-Lite Company, Chicago, IL) was used for 5- and 6-year-old participants, and

Table 1
Demographic information on each group

	Full-term controls	VLBW children
Gender distribution	9 F:10 M	10 F:9 M
Age (years:months)	6:10 (S.D. 15.4 months) range 4:11 to 8:11	6:10 (S.D. 11.7 months) range 5:2 to 8:5
Birthweight (g)	3525 (S.D. 370) range 2983–4457	1198 (S.D. 245) range 732–1483
Gestational age (weeks)	39.8 (S.D. 1.1) range 38–42	29 (S.D. 1.8) range 25–32
PPVT-III (standard score)	110.9 (S.D. 6.9) range 102–124	103.8 (S.D. 9.8) range 80–119
Maternal education (mode)	6 ^a	5 ^a
Paternal education (mode)	3 ^a	4 ^a
Family income (mode)	7 ^b	7 ^b

Mean values (standard deviations) are shown for age, birthweight, weeks gestation and PPVT-III standard scores. Modal values are indicated for income and parental education levels.

^a 1 = less than 7th grade; 2 = 7th to 9th grade; 3 = 10th to 11th grade; 4 = completed high school; 5 = some post-secondary training; 6 = completed post-secondary degree/diploma; 7 = completed graduate degree.

^b 1 = under CAD\$ 11,000; 2 = CAD\$ 11,000–CAD\$ 20,999; 3 = CAD\$ 21,000–CAD\$ 30,999; 4 = CAD\$ 31,000–CAD\$ 40,999; 5 = CAD\$ 41,000–CAD\$ 50,999; 6 = CAD\$ 51,000–CAD\$ 75,000; 7 = over CAD\$ 75,000.

the Lighthouse Acuity Chart (Lighthouse International, New York, NY) for 7- and 8-year-olds. Different charts were used for the two age groups because we find that younger children are often confused by the number of letters on the Lighthouse chart; the Good-Lite test is a simpler, matching task that induces crowding of the target letters by surrounding them with bars rather than other letters. Stereoacuity was assessed with the Titmus test (Stereo Optical Company, Chicago, IL) and fusion with the Worth 4-dot fusion test (Bernell Company, Mishawaka, IN).

1.2.3. Tests of sensitivity to first- and second-order local motion

Stimuli for the tests of sensitivity to first- and second-order local motion were generated by a PowerMac G3 computer running Pixx™ 1.55 software, and were displayed on an Optquest monitor, 32° wide by 24° high when viewed from a distance of 57 cm, with a spatial resolution of 1024 × 768 pixels and a refresh rate of 75 Hz. The stimuli were created with the calibration tool included in the Pixx™ software, according to the procedures summarized in [Elleberg et al. \(2003b\)](#), and were identical to those used in previous studies of motion vision in normal and visually deprived children ([Elleberg et al., in press](#); [Elleberg et al., 2003b](#)).

The stimuli consisted of 1 c deg⁻¹ horizontal sinusoidal gratings, 10° wide by 10° high when viewed from a distance of 57 cm (see left panel of [Fig. 1](#)). The stimuli drifted either up or down for 1.5 s at a velocity of 6° s⁻¹. All stimuli consisted of static two-dimensional random noise (referred to as the carrier), the luminance of which was binary. Each noise element subtended 2 arc min × 2 arc min, and was assigned independently with a probability of 50% to be either ‘light’

or ‘dark’. The first-order stimuli were created by adding the noise carrier to a luminance-modulated sinusoidal grating of 1 c deg⁻¹. This created a sinusoidal modulation of luminance across the carrier, which appeared like a conventional luminance-modulated sinusoidal grating which moved either up or down during each trial. The amplitude of the luminance modulation (Michelson contrast or depth modulation) was defined as:

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

where L_{\max} and L_{\min} are the maximum and minimum mean local luminance averaged over adjacent pairs of noise dots.

The second-order stimuli were created by multiplying static two-dimensional random noise by a luminance-modulated sinusoidal grating (see right panel of [Fig. 1](#)). Detecting direction of motion in these stimuli (up versus down) required detecting the direction of motion of stripes defined by alternating regions of higher and lower contrast bars while the mean luminance was held constant. The amplitude of the contrast modulation (depth modulation) was defined as:

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

where C_{\max} and C_{\min} are the maximum and minimum mean local contrasts (Michelson) in the stimulus.

The space- and time-average luminance of the stimuli and background were maintained at 37 cd m⁻². Gamma-correction was verified by means of a Minolta LS-100 photometer. The luminance contrast of the first-order images was linearly related to the voltage of the Z-axis. Using the same procedure as [Smith and Ledgeway \(1996\)](#), we calibrated the second-order images to ensure that gamma-correction was

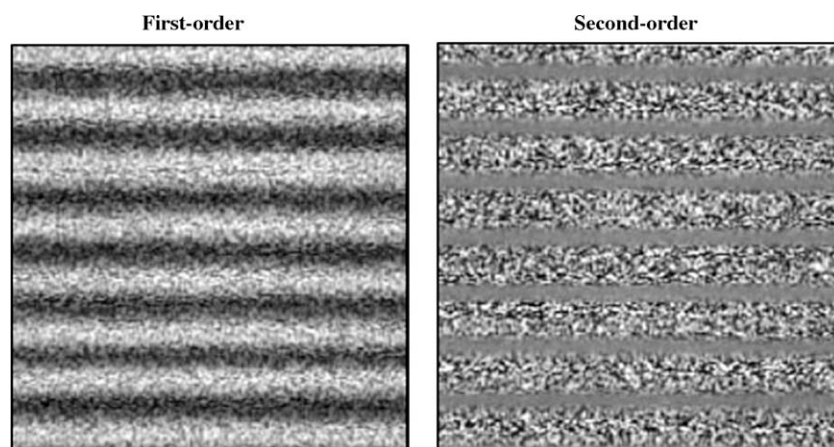


Fig. 1. An example of the stimuli used to measure the perception of first-order and second-order local motion. Horizontal stripes are created from differences in luminance (left panel) or contrast (right panel) and move vertically. The child’s task on each trial is to say whether the stripes are moving up or down. For the stimulus on the left, luminance is modulated sinusoidally to create first-order cues for the perception of motion. Specifically, higher luminance stripes alternate with lower luminance stripes. The difference in luminance between stripes is varied over trials, while the mean luminance remains constant. For the stimulus on the right, contrast is modulated sinusoidally to create second-order cues for the perception of motion. Specifically, the top stripe is a high contrast stripe made from black and white pixels. The adjacent stripe is a low contrast stripe made from slightly darker vs. slightly lighter grey pixels. The difference in contrast between stripes is varied over trials. Because the mean luminance of adjacent stripes is identical, the perception of the direction of motion cannot depend on first-order cues.

accurate with respect to the characteristics of these stimuli. Specifically, we measured the local luminance values of a stationary and of a drifting second-order stimulus, and adjusted the gamma-correction factor to eliminate any differences in luminance between the high and low contrast regions of the envelope. The correction factor was checked regularly throughout the course of the study. Further, small noise dots ($2 \text{ arc min} \times 2 \text{ arc min}$) were used so that the second-order stimuli would not contain detectable local luminance cues (Smith & Ledgeway, 1996).

To verify that any observed deficits were motion-specific, participants were also asked to discriminate the orientation (horizontal versus vertical) of static, first-order and second-order gratings that were identical to the gratings used in the dynamic conditions except that they were static rather than moving.

1.2.4. Test of global motion

The global motion stimulus was identical to that used previously with full-term, visually normal children and children with a history of visual deprivation from cataract (Elleberg et al., 2002). It consisted of an array of 300 black dots (luminance 4.7 cd m^{-2}) moving at 18° s^{-1} against a white background (luminance 98.3 cd m^{-2}). The dots had a radius of 15 arc min and a dot density of $0.75 \text{ dots deg}^{-1}$. On any given trial, a certain percentage of the dots (signal) moved coherently among an array of dots displaced in random directions (noise) (see Fig. 2). In each successive frame, all signal dots were displaced in the same direction by 0.25° , giving the perception of continuous motion, except that any particular dot lived for one frame (13.3 ms) so the viewer could not detect the direction of motion by concentrating on any one dot. Throughout each trial, a central fixation cross was displayed.

1.3. Procedure

Before testing began, the procedures were explained and parental consent for participation was obtained. For 5- and 6-year-olds, the testing was split into two sessions run on separate days, with each session lasting approximately 1 h (including adaptation and rest periods). Data were collected for only one of the motion tests (second-order local motion) for two of these participants (one control and one preterm child) because they were unable to return for the second testing session. Older children were able to complete the testing in one session with a 30 min break at the midpoint. All testing was performed with the child wearing optical correction, if required.

Prior to motion testing, acuity was assessed monocularly at 3 m (Good-Lite Acuity Chart) or 4 m (Lighthouse Acuity Chart). The requisite acuity to pass the Good-Lite was 20/25 for 5-year-olds and 20/20 for 6-year-olds. To pass the Lighthouse, 7- and 8-year-old children had to demonstrate acuity of 20/20. Testing of each eye was repeated with a +3 dioptre add over the eye to rule out hypermetropia greater than three dioptres. To pass the Titmus test, 6-, 7- and 8-year-olds had to have a stereoacuity of at least 40 s of arc, and 5-year-olds had to have a stereoacuity of at least 100 s of arc. To pass the Worth 4-dot test of fusion at near, children had to demonstrate binocular fusion. The choice of cut-offs for linear- and stereoacuity was based on clinical experience and the results of earlier studies (e.g., Bowering, Maurer, Lewis, & Brent, 1993). To pass the visual screening battery, passing scores had to be achieved on all tests.

Tests comprising the visual screening battery were interspersed with the tests of local and global motion processing to prevent fatigue. All motion tests were conducted in a dimly lit room and children were given 2 min to adjust to the testing

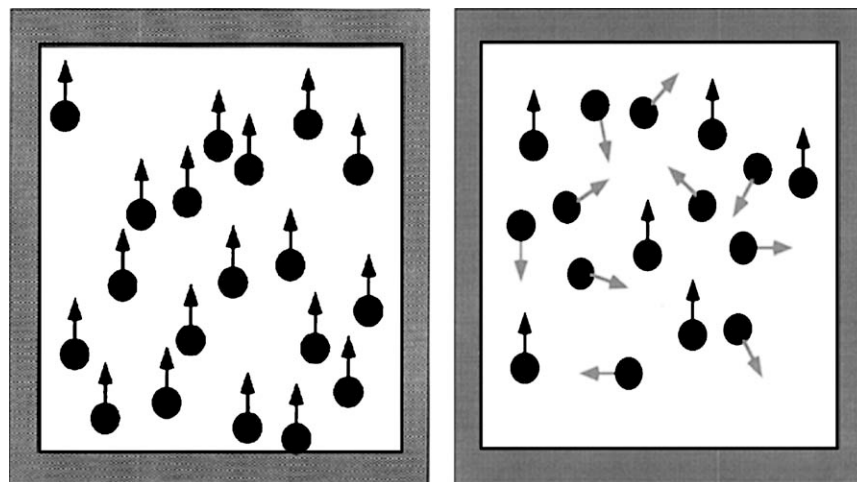


Fig. 2. Examples of stimuli used to test sensitivity to the direction of global motion. The pattern on the left has 100% coherent motion (all the dots are moving upwards) and the pattern on the right has a 37% coherent signal (6 of 16 dots are moving upward and the remaining dots are moving in random directions). The child's task was to say whether the overall direction of motion was upward or downward. Threshold was defined as the minimum percent coherence necessary to discriminate accurately whether the predominant direction was upward or downward.

conditions and room illumination before beginning. While completing the motion tests, children were positioned in a chin rest to minimize movement artefacts. We used a chin rest to make the testing conditions identical to our previous three studies of sensitivity to local and global motion in normally developing full-term children and children treated for cataract (Elleberg et al., *in press*; Elleberg et al., 2002; Elleberg et al., 2003b). In pilot work for those studies, we discovered that a padded chin rest is comfortable even for 5-year-olds, reduces head movements, and helps keep the eyes at the appropriate testing distance.

All motion tests were carried out monocularly with the eye with better acuity; in cases where acuity of the two eyes was equivalent, the tested eye was chosen at random. The untested eye was patched with 3 M Micropore tape. The global motion test was administered after local motion testing was completed for 10 of the 19 participants in each group; for the remaining participants global motion testing was carried out prior to local motion testing. During the motion tests the experimenter sat facing the child and entered responses on the keyboard while remaining naïve as to the direction of motion on test trials. Both verbal and hand gestures were accepted as responses, and in the case of a discrepancy, verbal clarification was required.

1.3.1. Local motion testing

Local motion testing began with the experimenter saying “We are going to play a game where you will see a grey box with moving stripes. Your job is to tell me if the stripes are moving up (experimenter points up) or moving down (experimenter points down)”. To verify that the child understood the task, two trials of second-order local motion were presented with feedback. The child was then given 10 trials with second-order stimuli moving at 1.5° s^{-1} and to proceed had to meet a criterion of indicating the direction of motion correctly on four trials in a row. Once this criterion was passed, children proceeded to the test phase. During the test phase, depth modulation was varied across trials according to a maximum-likelihood staircase procedure (Harvey, 1986). We defined threshold as the minimum amount of luminance (first-order) or contrast (second-order) modulation necessary to discriminate the direction of motion. Trials with static stimuli were similar except the experimenter said “Your job now is to tell me if the stripes are standing up (experimenter motions vertically) or lying down (experimenter motions horizontally)”.

Static and motion trials for first- and second-order stimuli were run in separate blocks. For first-order stimuli, static trials were carried out prior to the motion trials for 10 of the 19 participants in each group, and after the motion trials for the remaining participants. For second-order stimuli, static trials were carried out prior to the motion trials for 9 of the 18 participants in each group, and after the motion trials for the remaining participants (recall that one control and one preterm child were not tested with second-order stimuli). Testing in each block began with a practice run administered

under binocular viewing conditions. Feedback was provided for the practice staircase only.

1.3.2. Global motion testing

Prior to commencement of global motion testing, participants were given instructions and demonstration trials under binocular viewing conditions. The experimenter began by presenting four demonstration trials: two trials at 100% coherence and two trials at 50% coherence (i.e., 50% of the dots moved coherently either upwards or downwards and the rest moved in random directions). The child then had to specify the direction of perceived motion in two practice trials at each of these levels of coherence, and was given contingent feedback. The instructions were as follows: “You will see a bunch of dots on the screen that will be moving either up or down. At first all the dots will be moving in the same direction, but soon there will be other dots trying to fool you. Your job is to tell me if most of the dots are moving up (experimenter points up) or down (experimenter points down)”. The child began each trial fixating on a cross in the centre of the monitor and, throughout the trial, was reminded regularly to keep watching the cross. Global motion coherence thresholds were measured using a 2-down, 1-up staircase procedure (Levitt, 1971). Feedback was given during an initial practice staircase completed under binocular conditions. During the monocular test staircase, no feedback was given, but children were praised for their effort. In the 2-down, 1-up staircase procedure, the dot coherence decreased after two successive correct responses, and increased after every incorrect response. The first decrease involved a step size of half an octave (from 100% to 50% coherence), and thereafter reversals changed by a step size of one-quarter octave (where one octave is a halving or a doubling of a value). After the first reversal, testing continued until eight reversals were completed. Coherence thresholds were calculated using the mean coherence of the last six reversals.

2. Results

An analysis of variance (ANOVA) test revealed that preterm and control children were matched in age (in months), $F(1,36)=0.005$, $p=0.94$, and a series of Mann–Whitney U -tests showed that the groups were also matched in terms of mother’s educational attainment ($Z=-1.306$, $p=0.19$), father’s educational attainment ($Z=-0.685$, $p=0.49$), and family income ($Z=-0.11$, $p=0.91$) (see Table 1). The two groups were not matched, however, in terms of verbal intelligence, as indicated by the results of a second ANOVA conducted on standard scores obtained on the PPVT-III, $F(1,36)=6.64$, $p<0.05$. It is important to note, however, that while control children did obtain a slightly higher average score on this test (110.9 versus 103.8), only two of the preterm children obtained standard scores outside the normal range (80 and 85), with the remainder scoring between 94 and 119 (as compared to a range of

102–124 seen in the full-term control group). Moreover: (1) after controlling for age, there were no significant correlations between PPVT-III standard scores and threshold scores on any of the three motion-processing tests in the preterm sample ($p > 0.4$, in all cases); (2) re-running the analyses described below after excluding the two preterm children with PPVT-III scores below 90 did not alter the pattern of significant results in any way. Given this, we do not feel that the failure to match the groups precisely on this variable poses a major confound.

All control children passed the visual screening battery. Table 2 summarizes the results of the visual screening tests for preterm children.

2.1. Thresholds

Thresholds for discriminating the orientation of static gratings defined by first- and second-order cues, thresholds for discriminating the direction of first- and second-order local motion, and coherence thresholds for discriminating the direction of global motion were entered into a one-way multivariate analysis of covariance (MANCOVA) that controlled for participants' age (in months). There was a significant main effect of Group in this omnibus test, $F(5,29) = 4.12$, $p < 0.01$ (Wilks' lambda criterion), but no effect of Age. Due to a lack of homogeneity of variance, Welch's t -tests were used to explore group differences for

each variable (adjusted degrees of freedom indicated below). These follow-up tests revealed that preterm and full-term children did not differ in their depth modulation thresholds for discriminating the orientation of static gratings defined by either first-order cues [control $M = 0.0156$ (S.D. = 0.0024), preterm $M = 0.0176$ (S.D. = 0.0084), $t(20) = -1.03$, $p = 0.32$], or second-order cues [control $M = 0.0796$ (S.D. = 0.0499), preterm $M = 0.0736$ (S.D. = 0.0210), $t(24) = 0.49$, $p = 0.63$]. Thus, preterm children were able to perceive first- and second-order properties normally in stationary patterns. In contrast, preterm children had significantly elevated depth modulation thresholds, relative to controls, for discriminating the direction of first-order local motion [control $M = 0.0045$ (S.D. = 0.0004), preterm $M = 0.0123$ (S.D. = 0.0125), $t(17) = -2.63$, $p < 0.05$] and the direction of second-order local motion [control $M = 0.1690$ (S.D. = 0.0779), preterm $M = 0.3240$ (S.D. = 0.1678), $t(25) = -3.65$, $p < 0.005$]. Their coherence thresholds for global motion were also significantly higher than those of controls [control $M = 9.80$ (S.D. = 11.72), preterm $M = 29.81$ (S.D. = 29.20), $t(22) = -2.70$, $p < 0.05$]. After controlling for age (in months), birthweight in the preterm group did not correlate with any of the five measured thresholds (p -values ranging from 0.32 to 0.86).

Age-at-testing was not significantly correlated with thresholds for either type of local motion in the sample of control children, although it was negatively correlated with

Table 2

Summary table for preterm children on screening, orientation discrimination (static) and motion-processing tasks

Case	Status	Visual screening	FOS DEF	SOS DEF	FOM DEF	SOM DEF	GLOB DEF
15	n	Fail ^a	0.78	0.63	1.05	1.39	0.59
2	ROP	Pass	0.96	0.61	0.82	1.44	1.54
18	ROP	Fail ^b	0.88	0.98	1.04	0.90	0.57
14	n	Pass	1.17	1.71	1.13	1.41	0.90
17	PVBD	Fail ^{b,c}		1.21		0.71	
1	ROP/PVBD	Fail ^{a,b,c}	0.73	0.83	2.09	1.17	1.81
19	PVBD	Pass		1.08		2.05	
7	PVBD	Fail ^b	0.69	0.53	0.73	6.95	0.53
9	n	Pass	0.54	1.12	1.52	2.24	1.84
8	PVBD	Pass	0.71	0.94	8.07	2.41	0.44
10	n	Fail ^{b,d}	1.37	1.08	8.48	2.64	1.17
16	n	Fail ^b	0.80	1.26	0.89	1.56	2.17
13	ROP	Fail ^b	2.11	1.73	1.13	1.11	7.47
5	n	Fail ^b	1.63	0.80	1.09	0.63	13.19
4	n	Fail ^b	1.34	1.93	1.03	1.03	15.68
11	ROP	Fail ^{a,b,c}	2.42	1.27	10.54	3.85	2.71
12	n	Fail ^b	1.10	0.32	2.42	7.94	6.81
6	PVBD	Pass	0.69	0.85	3.42	2.58	19.97
3	PVBD	Fail ^b	1.50	1.36	3.16	4.07	36.47

Deficit ratios were computed by taking each preterm child's threshold on a given test and dividing it by the corresponding threshold obtained by that child's full-term control. Deficit ratios designated as abnormal (shown in boldface) were those that had a value of at least 2, indicating that the preterm child's threshold was at least twice that of his/her control. Deficit scores could not be computed for cases 17 and 19 for first-order or global tasks due to missing data. [ROP = retinopathy of prematurity; PVBD = periventricular brain damage; n = normal (no ROP or periventricular brain damage); FOS DEF, SOS DEF, FOM DEF, SOM DEF and GLOB DEF refer to deficit scores for first- and second-order static stimuli, first- and second-order local motion stimuli, and global motion stimuli, respectively].

^a Abnormal acuity in fellow (untested) eye (but not tested eye).

^b Failed Titmus test of stereoacuity.

^c Unilateral amblyopia (at least one line difference in acuity between the eyes).

^d Failed Worth 4-dot fusion test.

coherence thresholds for global motion, $r = -0.572$, $p < 0.05$. In other words, while control children's ability to discriminate local motion had reached stable levels, their ability to discriminate global motion was continuing to improve with age.

Threshold scores were generally more variable in preterm children than in controls. Unlike controls, sensitivity to local motion tended to show some improvement with increasing age (although this trend was significant for second-order local motion only, $r = -0.50$, $p < 0.05$). Sensitivity to global motion, however, did not improve with increasing age in this group, $r = 0.216$, $p = 0.390$.

2.2. Deficit ratios

In order to be able to compare preterm children's performance across tasks directly, scores needed to be converted to a common metric. Because performance on some of the experimental tests showed age-related changes (see above), Z scores were not the appropriate metric. Instead, deficit ratios were calculated for each preterm child by dividing that child's threshold score for correct discrimination of each type of stimulus by the corresponding threshold score of his/her age-matched control. Pairs were created by matching the youngest preterm child with the youngest control, and so on. The mean difference between the ages of children in a given pair at the time of testing was 1.5 weeks (median age difference: 1 month). These age-matched pairs, while not matched for gender in all cases, did not differ significantly in maternal and paternal education levels, nor in family income (Wilcoxon signed ranks test, $p > 0.2$ in all cases).

Ratio scores were entered into a repeated measures ANOVA, using a Greenhouse–Geisser adjustment to the degrees of freedom to account for the observed lack of homogeneity of variance in the data. The main effect of task was significant, $F(1.3, 20.2) = 4.175$, $p < 0.05$. Follow-up LSD tests revealed no differences between deficit ratios seen in the two static conditions. Indeed, the mean ratios of 1.14 (S.D. = 0.13) and 1.06 (S.D. = 0.11) seen with first-order and second-order static stimuli, respectively, were close to 1, indicating that the performance of preterm and control children was very similar in these conditions. Deficit ratios in the three conditions involving dynamic stimuli were significantly higher than those seen with static stimuli. Although mean ratios appeared largest for the global motion stimuli, there was a great deal of variability in performance on this task among preterm children (see Table 2). As a result, the mean deficit ratios obtained in the three dynamic conditions did not differ statistically (see Fig. 3).

2.3. The relationship between motion processing, stereoacuity and amblyopia

As can be seen in Table 2, 12 of the 19 preterm children failed the Titmus test of stereoacuity. To examine the relationship between stereoacuity and motion-processing abili-

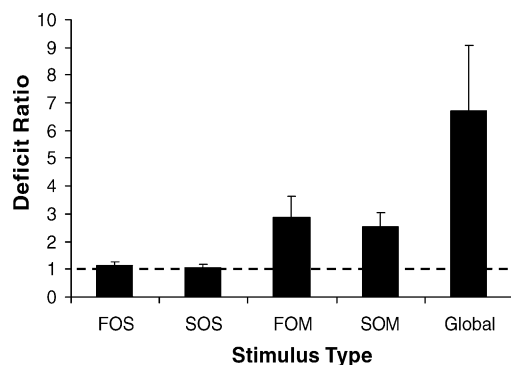


Fig. 3. Mean deficit ratios (S.E.) in premature children for the correct discrimination of the orientation of static gratings defined by first-order (FOS) or second-order (SOS) cues, and for the correction discrimination of the direction of first-order local motion (FOM), second-order local motion (SOM), and global motion. Note that, as these ratios were calculated by dividing each premature child's threshold score on a particular test with the corresponding threshold score of his/her age-matched control, a mean ratio score of 1 (shown by the dashed line) would indicate that the preterm group had exactly the same mean threshold as the control group (i.e., no deficit).

ties, correlations between measured stereoacuties and deficit ratios for first- and second-order local motion and for global motion coherence were computed for the preterm children. Only the correlation with the deficit ratio on the global motion task was significant, $r(17) = 0.60$, $p < 0.05$. Inspection of Table 2, however, reveals one child who performed normally on all of the motion tasks (case 18) who had failed the Titmus test, and one child who performed in the abnormal range on all of the motion tasks (case 6) who had normal stereoacuity. These results suggest that the motion-processing deficits we observed are not due to impaired stereoacuity, even if problems with the analysis of global motion and stereo deficits may frequently co-occur.

Only three of the children with abnormal stereoacuties had unilateral amblyopia (defined here as at least one line difference in acuity between the eyes; cases 17, 1 and 11), and when we re-ran both the MANCOVA on threshold scores and the deficit ratio analysis, excluding these three children, the results were unchanged. We think it unlikely, then, that the deficits we observed in our preterm sample were associated with amblyopia.

2.4. Patterns of impairment

Deficit ratios were abnormal (≥ 2 , i.e., at least one octave) for one or more of the three types of motion stimuli in 14 of the 19 preterm children (73.7%; see Table 2). In four children (cases 11, 12, 6 and 3), these clinically significant impairments were evident with all three types of motion processing. Interestingly, however, isolated impairments in each form of motion processing were also observed. Thus, one child (case 1) showed an isolated deficit in the processing of first-order local motion, two (cases 7 and 9) showed an isolated deficit in the processing of second-order local motion, and three (cases 16, 5 and 4) showed an isolated global

motion-processing deficit. Correlations between deficit ratios in all three tests were also assessed in the preterm sample, and none of these correlations were found to be significant ($p > 0.45$ in all cases). These results suggest that these three forms of motion processing may involve different neural mechanisms.

2.5. *The relationship between motion processing, ROP and periventricular brain damage*

Some of the preterm children in the present sample had experienced either mild periventricular brain damage and/or mild ROP that had undergone spontaneous regression (see Table 2). Due to the limited sample size, it was not possible to subdivide the preterm sample along these lines to make statistical comparisons. It is interesting to note, nonetheless, that three of five children affected by ROP and all of the children with periventricular brain damage for whom complete data were available showed abnormal performance on at least one motion task. It was also the case, however, that six of eight preterm children with no history of either form of pathology were impaired on at least one of the tasks. In one of these cases (case 9) all visual screening tests were performed normally.

3. Discussion

The most striking finding in the current study was that under the present testing conditions premature children, as a group, were impaired relative to age-matched controls on all three types of motion processing tested. These deficits were motion-specific. They could not be reduced to deficits in processing luminance or contrast, given that impairments were not evident in the static conditions that measured thresholds for detecting the orientation of gratings defined by the same first-order and second-order properties. They were not related to deficient stereovision or amblyopia. It is also unlikely that attentional problems could account for these difficulties as preterm children performed normally in the static conditions, which place comparable demands on attentional resources. Although there were differences between preterm and control children in verbal ability, we think it unlikely that the observed motion-processing problems reflect some general effect associated with “poor outcomes” as all of the preterm children had had normal neurodevelopmental assessments at 18–24 months corrected age, there were no significant correlations between PPVT-III standard scores and performance on any of the motion tests, and all but two (cases 13 and 11) had normal thresholds for discriminating the orientation of both first-order and second-order static gratings.

Although group differences were observed with all three types of motion processing, individual cases showed isolated impairments in the perception of first-order local motion, second-order local motion, or global motion. This suggests that different neural mechanisms may be involved in the pro-

cessing of these three types of motion, a conclusion strengthened by our finding that deficit ratios on the three motion-processing tasks were not correlated with one another. These findings complement other recent reports suggesting that first- and second-order cues are processed by separate neural mechanisms (Chubb & Sperling, 1988; Elleberg et al., 2003a; Greenlee & Smith, 1997; Ledgeway & Smith, 1994; Mareschal & Baker, 1998; Mareschal & Baker, 1999; Smith et al., 1998; Vaina & Cowey, 1996; Vaina, Cowey, & Kennedy, 1999; Vaina, Makris, Kennedy, & Cowey, 1998; Vaina, Soloviev, Bienfang, & Cowey, 2000; Zhou & Baker, 1993; but see Seiffert, Somers, Dale, & Tootell, 2003). They also suggest that the observed deficits in global motion analysis did not stem simply from problems in discerning either first- or second-order local cues. (Note that the stimuli used in the motion coherence task employed here were not defined exclusively by first- or second-order cues, although their processing probably depended primarily on the former.)

Control children showed no significant age-related changes in sensitivity to either form of local motion. In other words, their performance appeared stable between the ages of 5 and 9 years. In stark contrast to controls, preterm children did show age-related improvement (a decline in threshold scores) for second-order local motion. The results of earlier work using identical stimuli suggest that, at the velocity used here (6° s^{-1}), sensitivity to second-order local motion matures more slowly than sensitivity to first-order local motion (Elleberg et al., 2003b). What we may be observing, then, is a delay that shows improvement with time, rather than a persistent deficit, on this test. Additional studies using older samples of premature children may shed light on this issue.

Unlike local motion, sensitivity to global motion did not show age-related improvement in preterm children. Moreover, when deficits were present on this task they were large. Thus, if we consider only the 41–47% of the preterm children who performed in the abnormal range on any one of the motion-processing tasks, their deficit ratios were 2.4–3.4 times greater with global motion than with either form of local motion. We suspect that deficits on this task may even increase in size after age 5–6, as typically developing children continue to improve. As analysis of global motion coherence involves area MT (Newsome & Paré, 1988; Schenk & Zihl, 1997), these results would be consistent with dysfunction in this region. Other work has revealed what appears to be a persistent deficit (rather than a simple “delay” or “maturational lag”) in another form of motion processing – motion-defined form recognition – in extremely low-birthweight children tested at a mean age of 11 years (Downie et al., 2003). Performance on this latter task likely involves area V3B (the kinetic occipital area)—an extrastriate region located posterior to area MT (Smith et al., 1998; Van Oostende et al., 1997).

The small sample size in the present study made it impossible to compare statistically the impact of mild periventricular brain damage or ROP on visual development. Nonetheless, while the presence of either form of pathology appeared to

increase a child's risk for a motion-processing impairment, it is worth noting that some children with no history of ROP who also showed no evidence of periventricular brain damage in neonatal cranial ultrasound scans were found to be impaired on at least one of the tasks. Although it is quite possible that our cranial ultrasounds were simply not sensitive enough to detect subtle forms of pathology in these children (cf. Arzoumanian et al., 2003; Inder, Anderson, Spencer, Wells, & Volpe, 2003; Miller et al., 2003), it is also possible that the atypical visual experiences associated with their preterm birth interfered with the normal development and functioning of their motion-processing systems.

4. Conclusions

The present report provides evidence that, as a group, very low birthweight children are at risk for impairments in the processing of local motion defined by luminance cues, local motion defined by contrast cues, and global motion. The patterns of deficit and sparing also support the conclusion that these three forms of motion processing may involve separate neural mechanisms. The research described here adds to our understanding of the organization and functional development of motion-processing subsystems in humans, and of the impact of prematurity and associated complications on visual development. It also highlights the fact that even those premature children with relatively uncomplicated medical histories need to be followed carefully. If motion-processing deficits do contribute to problems with visuomotor control, assessment of motion sensitivity in infancy may allow for earlier identification of children at risk for difficulties in this area.

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References

Arzoumanian, Y., Mirmiran, M., Barnes, P. D., Woolley, K., Ariagno, R. L., Moseley, M. E., et al. (2003). Diffusion tensor brain imaging findings at term-equivalent age may predict neurologic abnormalities in low birth weight preterm infants. *American Journal of Neuroradiology*, 24, 16–53.

Aylward, G. P. (2002). Cognitive and neuropsychological outcomes: More than IQ scores. *Mental Retardation and Developmental Disabilities Research Reviews*, 8, 234–240.

Bowering, E. R., Maurer, D., Lewis, T. L., & Brent, H. P. (1993). Sensitivity in the nasal and temporal hemifields in children treated for cataract. *Investigative Ophthalmology and Visual Science*, 34, 3501–3509.

Chubb, C., & Sperling, G. (1988). Drift-balance random stimuli: A general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America A, Optics and Image Science and Vision*, 5, 1986–2007.

Committee for the Classification of Retinopathy of Prematurity. (1984). The international classification of retinopathy of prematurity. *Pediatrics*, 74, 127–133.

Dowdeswell, H. J., Slater, A. M., Broomhall, J., & Tripp, J. (1995). Visual deficits in children born at less than 32 weeks' gestation with and without major ocular pathology and cerebral damage. *British Journal of Ophthalmology*, 79, 447–452.

Downie, A. L. S., Frisk, V., & Jakobson, L. S. (submitted for publication). The impact of periventricular brain injury on reading and spelling abilities in the late elementary and adolescent years.

Downie, A. L. S., Jakobson, L. S., Frisk, V., & Ushycky, I. (2003). Periventricular brain injury, visual motion processing, and reading and spelling abilities in children who were extremely low birthweight. *Journal of the International Neuropsychological Society*, 9, 440–449.

Dumoulin, S. O., Bittar, R. G., Kabani, N. J., Baker, C. L., Le Goulahe, G., Pike, G. B., et al. (2000). A new anatomical landmark for reliable identification of human area V5/MT: A quantitative analysis of sulcal patterning. *Cerebral Cortex*, 10, 454–463.

Dunn, L. M., & Dunn, L. M. (1997). *Peabody picture vocabulary test* (3rd ed.). Circle Pines, MN: American Guidance Service.

Dupont, P., De Bruyn, B., Vandenberghe, R., Rosier, A.-M., Michiels, J., Marchal, G., et al. (1997). The kinetic occipital region in human visual cortex. *Cerebral Cortex*, 7, 283–292.

D'Zmura, M., & Lennie, P. (1986). Shared pathways for rod and cone vision. *Vision Research*, 26, 1273–1280.

Elleberg, D., Lavoie, K., Lewis, T. L., Maurer, D., Lepore, F., & Guillemot, J.-P. (2003). Longer VEP latencies and slower reaction times to the onset of second-order motion than to the onset of first-order motion. *Vision Research*, 43, 651–658.

Elleberg, D., Lewis, T. L., Defina, N., Maurer, D., Brent, H. P., Guillemot, J.-P., et al. (in press). Greater losses in the sensitivity to second-order local motion than to first-order local motion after early visual deprivation in humans. *Vision Research*.

Elleberg, D., Lewis, T. L., Maurer, D., Brar, S., & Brent, H. P. (2002). Better perception of global motion after monocular than after binocular deprivation. *Vision Research*, 42, 169–179.

Elleberg, D., Lewis, T. L., Meghji, K. S., Maurer, D., Guillemot, J.-P., & Lepore, F. (2003). Comparison of sensitivity to first- and second-order local motion in 5-year-olds and adults. *Spatial Vision*, 16, 419–428.

Forslund, M., & Bjerre, I. (1990). Follow-up of preterm children: II. Growth and development at four years of age. *Early Human Development*, 24, 107–118.

Frisk, V., Whyte, H., & Barnes, M. A. (1997). *Adverse effects of periventricular brain damage: Part 1: Cognitive weaknesses at school entry*. Unpublished manuscript.

Fulton, A. B., Hansen, R. M., Petersen, R. A., & Vanderveen, D. K. (2001). The rod photoreceptors in retinopathy of prematurity: An electroretinographic study. *Archives of Ophthalmology*, 119, 499–505.

Gouras, P., & Link, K. (1966). Rod and cone interaction in dark-adapted monkey ganglion cells. *Journal of Physiology*, 184, 499–510.

Greenlee, M. W., & Smith, A. T. (1997). Detection and discrimination of first- and second-order motion in patients with unilateral brain damage. *Journal of Neuroscience*, 17, 804–818.

Harvey, L. O. (1986). Efficiency estimation of sensory thresholds. *Behavior Research Methods, Instruments, & Computers*, 18, 623–632.

Hawken, M. J., Parker, A. J., & Lund, J. S. (1988). Laminar organization and contrast sensitivity of direction-selective cells in the striate

- cortex of the old world monkey. *Journal of Neuroscience*, 8, 3541–3548.
- Inder, T. E., Anderson, N. J., Spencer, C., Wells, S., & Volpe, J. J. (2003). White matter injury in the premature infant: A comparison between serial cranial sonographic and MR findings at term. *American Journal of Neuroradiology*, 24, 805–809.
- Jakobson, L. S., Frisk, V., Downie, A. L. S., & Whyte, H. (2003). *Direct and indirect effects of motion-processing deficits on visual and visuomotor functioning in children born extremely prematurely*. Poster presented at the biennial meeting of the Society for Research in Child Development.
- Jakobson, L. S., Frisk, V. A., Knight, R. M., Downie, A. L. S., & Whyte, H. (2001). The relationship between periventricular brain injury and deficits in visual processing among extremely-low-birthweight (<1000 g) children. *Journal of Pediatric Psychology*, 26, 503–512.
- Ledgeway, T., & Smith, A. T. (1994). Evidence for separate motion-detecting mechanisms for first- and second-order motion in human vision. *Vision Research*, 34, 2727–2740.
- Lee, B. B., Pokorny, J., Smith, V. C., Martin, P. R., & Valberg, A. (1990). Luminance and chromatic modulation sensitivity of macaque ganglion cells and human observers. *Journal of the Optical Society of America A, Optics and Image Science and Vision*, 7, 2223–2236.
- Lee, B. B., Smith, V. C., Pokorny, J., & Kremers, J. (1997). Rod inputs to macaque ganglion cells. *Vision Research*, 37, 2813–2828.
- Lennie, P. (1993). Roles of M and P pathways. In R. Shapley & D. M.-K. Lam (Eds.), *Contrast sensitivity*. Cambridge: MIT Press.
- Levitt, H. (1971). Transformed up-down methods in psychoacoustics. *Journal of the Acoustical Society of America*, 49, 467–477.
- Mareschal, I., & Baker, C. L., Jr. (1998). Temporal and spatial response to second-order stimuli in cat area 18. *Journal of Neurophysiology*, 80, 2811–2823.
- Mareschal, I., & Baker, C. L., Jr. (1999). Cortical processing of second-order motion. *Visual Neuroscience*, 16, 527–540.
- Miller, S. P., Cozzio, C. C., Goldstein, R. B., Ferriero, D. M., Partridge, J. C., Vigneron, D. B., et al. (2003). Comparing the diagnosis of white matter injury in premature newborns with serial MR imaging and transfontanel ultrasonography findings. *American Journal of Neuroradiology*, 24, 1661–1669.
- Newsome, W. T., & Paré, E. B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *Journal of Neuroscience*, 8, 2201–2211.
- Ornstein, M., Ohlsson, A., Edmonds, J., & Asztalos, E. (1991). Neonatal follow-up of very low birthweight/extremely low birthweight infants to school age: A critical overview. *Acta Paediatrica Scandinavica*, 80, 741–748.
- Palmer, E. A., Flynn, J. T., Hardy, R. J., Phelps, D. L., Phillips, C. L., Schaffer, D. B., et al. (1991). Incidence and early course of retinopathy of prematurity. *Ophthalmology*, 98, 1628–1640.
- Papile, L., Burstein, J., Burstein, R., & Koffler, H. (1978). Incidence and evolution of subependymal and intraventricular hemorrhage: A study of infants with birth weights less than 1500 grams. *Journal of Pediatrics*, 92, 529–534.
- Purpura, K., Kaplan, E., & Shapley, R. M. (1988). Background light and the contrast gain of primate P and M retinal ganglion cells. *Proceedings of the National Academy of Sciences of the United States of America*, 85, 4534–4537.
- Ross, G., Evelyn, L., & Auld, P. A. M. (1996). Cognitive abilities and early precursors of learning disabilities in very-low-birthweight children with normal intelligence and normal neurological status. *International Journal of Behavioral Development*, 19, 563–580.
- Ross, G., Lipper, E. G., & Auld, P. A. M. (1991). Educational status and school-related abilities of very low birthweight premature children. *Pediatrics*, 88, 1125–1134.
- Schenk, T., Mai, N., Ditterich, J., & Zihl, J. (2000). Can a motion-blind patient reach for moving objects? *European Journal of Neuroscience*, 12, 3351–3360.
- Schenk, T., & Zihl, J. (1997). Visual motion perception after brain damage: I. Deficits in global motion perception. *Neuropsychologia*, 35, 1289–1297.
- Seiffert, A. E., Somers, D. C., Dale, A. M., & Tootell, R. B. (2003). Functional MRI studies of human visual motion perception: Texture, luminance, attention and after-effects. *Cerebral Cortex*, 13, 340–349.
- Smith, A. T., Greenlee, M. W., Sing, K. D., Kramer, F. M., & Hennig, J. (1998). The processing of first- and second-order motion in human visual cortex assessed by functional magnetic resonance imaging (fMRI). *Journal of Neuroscience*, 18, 3816–3830.
- Smith, A. T., & Ledgeway, T. (1996). Separate detection of moving luminance and contrast modulations: Fact or artifact? *Vision Research*, 37, 45–62.
- Sun, H., Pokorny, J., & Smith, V. C. (2001). Control of the modulation of human photoreceptors. *Color Research and Application*, 26(Suppl.), S69–S75.
- Taylor, H. G., Klein, N., Minich, N. M., & Hack, M. (2000). Middle-school-age outcomes in children with very low birthweight. *Child Development*, 71, 1495–1511.
- Tootell, R. B. H., Reppas, J. B., Kwong, K. K., Malach, R., Born, R. T., Brady, T. J., et al. (1995). Functional analysis of human MT and related visual cortical areas using functional magnetic resonance imaging. *Journal of Neuroscience*, 15, 3215–3230.
- Vaina, L. M., & Cowey, A. (1996). Impairment of the perception of second-order motion but not first-order motion in a patient with unilateral focal brain damage. *Proceedings of the Royal Society of London B, Biological Sciences*, 263, 1225–1232.
- Vaina, L. M., Cowey, A., & Kennedy, D. (1999). Perception of first- and second-order motion: Separable neurological mechanisms? *Human Brain Mapping*, 7, 67–77.
- Vaina, L. M., Makris, N., Kennedy, D., & Cowey, A. (1998). The selective impairment of the perception of first-order motion by unilateral cortical brain damage. *Visual Neuroscience*, 15, 333–348.
- Vaina, L. M., Soloviev, S., Bienfang, D. C., & Cowey, A. (2000). A lesion of cortical area V2 selectively impairs the perception of the direction of first-order visual motion. *Neuroreport*, 11, 1039–1044.
- Van Oostende, S., Snaert, S., Van Hecke, P., Marchal, G., & Orban, G. A. (1997). The kinetic occipital (KO) region in man: An fMRI study. *Cerebral Cortex*, 7, 690–701.
- Virsu, V., & Lee, B. B. (1983). Light adaptation in cells of macaque lateral geniculate nucleus and its relation to human light adaptation. *Journal of Neurophysiology*, 50, 864–878.
- Virsu, V., Lee, B. B., & Creutzfeldt, O. D. (1987). Mesopic spectral responses and the Purkinje shift of macaque lateral geniculate nucleus cells. *Vision Research*, 27, 191–200.
- Volpe, J. J. (1995). *Neurology of the newborn* (3rd ed.). Philadelphia, PA: W.B. Saunders Company.
- Wiesel, T. N., & Hubel, D. H. (1966). Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. *Journal of Neurophysiology*, 29, 1115–1156.
- Zeki, S., Perry, R. J., & Bartels, A. (2003). The processing of kinetic contours in the brain. *Cerebral Cortex*, 13, 189–202.
- Zhou, Y. X., & Baker, C. L., Jr. (1993). A processing stream in mammalian vision cortex neurons for non-Fourier responses. *Science*, 261, 98–101.