# Comparison of sensitivity to first- and second-order local motion in 5-year-olds and adults

# DAVE ELLEMBERG<sup>1,2,\*</sup>, TERRI L. LEWIS<sup>2</sup>, KARIM S. MEGHJI<sup>2</sup>, DAPHNE MAURER<sup>2</sup>, JEAN-PAUL GUILLEMOT<sup>1,3</sup> and FRANCO LEPORE<sup>1</sup>

<sup>1</sup> Groupe de Recherche En Neuropsychologie Expérimentale, Université de Montréal, Montréal, Québec, Canada

<sup>2</sup> McMaster University, Hamilton, Ontario, Canada

<sup>3</sup> Université du Québec a Montréal, Montréal, Québec, Canada

Received 16 July 2002; revised 8 May 2003; accepted 8 May 2003

**Abstract**—We compared sensitivity to first- versus second-order motion in 5-year-olds and adults tested with stimuli moving at slower  $(1.5^{\circ} \text{ s}^{-1})$  and faster  $(6^{\circ} \text{ s}^{-1})$  velocities. Amplitude modulation thresholds were measured for the discrimination of the direction of motion (up *vs.* down) for luminance-modulated (first-order) and contrast-modulated (second-order) horizontal sine-wave gratings. At the slower velocity  $(1.5^{\circ} \text{ s}^{-1})$ , the differences in threshold between 5-year-olds and adults were small but significant for both first- and second-order stimuli (0.02 and 0.05 log units worse than adults' thresholds, respectively). However, at the faster velocity ( $6^{\circ} \text{ s}^{-1}$ ), the differences in threshold between the children and adults were 8 times greater for second-order motion than for first-order motion. Specifically, children's thresholds were 0.16 log units worse than those of adults for second-order motion compared to only 0.02 log units worse for first-order motion. The different pattern of results for first-order and second-order motion at the faster velocity ( $6^{\circ} \text{ s}^{-1}$ ) is consistent with models positing different mechanisms for the two types of motion and suggests that those mechanisms mature at different rates.

Keywords: Visual development; children; adults; first-order motion; second-order motion.

# INTRODUCTION

The perception of motion can arise from displacements in luminance (first-order cues) or from displacements in other physical characteristics of an image, such as its texture, that are visible even when there is no change in mean luminance (second-order cues). Mathematical models of the processing of first- and second-order motion (Wilson *et al.*, 1992), supported by psychophysical (Chubb and Sperling,

<sup>\*</sup>To whom correspondence should be addressed at McGill Vision Research Unit, 687 Pine Ave. West, Room H4-14, Montreal, Quebec, Canada H3A 1A1. E-mail: dave.ellemberg@staff.mcgill.ca

1988; Ledgeway and Smith, 1994), electrophysiological (Zhou and Baker, 1993; Mareschal and Baker, 1998, 1999), human imaging (Smith et al., 1998), and neuropsychological (Vaina and Cowey, 1996; Greenlee and Smith, 1997; Vaina et al., 1998) data, suggest that the processing of second-order motion involves neuronal mechanisms that are different from those involved in the processing of first-order motion. For example, humans do not integrate alternating frames containing first- and second-order local motion into an unambiguous percept of motion (Ledgeway and Smith, 1994), and their sensitivity to first- or second-order local motion is not affected by adaptation to motion of the other type (Nishida et al., 1997). Further, both the latency of the visual evoked potential and the reaction time for a psychophysical response are longer for the onset of second-order motion than for the onset of first-order motion (Ellemberg et al., 2003). Finally, functional magnetic resonance imaging studies indicate that, although some visual areas (including V1, V2, and V5) respond equally to both types of motion, areas V3 and VP respond more strongly to second-order motion than to first-order motion (Smith et al., 1998).

Only one study has examined the perception of first-order versus second-order motion during development (Atkinson et al., 1993; reviewed in Braddick et al., 1996). Infants aged 8-12 weeks and 16-20 weeks spent more time looking at a stimulus that contained either first- or second-order motion than at a nondirectional control stimulus, and the difference was larger for first- than for secondorder motion. These findings indicate that infants as young as 2 months of age can detect both first- and second-order motion. However, it is difficult to draw conclusions about the differential development of sensitivity to the two types of motion because the authors did not measure thresholds. Several other studies tested the development of motion perception (Volkmann and Dobson, 1976; Kaufmann et al., 1985; Dannemiller and Freedland, 1989; Aslin and Shea, 1990; Bertenthal and Bradbury, 1992; Dobkins and Teller, 1996; Roessler and Dannemiller, 1997), but none compared sensitivity to first- versus second-order cues to motion. Despite the wide differences in stimuli and threshold criteria amongst these studies, they agree that until at least 6 months of age (the oldest age tested) sensitivity at slower velocities is more immature than sensitivity at faster velocities (but see Wattam-Bell, 1991). Because the perception of velocity is determined by the detection of the spatial structure of the moving stimulus and by its rate of temporal change, it has been suggested that infants' especially poor sensitivity at slower velocities is related to their poor spatial resolution (i.e. reduced sampling density of foveal receptors) and especially poor contrast sensitivity at low temporal frequencies (Freedland and Dannemiller, 1987; Kaufmann, 1995; Roessler and Dannemiller, 1997).

Thus, little is known about the development of motion perception beyond infancy or about sensitivity to the direction of first-*versus* second-order motion at any time during development. The goal of the present study was to compare sensitivity to first-*versus* second-order motion in 5-year-olds and adults tested with stimuli moving at slower  $(1.5^{\circ} \text{ s}^{-1})$  and faster  $(6^{\circ} \text{ s}^{-1})$  velocities. We measured thresholds

for the discrimination of direction using patterns of random noise that were either added to (first-order stimulus) or multiplied by (second-order stimulus) a sinusoidal grating modulated in luminance.

#### METHODS

# Subjects

The subjects were 24 adults (mean age = 20.4 years, range 19.1–22.9 years) and 24 children who were 5 years of age ( $\pm 1$  month). None of the subjects had a history of eye problems, and all met our criteria on a visual screening examination. Specifically, adults had a linear letter acuity (Lighthouse Visual Acuity Chart) of at least 20/20 in each eye without optical correction, worse acuity with a +3 dioptre add (to rule out hypermetropia of greater than 3 dioptres), fusion at near on the Worth four dot test, and stereoacuity of at least 40 arc sec on the Titmus test. The 5-year-olds met the same criteria except that they were required to have a visual acuity of at least 20/25 when tested with the Good-lite Crowding cards. Specifically, children were shown flash cards (Good-lite, catalogue # 1010), each containing one letter (H, O, T, or V) flanked by six comparably-sized vertical bars to the left and to the right. The smallest letter that children identified (by pointing to the match on a hand-held card) provided a measure of visual acuity.

# Apparatus and stimuli

The stimuli were generated by a Macintosh G3 computer by means of Pixx 1.55 software<sup>TM</sup>, and were displayed on a Two-Page Display/21 gs Radius monochrome monitor,  $32^{\circ}$  wide by  $25^{\circ}$  high. The monitor had a frame rate of 75 Hz and a pixel resolution of  $1152 \times 870$ .

The stimuli consisted of 1 c deg<sup>-1</sup> horizontal sinusoidal gratings, 10° wide by 10° high when viewed from a distance of 50 cm. The stimuli drifted either up or down for 1.5 s at a velocity of 1.5 or 6° s<sup>-1</sup>. All stimuli consisted of static two-dimensional random noise (referred to as the carrier), the luminance of which was binary. Each noise element subtended  $2 \times 2$  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<sup>-1</sup>. This created a sinusoidal modulation of luminance across the carrier, which appeared like a conventional luminance-modulated sinusoidal grating. The amplitude of the luminance modulation (Michelson contrast or depth modulation) was defined as:

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 the carrier by a luminancemodulated sinusoidal grating (e.g. Smith and Ledgeway, 1997). This produced a sinusoidal modulation of the contrast of the carrier. The stimulus consisted of a series of alternating regions of higher and lower contrast between noise dots, with every region having the same mean luminance. The amplitude of the contrast modulation (depth modulation) was defined as:

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 24 cd m<sup>-2</sup>. 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 (1997), we calibrated the second-order images to ensure that gamma-correction was 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 × 2 arc min) were used so that the second-order stimuli would not contain detectable local luminance cues (Smith and Ledgeway, 1997).

# Procedure

The procedures were explained and informed consent was obtained from the adults and from parents of the 5-year-olds. The experimental protocol was approved by the Committee on the Ethics of Research on Human Subjects, McMaster University. Because the data are to be compared to those from children with monocular eye problems, all subjects were tested monocularly, half in each group with the right eye and half with the left eye. The eye not being tested was patched with 3M Micropore<sup>TM</sup> tape. The subject was seated 50 cm from the stimuli with the chin positioned on a chin-rest. Parents sat in the testing room out of their child's sight and were asked to remain silent throughout the testing.

Subjects were instructed to fixate a target in the centre of the screen that appeared between trails and then were asked to judge whether the stripes were moving upward or downward. The experimenter said: '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 down (experimenter points down)'. The experimenter entered the responses by means of the keyboard. The experimenter watched the participant's viewing eye continuously to ensure that he/she was looking at the centre of the screen. To verify that subjects understood the task, they were first presented with a 10-trial block of second-order stimuli at 100% depth modulation which were moving at  $1.5^{\circ}$  s<sup>-1</sup>. To be included in the study, participants had to judge correctly the direction of motion (up or down)

on four consecutive trials. All subjects met this criterion, usually in the first four trials.

All subjects were tested in each of four conditions: first- and second-order motion x two velocities  $(1.5 \text{ and } 6^{\circ} \text{ s}^{-1})$ . To control for any effects of fatigue and/or practice, half of the participants in each group first completed trials with first-order motion; the other half first completed trials with second-order motion. Within each type of motion, the velocities were tested in a random order. Thresholds for the discrimination of the direction of motion (up or down) were calculated with a ML-TEST staircase procedure (Harvey, 1986), and were defined as the minimum depth modulation necessary to detect the direction of motion. Before beginning the test with each type of motion (first- or second-order), each subject was given a practice staircase with feedback after each trail. At the end of each practice run, subjects were asked if they understood the task and if so, testing began. No feedback was given during the test but children were praised periodically and were reminded to watch carefully. All adults completed testing in one session. Thirteen of the 5-year-olds completed testing within one session lasted no more than 1 hour.

#### RESULTS

The mean depth modulation thresholds for the 5-year-olds and for the adults are presented in Fig. 1. Circles represent the mean thresholds for the 5-year-olds and the squares represent the mean thresholds for the adults. Filled symbols represent first-order motion and open symbols represent second-order motion. Because it can be argued that thresholds for first- and second-order motion are on different scales, we compared the thresholds of the adults and 5-year-olds for each of the four conditions (two types of motion at two velocities) in separate two-tailed *t*-tests. The results of these analyses indicate that for each of the four conditions, 5-year-olds had significantly higher thresholds than adults (in all cases, p < 0.01). To compare the data across the four conditions, we transformed the thresholds into immaturity scores. For each condition, we paired each 5-year-old to the adult tested in the same ordinal position and subtracted their log thresholds. These ratios, which we call the immaturity scores, were then compared for each of the four conditions in a repeated measures analysis of variance (ANOVA). The ANOVA revealed an interaction between type of motion and velocity  $F_{1,23} = 19.05$  (p < 0.01). The post-hoc analysis on the interaction revealed that the immaturity score for secondorder motion at the faster velocity ( $6^{\circ}$  s<sup>-1</sup>), was significantly higher than that for each of the three other conditions (p < 0.01). There were no other significant differences. Together, these findings indicate that 5-year-olds are less sensitive than adults for each condition, that the reductions in sensitivity are greatest for secondorder motion at the fastest speed, and that the reductions in sensitivity are equal for the other three conditions.



**Figure 1.** Mean thresholds (log depth modulation) for the discrimination of the direction of firstversus second-order motion in 5-year-olds (circles) and in adults (squares). Solid symbols represent the mean log thresholds for first-order motion and the open symbols represent the mean log thresholds for second-order motion. Depth modulation represents modulation of the luminance of first-order gratings and modulation of the contrast of second-order gratings.

# DISCUSSION

Our findings indicate that, at least under some conditions, sensitivity to secondorder motion develops more slowly than sensitivity to first-order motion. Five-yearolds were significantly less sensitive than adults for each condition tested. The thresholds of 5-year-olds were elevated slightly and equally for first-order stripes moving at  $1.5^{\circ}$  s<sup>-1</sup> or  $6^{\circ}$  s<sup>-1</sup> and for second-order stripes moving at  $1.5^{\circ}$  s<sup>-1</sup> (0.02) to 0.05 log units worse). However, at the faster velocity ( $6^{\circ}$  s<sup>-1</sup>), the thresholds of 5-year-olds were elevated 8 times more for second-order motion (0.16 log units worse than adults) than for first-order motion (0.02 log units worse than adults). The different pattern of result for first-order and second-order motion at the faster velocity suggests that sensitivity to these two types of motion develops, at least in part, at different rates. These results are akin to those for the development of texture segmentation. In human infants and in kittens, segmentation of textures based on orientation differences (a second-order cue) emerges later and is slower to develop than segmentation based on luminance differences (a first-order cue) (Atkinson and Braddick 1992; Sireteanu and Rieth, 1992; Wilkinson and Lessard, 1995; see Sireteanu, 2000 for a review).

Although non-visual factors, such as differences between the 5-year-olds and adults in attention or eye movements, may have contributed to the difference in threshold, they cannot account for the significant differences in the extent of

the immaturity for different conditions. All tasks measured thresholds, yet the difference between the thresholds of 5-year-olds and adults was much larger for second-order motion at the faster velocity than for the other three conditions. The 5-year-olds' performance also does not appear to be related to differences in the adults' sensitivity in the different conditions. For example, the 5-year-olds were about 2 times less sensitive to the motion of second-order images at the faster than at the slower velocities, whereas adults were almost equally sensitive in the two conditions.

Our data indicate that for second-order stimuli, differences between 5-year-olds and adults are three times greater at the faster than at the slower velocity (0.16 and 0.05 log units worse than adults at the faster and slower velocities, respectively). This pattern of results is very different from that observed in young infants where sensitivity to first-order stimuli moving at  $1.5^{\circ}$  s<sup>-1</sup> is far more immature than sensitivity to first-order stimuli moving at faster velocities (Volkmann and Dobson, 1976; Kaufmann *et al.*, 1985; Dannemiller and Freedland, 1989; Aslin and Shea, 1990; Bertenthal and Bradbury, 1992; Roessler and Dannemiller, 1997; but see Wattam-Bell 1991). Therefore, our findings suggest that, contrary to the pattern for first-order stimuli during infancy, sensitivity to second-order motion develops more slowly at faster than at slower velocities during childhood.

Under the present testing conditions, we cannot determine whether the pattern of results for the slower *versus* faster velocity is a consequence of differences in sensitivity to velocity or to temporal frequency. Because temporal frequency is equal to velocity multiplied by spatial frequency, and because we kept spatial frequency constant at 1 c deg<sup>-1</sup>, temporal frequency varied directly with velocity: 1.5 and 6 Hz for the slower  $(1.5^{\circ} \text{ s}^{-1})$  and faster velocities  $(6^{\circ} \text{ s}^{-1})$ , respectively. Studies with adults have suggested that velocity, rather than temporal frequency, is the critical variable for the velocities used in the current study (McKee *et al.*, 1986). Within this range, McKee *et al.* (1986) found that velocity discrimination is affected little by large random changes in spatial frequency, and hence affected little by the temporal frequency of the pattern to be discriminated (but see Burr and Ross, 1982; Smith and Edgar, 1991).

The motion energy model, supported by both psychophysical and physiological data, provides a structure for understanding the development of motion sensitivity (Adelson and Bergen, 1985; Emerson *et al.*, 1992). The model suggests that sensitivity to first-order motion depends on the integration over space and time of the outputs of bandpass linear spatio-temporal filters. However, this mechanism is blind to second-order stimuli because it relies on the presence of spatial Fourier components in the luminance domain. Therefore, sensitivity to second-order motion depends on a non-linear transformation that introduces first-order characteristics into the neural representation of the second-order image. Early distortion products of pre-cortical origin (e.g. at the level of photoreceptors) have been suggested as a possible source of non-linearity (Burton, 1973; Henning *et al.*, 1975; Nachmias and

Rogowitz, 1983). However, several studies refuted this hypothesis (Langley *et al.*, 1996; Badcock and Derrington, 1989; Zhou and Baker, 1993, 1994).

Computational modeling supported by psychophysical and electrophysiological data suggests that the detection of second-order motion requires at least two additional processing steps that are subsequent to the first stage linear filter in the primary visual cortex (Chubb and Sperling, 1988, 1989; Wilson et al., 1992; Baker, 1999). The 'filter-rectify-filter' model suggests that early linear filtering is followed by a non-linear processing stage (e.g. full-wave rectification, half-wave rectification, or squaring) that introduces first-order characteristics into the neural representation of the second-order image, and a second stage filtering at a lower scale. Despite the fact that the bulk of the data supports this two-stream model, there are some findings that seem to support single pathway models (Johnston and Clifford, 1995; Taub et al., 1997; Baloch et al., 1999). Although our data cannot distinguish between these models, they are consistent with the hypothesis that each type of motion is processed, at least in part, by separate mechanisms. Because the immaturities were greater for second-order motion, our results suggest that the additional non-linear processing necessary for the extraction of second-order motion matures more slowly than the mechanisms underlying the extraction of firstorder motion.

In summary, we found a different developmental pattern for sensitivity to firstorder *versus* second-order local motion when stripes moved at  $6^{\circ}$  s<sup>-1</sup>. At that velocity, 5-year-olds were especially immature for second-order motion but nearly adult-like for first-order motion. These findings are consistent with the hypothesis that each type of motion is processed, at least in part, by separate mechanisms.

# Acknowledgements

This research was supported by the Medical Research Council of Canada and Canadian Institutes of Health Research grants (MT-11710, MA-11710, and MOP-36430) to Daphne Maurer, NSERC grants to Franco Lepore and Jean-Paul Guillemot and Canada Research CHAIR to Franco Lepore. Dave Ellemberg was supported in part by a research scholarship from Fight for Sight, Prevent Blindness America, and by a scholarship from the Medical Research Council of Canada (E.A. Baker Award). We also wish to thank Peter April for providing us with the Pixx Software (see web site for more details: www.vpixx.com) used to generate the stimuli.

# REFERENCES

- Adelson, E. H. and Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion, J. Opt. Soc. Amer. A. 2, 284–299.
- Aslin, R. N. and Shea, S. L. (1990). Velocity thresholds in human infants: Implications for the perception of motion, *Develop. Psychol.* 26, 589–598.
- Atkinson, J. and Braddick, O. (1992). Visual segmentation of oriented textures by infants, *Behavioural Brain Research* **49**, 123–131.

- Atkinson, J., Braddick, O. and Wattam-Bell, J. (1993). Infant cortical mechanisms controlling OKN, saccadic shifts, and motion processing, *Investigative Ophthalmol. Visual Sci.* **34**, 1357, Abstract.
- Badcock, D. R. and Derrington, A. M. (1989). Detecting the displacement of spatial beats: no role for distortion products, *Vision Research* 29, 731–739.
- Baker, C. L. (1999). Central neural mechanisms for detecting second-order motion, *Current Opinion* in Neurobiology 9, 461–466.
- Baloch, A. A., Grossberg, S., Mingolla, E. and Nogueira, C. A. M. (1999). Neural model of firstorder and second-order motion perception and magnocellular dynamics, *J. Opt. Soc. Amer. A.* 16, 953–978.
- Bertenthal, B. I. and Bradbury, A. (1992). Infants' detection of shearing motion in random-dot displays, *Developmental Psychology* 28, 1056–1066.
- Braddick O., Atkinson, J. and Hood, B. (1996). Striate cortex, extrastriate cortex, and colliculus: some new approaches, in: *Infant Vision*, Vital-Durand, F., Braddick, O. and Atkinson, J. (Eds), pp. 203–220. Oxford.
- Burr, D. C. and Ross, J. (1982). Contrast sensitivity at high velocities, Vision Research 22, 479-484.
- Burton, G. J. (1973). Evidence for non-linear response process in the visual system from measurements on the thresholds of spatial beat frequencies, *Vision Research* **13**, 1211–1255.
- Chubb, C. and Sperling, G. (1988). Drift-balanced random stimuli: a general basis for studying non-Fourier motion perception, *J. Opt. Soc. Amer. A.* **5**, 1986–2007.
- Dannemiller, J. L. and Freedland, R. L. (1989). The detection of slow stimulus movement in 2- to 5-month-olds, J. Exp. Child Psychol. 47, 337–355.
- Dobkins, K. R. and Teller, D. Y. (1996). Infant contrast detectors are selective for direction discrimination, *Vision Research* 36, 281–294.
- Ellemberg, D., Lavoie, K., Lewis, T. L., Maurer, D., Lepore, F. and Guillemot, J.-P. (2003). Longer VEP latencies and slower reactions times to the onset of second-order motion than to the onset of first-order motion, *Vision Research* 43, 651–658.
- Emerson, R. C., Bergen, J. R. and Adelson, E. H. (1992). Directionally selective complex cells and the computation of motion energy in cat visual cortex, *Vision Research* **32**, 203–218.
- Freedland, R. L. and Dannemiller, J. L. (1987). Detection of stimulus motion in 5- month-old infants, J. Exp. Psychol.: Human Perception and Performance 13, 566–576.
- Greenlee, M. W. and Smith, A. T. (1997). Detection and discrimination of first- and second-order motion in patients with unilateral brain damage, J. Neurosci. 17, 804–818.
- Harvey, L. O. (1986). Efficient estimation of sensory thresholds, *Behavior Research Methods*, *Instruments and Computers* 18, 623–632.
- Henning, G. B., Hertz, B. G. and Broadbent, D. E. (1975). Some experiments bearing on the hypothesis that the visual system analyses spatial patterns in independent bands of spatial frequency, *Vision Research* 15, 887–897.
- Johnston, A. and Clifford, C. W. G. (1995). Perceived motion of contrast- modulated gratings: predictions of the multi-channel gradient model and the role of full-wave rectification, *Vision Research* **35**, 1771–1783.
- Kaufmann, F. (1995). Development of motion perception in early infancy, *Europ. J. Pediatrics* **154**, S48–S53.
- Kaufmann, F., Stucki, M. and Kaufmann-Hoyoz, R. (1985). Infant Behavior and Development 8, 89–98.
- Langley, K., Fleet, D. J. and Hibbard, P. B. (1996). Linear filtering precedes nonlinear processing in early vision, *Current Biology* 6, 891–896.
- Ledgeway, T. and Smith, A. T. (1994). Evidence for separate motion-detecting mechanisms for first and second order motion in human vision, *Vision Research* **34**, 2727–2740.
- Mareschal, I. and Baker, C. L. (1998). Temporal and spatial responses to second-order stimuli in cat area 18, J. Neurophysiol. 80, 2811–2873.

- Mareschal, I. and Baker, C. L. (1999). Cortical processing of second-order motion, Visual Neuroscience 16, 527–540.
- McKee, S. P., Silverman, G. H. and Nakayama, K. (1986). Precise velocity discrimination despite random variations in temporal frequency and contrast, *Vision Research* **26**, 599–608.
- Nachmias, J. and Rogowitz, B. E. (1983). Masking by spatially modulated gratings, *Vision Research* 23, 1621–1624.
- Nishida, S., Ledgeway, T. and Edwards, M. (1997). Dual multiple-scale processing for motion in the human visual system, *Vision Research* 37, 2685–2698.
- Roessler, J. S. and Dannemiller, J. L. (1997). Changes in human infants' sensitivity to slow displacements over the first 6 months, *Vision Research* **37**, 417–423.
- Sireteanu, R. (2000). Texture segmentation, "pop-out", and feature binding in infants and children, in: *Progress in Infancy Research*, Rovee-Collier, C., Lipsitt, L. and Hayne, H. (Eds), Vol. 1, pp. 183–250. Lawrence Erlbaum Associates (Publishers).
- Sireteanu, R. and Rieth, C. (1992). Texture segregation in infants and children, *Behavioural Brain Research* **49**, 133–139.
- Smith, A. T. and Edgar, G. K. (1991). The separability of temporal frequency and velocity, *Vision Research* 31, 321–326.
- Smith, A. T. and Ledgeway, T. (1997). Separate detection of moving luminance and contrast modulations: fact or artifact? *Vision Research* 37, 45–62.
- Smith, A. T., Greenlee, M. W., Sing, K. D., Kramer, F. M. and Hennig, J. (1998). The processing of first- and second-order motion in human visual cortex assessed by functional magnetic resonance imaging (fMRI), *J. Neurosci.* 18, 3816–3830.
- Taub, E., Victor, J. D. and Conte, M. M. (1997). Nonlinear preprocessing in short-range motion, *Vision Research* 11, 1459–1477.
- Vaina, L. M. and Cowey, A. (1996). Impairment of the perception of second- order motion but not first-order motion in a patient with unilateral focal brain damage, *Proc. Roy. Soc. London* 263, 1225–1232.
- Vaina, L. M, Makris, N., Kennedy, D. and Cowey, A. (1998). The selective impairment of the perception of first-order motion by unilateral cortical brain damage, *Visual Neuroscience* 15, 333–348.
- Volkmann, F. C. and Dobson, M. V. (1976). Infant responses of ocular fixation to moving visual stimuli, J. Exp. Child Psychol. 22, 86–99.
- Wattam-Bell, J. (1991). Development of motion-specific cortical responses in infancy, *Vision Research* **31**, 287–297.
- Wilkinson, F. and Lessard, J. (1995). Orientation, density and size as cues to texture segmentation in kittens, *Vision Research* **35**, 2463–2478.
- Wilson, H. R., Ferrara, V. P. and Yo, C. (1992). A Psychophysically motivated model for twodimensional motion perception, *Visual Neuroscience* 9, 79–97.
- Zhou, Y.-X. and Baker, C. L. (1993). A processing stream in mammalian visual cortex neurons for non-Fourier responses, *Science* 261, 98–101.
- Zhou, Y.-X. and Baker, C. L. (1994). Envelope-responsive neurons in areas 17 and 18 of cat, J. Neurophysiol. 72, 2134–2150.