The effect of blur on cortical responses to global form and motion

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Global form and motion sensitivity undergo long development in childhood with motion sensitivity rather than form being impaired in a number of childhood disorders and both impaired in adult clinical populations. This suggests extended development and vulnerability of extrastriate cortical areas associated with global processing. However, in some developmental and clinical populations, it remains unclear to what extent impairments might reflect deficits at earlier stages of visual processing, such as reduced visual acuity and contrast sensitivity. To address this, we investigated the impact of degraded spatial vision on cortical global form and motion processing in healthy adults. Loss of high spatial frequencies was simulated using a diffuser to blur the stimuli. Participants completed behavioral and EEG tests of global form and motion perception under three levels of blur. For the behavioral tests, participants' form and motion coherence thresholds were measured using a two-alternative, forced-choice procedure. Steady-state visual evoked potentials were used to measure cortical responses to changes in the coherence of global form and motion stimuli. Both global form and global motion perception were impaired with increasing blur as measured by elevated behavioral thresholds and reduced cortical responses. However, form thresholds showed greater impairment in both behavioral and EEG measures than motion thresholds at the highest levels of blur. The results suggest that high spatial frequencies play an important role in the perception of both global form and motion but are especially significant for global form. Overall, the results reveal complex interactions between low-level factors and global visual processing, highlighting the importance of taking these factors into account when investigating extrastriate function in low vision populations.

Introduction

Global form and motion perception are midlevel visual skills involving processing in the extrastriate visual cortex and beyond. Both global form and motion perception require the integration of low-level visual

information into a global construct. Global form perception can be studied by presenting an array of line segments aligned into a global structure or direction. Participants are then required to judge the structure or the direction at different coherence levels to establish their coherence threshold. The coherence of the pattern refers to the proportion of the lines that collectively make up the form as opposed to being randomly oriented. Therefore, the greater the coherence level of the form, the easier its detection becomes. The analogous global motion task requires participants to detect the direction of motion in an array of coherently moving dots. Again, the coherence level of these dots can be varied to establish a participant's threshold.

Form perception is known to be predominantly processed in ventral stream areas, such as V4 (Gallant, Shoup, & Mazer, 2000; Ostwald, Lam, Li, & Kourtzi, 2008; Wilkinson et al., 2000), and motion perception is dominated by dorsal stream areas, such as middle temporal (MT)/V5 and medial superior temporal (Braddick et al., 2001; Harvey, Braddick, & Cowey, 2010; Rees, Friston, & Koch, 2000). This functional segregation allows for differences in the development and potential vulnerabilities of the two pathways to be explored. As a result, global form and motion perception have been studied extensively in both typically developing (Atkinson et al., 2004; Braddick, Atkinson, & Wattam-Bell, 2003; Golarai, 2009; Gunn et al., 2002) and atypical populations (Atkinson et al., 1997; Ellemberg, Lewis, Maurer, Brar, & Brent, 2002; Kogan et al., 2004; Lewis et al., 2002; Taylor, Jakobson, Maurer, & Lewis, 2009).

Typically developing infants first display a preference to coherent global form, as compared with incoherent, at around 12 weeks (Atkinson et al., 2004). Psychophysical thresholds then improve throughout infancy and childhood until as late as 14 years of age (e.g., Kovács, Kozma, Fehér, & Benedek, 1999) although by around 8 years of age form coherence sensitivity is close to adult values in many studies (e.g., Atkinson & Braddick, 2005). Sensitivity to global motion emerges between 6 and 8 weeks of age (Wattam-Bell, 1996) with adult-like abilities reported between 6 and 11 years of age (Ellemberg et al., 2002; Braddick et al., 2003; Gunn et al., 2002) although thresholds for some types of coherent motion stimuli develop until as late as 14 years of age (Hadad, Maurer, & Lewis, 2011).

In clinical groups who have experienced early visual deprivation due to congenital cataracts, both form and motion thresholds are affected. On average, bilateral cataract participants, treated within the first year of life, show form coherence thresholds that are 1.6 times worse than controls, and motion coherence thresholds can be up to five times worse (Ellemberg et al., 2002; Ellemberg, Lewis, Maurer, Lui, & Brent, 1999; Lewis et

al., 2002). Global motion deficits have been found to be worse in children with binocular as opposed to monocular cataracts, suggesting that early visual input from one eye is sufficient to drive the development of extrastriate brain areas. This is in contrast with low-level visual abilities, such as acuity and contrast sensitivity, which present greater deficits following monocular as opposed to binocular deprivation (e.g., Ellemberg, Lewis, Maurer, & Brent, 2000; Ellemberg et al., 1999; Lewis, Maurer, & Brent, 1995; Maurer & Lewis, 2001). This is thought to be due to unbalanced competition between the two eyes (Maurer & Lewis, 2001).

Motion thresholds in cataract patients are relatively higher than form thresholds suggesting an increased vulnerability to visual deprivation. This is in line with theories of dorsal stream vulnerability in which visual functions mediated by the dorsal stream are more vulnerable to developmental delay than those mediated by the ventral stream. This has been shown in a range of visual and developmental disorders (Atkinson & Braddick, 2007, 2011; Atkinson et al., 1997; Braddick et al., 2003; Gunn et al., 2002; Spencer et al., 2000; Taylor et al., 2009). The reasons for this selective vulnerability of the dorsal stream may lie in the need for precise neural timing of visual information in the perception of global motion, which is not so critical for form perception (Braddick et al., 2003).

One important factor not to be overlooked when studying both developmental and clinical groups is the possible influence of impairments in low-level vision, e.g., reduced contrast sensitivity at high spatial frequencies, leading to reduced visual acuity. Sensitivity to high spatial frequencies is required to detect fine detail. The degree to which global form and motion perception depends on different spatial frequencies is unclear. Reduced sensitivity at high frequencies may increase global form and motion thresholds by degrading the low-level visual information available to participants. If this is the case, then participants less sensitive to high frequencies (i.e., those with poor acuity), such as infants and low vision populations, may have an impaired ability to perceive local elements, processed at lower levels of the visual system, e.g., V1, rather than their global organization, processed in extrastriate cortical areas, such as V4 and MT/V5.

Acuity and contrast sensitivity continue to develop up until at least 5 years of age. In the first few months of life, acuity is poor, improving at approximately 1 c/° per month during the first year (Atkinson & Braddick, 1981; Atkinson, Braddick, Moar, 1977b; Norcia & Tyler, 1985). Contrast sensitivity develops rapidly over the first weeks of life (Atkinson, Braddick, & Moar, 1977a; Norcia, Tyler, & Hamer, 1990) reaching adult-like levels by 5 years (Atkinson, French, & Braddick, 1981). Because this is the period when global sensitivity

first emerges, the possible influence of poor acuity on this should not be ignored. Clinical populations, such as congenital cataract patients, also have reduced visual acuity and contrast sensitivity although these improve rapidly after cataracts are removed (Birch & Stager, 1988; Ellemberg et al., 2000; Ellemberg et al., 1999; Jacobson, Mohindra, & Held, 1981; Kugelberg, 1992; Lewis et al., 1995).

Previous research into the influence of high spatial frequency loss on form and motion perception has focused on testing psychophysical thresholds while participants wear blurring lenses. By fitting participants with positive diopter lenses, it is possible to filter out the majority of high spatial frequencies to which a participant is exposed. This optical blur can therefore be used to simulate reduced sensitivity to high spatial frequencies (poor visual acuity).

Zwicker, Hoag, Edwards, Boden, and Giaschi (2006) investigated the effects of positive diopter lenses, ranging from +0.75 to +4.00 diopters (D), in a psychophysical experiment of global form and motion processing. They found that, although global form coherence thresholds were reduced with increased blur, global motion thresholds were unaffected (Zwicker et al., 2006). This suggests that form perception may be more reliant on high spatial frequencies than global motion perception.

Braddick, Akthar, Anker, and Atkinson (2007) examined the effects of optical blur, induced with positive diopter lenses, on form and motion coherence thresholds. Participants were required to identify either rotational motion or stationary concentric circles at varying coherence levels in a two-alternative, forced-choice (2AFC) task. Up to +5D of blur did not significantly increase thresholds from baseline; however, at higher levels (+7D or more), impairments were seen (Braddick et al., 2007).

The interaction between spatial frequencies and dot displacement in motion stimuli also appears to be important. Cleary and Braddick (1990) found that the upper displacement limit (d_{max}) increased when high spatial frequencies were removed from random dot kinematograms. Mirroring this, Barton, Rizzo, Nawtrot, and Simpson (1996) found that blur equivalent to +3.25D worsened direction discrimination when dot displacement was low (less than 16′), but conversely, discrimination was increased when displacement was high (greater than 21′). This suggests that high spatial frequencies may aid global motion perception but only when dot displacement is relatively low (Barton et al., 1996; Cleary & Braddick, 1990). This highlights the complexity of the global motion system and the need to take multiple aspects of stimuli into consideration when determining the influence of different spatial frequencies.

Previous studies into the effects of optical blur have focused on behavioral tests; however, another method widely employed in developmental and clinical research is EEG. EEG provides a measure of cortical visual processing without the need for participants to understand the task and is therefore a powerful tool when used with infants and other nonverbal populations.

Steady-state visual evoked potentials (SSVEPs) have been used to study the development of global form and motion processing (Hou, Gilmore, Pettet, & Norcia, 2009; Norcia et al., 2005; Palomares, Pettet, Vildavski, Hou, & Norcia, 2009; Wattam-Bell et al., 2010; Weinstein et al., 2012). SSVEPs measure cortical responses to global form and motion through the use of rapidly alternating coherent and incoherent stimuli. Global motion SSVEPs develop more rapidly than form SSVEPs in infancy, and by 5 months of age, a majority of infants show a motion response compared with around 50% showing a form response although the scalp topography of both responses is still markedly immature at that age (Wattam-Bell et al., 2010). However, as with behavioral measures, it remains unclear how far these SSVEP results reflect immaturities in extrastriate networks rather than reduced visual input to these regions due to loss of high spatial frequencies. This question also applies when studying other groups with reduced vision, such as populations with visual impairments.

The current study examined the impact of blur on both behavioral measures of sensitivity to global form and motion and cortical measures, using SSVEPs. Optical blur created with positive diopter lenses as used in previous studies (Barton et al., 1996; Braddick et al., 2007; Zwicker et al., 2006) does not have a smooth modulation transfer function, resulting in some high spatial frequencies still being perceptible, albeit with phase distortions ("spurious resolution"). To address this, the current study used a diffusing sheet, which acts as a low-pass filter. This method has been used extensively in vision research as a means of creating blur (Enoch & Williams, 1983; Essock, Williams, Enoch, & Raphael, 1984; Legge, Pelli, Rubin, & Schleske, 1985; Westheimer & McKee, 1980; Williams, Enoch, & Essock, 1984). This study also tested a wider range of blur than used in the previously described studies (Barton et al., 1996; Braddick et al., 2007; Zwicker et al., 2006) in order to measure the impact of the large degree of blur that would be experienced by some visually impaired populations.

Methods and materials

Participants

Twenty adults (seven males, 18–47 years, $M = 25.2$) participated in the study. All participants had normal
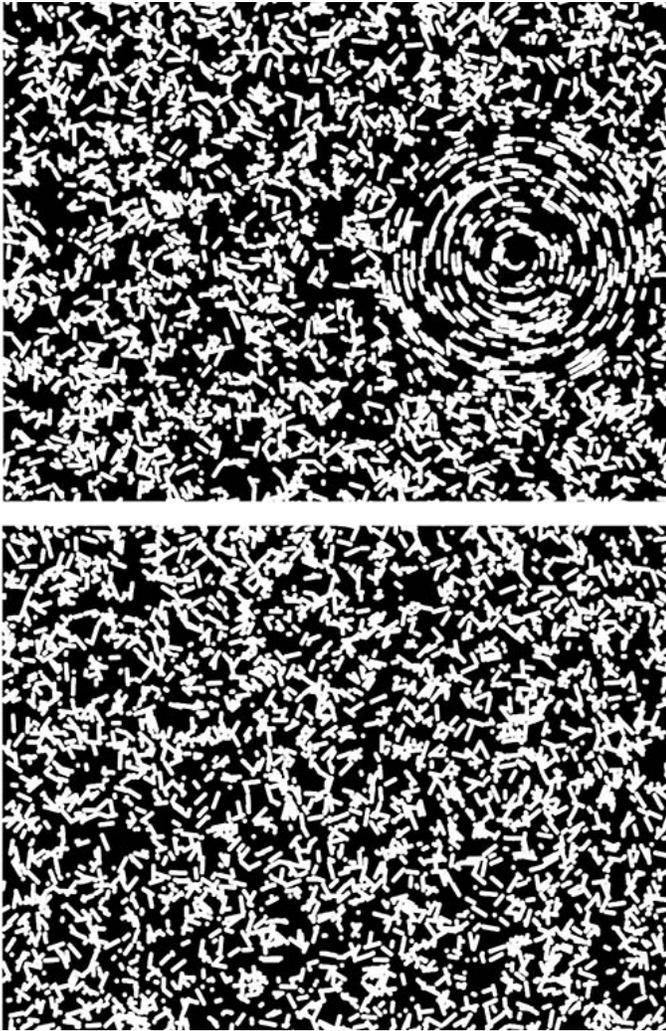
Figure 1. Example of the form and motion task. Form stimuli are shown here but also demonstrate the motion task in which each line segment represents the motion trajectory of a single dot. The upper image shows 100% coherence, and the lower image shows 12.5% coherence.

or corrected-to-normal vision and no known neurological problems. Written informed consent was given by each participant before the experiment commenced.

Stimulus generation and task design

Behavioral and EEG stimuli were generated in Matlab (version 2012a, The MathWorks Inc., Natick, MA) using Psychophysics Toolbox (Brainard, 1997) and displayed on a Mitsubishi Diamond Pro SB2070 22-in. CRT monitor with a resolution of 1280 × 1024 pixels and a 60-Hz refresh rate. Tests were completed at a distance of 60 cm at which the display size was 37° × 28°. Participants completed the behavioral tests followed by the EEG.

Behavioral tests

Coherent form and motion stimuli consisted of 2,000 white dots, each with a 6-pixel diameter and 0.29° visual angle, plotted against a black background. To create the motion stimuli, eight dots were plotted in successive frames, creating motion along an arc trajectory at 8.6°/s with a lifetime of 133 ms. Within each frame, one/eighth dot lifetimes were randomly restarted, creating the overall impression of multiple motion trajectories of varying lengths. Form stimuli were matched to the motion stimuli, plotting dots from individual frames simultaneously to create stationary short arc segments. Line segments were one to eight dots in length with an average length of 1.3°. The starting locations of dots and of line segments were randomly distributed across the display area for each trial. In each case, coherently plotted elements were arranged in a circular structure with a common center of curvature. This produced a region of concentric structure subtending 16°. Outside this region, the arcs were randomly oriented.

The task employed a 2AFC design in which coherent form or motion was displayed on one side of the screen, centered 10° from the screen center. The participant's task was to judge the side containing coherent form or motion. Trials varied in their level of coherence by varying the ratio of coherent to random elements within the circular target region. Participants were asked to fixate on a white central cross while stimuli were presented, at random, on the left or right of fixation as shown in Figure 1.

Stimuli were presented for 1 s, after which time a black screen appeared. The participant then had as much time as he or she wanted to indicate the location of the target using either a right- or left-hand button.

Participants viewed a total of 90 form and 90 motion trials per blur level, and their coherence threshold was calculated from this. In each trial, coherence (percentage of coherent elements within the target region) was varied according to the PSI adaptive method (Kontsevich & Tyler, 1999), which estimated the threshold as the 75% point on the psychometric function.

SSVEP

Stimuli were matched in design to those used in the behavioral tests, containing 2,000 white dots, each with a 6-pixel diameter (0.29° visual angle), plotted against a black background. Unlike the behavioral stimuli, however, these were displayed centrally and filled the entire display (37° × 28°) as no active task was employed. Participants were instead required to passively view the form or motion stimuli. These stimuli
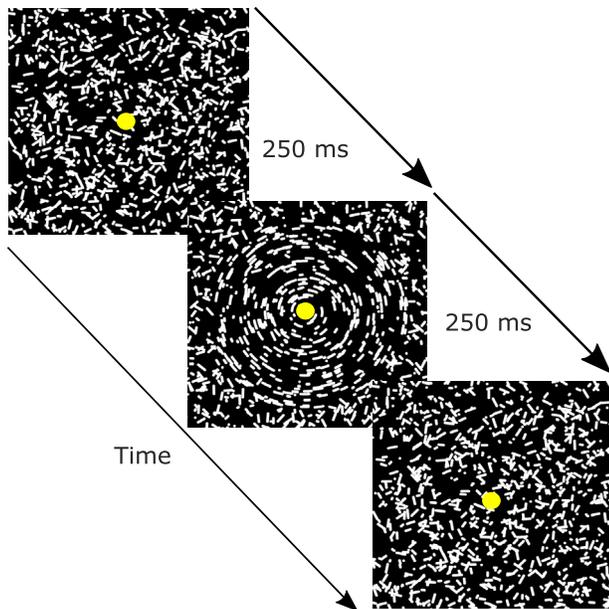
Figure 2. Example of the global form stimulus alternating between 100% coherence and 0% coherence. The figure also demonstrates the motion stimulus in which the arcs represent the trajectories of moving dots.

have been used and described in previous research (Wattam-Bell et al., 2010).

Trials alternated between 100% coherence and 0% coherence at a rate of four reversals/s. In the coherent phase, the line segments or dots aligned to create a circular form or rotational motion, respectively, as shown in Figure 2. In the incoherent phase, line segments or dots were oriented randomly within the display.

Participants were instructed to remain as still as possible during the EEG recording. A yellow fixation dot was present in the center of the display throughout the experiment, and participants were instructed to fixate this.

SSVEP recording

Recordings were made using a 128-electrode HydroCel Geodesic Sensor Net v.1.0 (Electrical Geodesics Inc., Eugene, OR) using the vertex as the reference. Impedance was measured at 20 Hz, and individual electrodes were adjusted so that impedance fell below 50 kΩ.

Stimuli were presented in alternating 10-s blocks of form and motion. The separate runs for each level of blur consisted of 10 blocks each of form and motion, giving a total of 200 cycles for each stimulus. Participants completed two runs per diffuser setting with the diffuser order randomized to avoid potential order effects.

SSVEP analysis

SSVEP signals were digitized at 250 samples/s and a low-pass filter was applied (20 Hz, 12 dB/octave). Channels were excluded if their standard deviation exceeded 800 μV, and the remaining channels were rereferenced to an average reference. VEP data was divided into 500-ms epochs (one stimulus cycle at 2 Hz), excluding any epochs with a total voltage excursion greater than 200 μV. Channels containing fewer than 30 artifact-free epochs were discarded. The preprocessing procedure was based on standard SSVEP practice (Odom et al., 2010; Picton et al., 2000).

F1 and F2

Fourier analysis was used to extract SSVEP amplitudes and phases at the fundamental frequency (F1 = 2 Hz) and the second harmonic (F2 = 4 Hz). The presence of a significant response at each harmonic was tested with the T^2_{circ} statistic (Victor & Mast, 1991) in both first-level (individual) and second-level (group) analyses as described in Wattam-Bell et al. (2010). This statistic is designed specifically for analyzing SSVEPs and provides a measure of the signal-to-noise ratio, taking into account the phase and amplitude of the signal at each harmonic.

The fundamental frequency (F1) at a rate of 2 Hz represented responses at the same frequency as the stimulus cycle. A significant F1 therefore represents activation in response to changes in the global structure of the stimuli with an asymmetric response to coherence onset versus offset.

A significant F2 (4 Hz) represents responses to changes in the stimulus configuration brought on by every stimulus switch. F2 therefore includes responses to local changes in the stimulus configuration. Neural responses to global changes may also be present in F2; however, F1 will only contain signal arising from global changes. This was verified by Braddick et al. (2006), who found that the amplitude of F1 dropped to zero as the coherence was reduced to 0%, for both form and motion stimuli, while F2 amplitudes remained consistently strong. A control experiment including a condition in which all stimuli were 0% coherent was run to check the contribution of global responses to F2 amplitudes; this is described in the Supplementary Material.

Comparability of form and motion stimuli

We used coherent form and motion stimuli that were matched as in previous studies (Atkinson & Braddick, 2005; Wattam-Bell et al., 2010) so that the regions of

	0 cm (+2.5D)	2 cm (+5.5D)	3 cm (+10D)
Mean acuity (LogMAR)	0.53	0.88	1.20

Table 1. Average visual acuity of three participants under the three blur conditions (with equivalent dioptric strength).

the visual field over which local form and motion information needs to be integrated are directly comparable. In other important respects, the stimuli cannot be made directly comparable—for example, because the motion case requires spatial integration over time, the moving stimulus is a dot (that describes a line over time). The stimuli thus have different spatial (and spatiotemporal) content—e.g., the motion stimuli (dots) have less low-spatial frequency information than the form stimuli (lines) although they also have temporal information that the form stimuli do not. Because of the presence of such differences, our analysis does not treat the stimuli as exactly matched in all respects except for the single difference of having form- versus motion-related coherence. We do not directly compare discrimination thresholds but first convert them to z-scores. We also do not directly compare F1 amplitudes but analyze them separately.

Visual blur

Blur was achieved using a diffuser placed over the screen, acting as a low-pass filter. The filter consisted of an A3, 800-μ polypropylene sheet (Gerprint, Peru) mounted onto a frame that stood in front of the monitor.

The distance between the filter and the screen was varied to create different levels of blur. The distances were selected to allow comparison with previous studies using dioptric blur (Barton et al., 1996; Braddick et al., 2007; Zwicker et al., 2006). To do this, three positive diopter lenses were initially selected: +2.5, +5.5, and +10. Three participants completed a binocular letter acuity chart at 60 cm on the test monitor while wearing each lens. The chart consisted of lines of letters selected at random from DHKNORSVZ and presented in the Sloan acuity font (Pelli, Robson, & Wilkinson, 1988). Letters were presented in lines of four with each line presenting successively smaller letters. When participants incorrectly identified two letters in a row, the test was stopped, and their acuity was calculated in LogMAR based on the viewing distance and letter size. After assessment with the lenses, participants had their acuity assessed using the filter at 0.5-cm distances from the monitor, and the distance producing a comparative acuity to the dioptric blur was noted. Based on this, distances of 0 cm, 2 cm, and 3 cm were found to reduce acuity to a comparable degree to the +2.5, +5.5, and +10 diopter lenses, respectively.
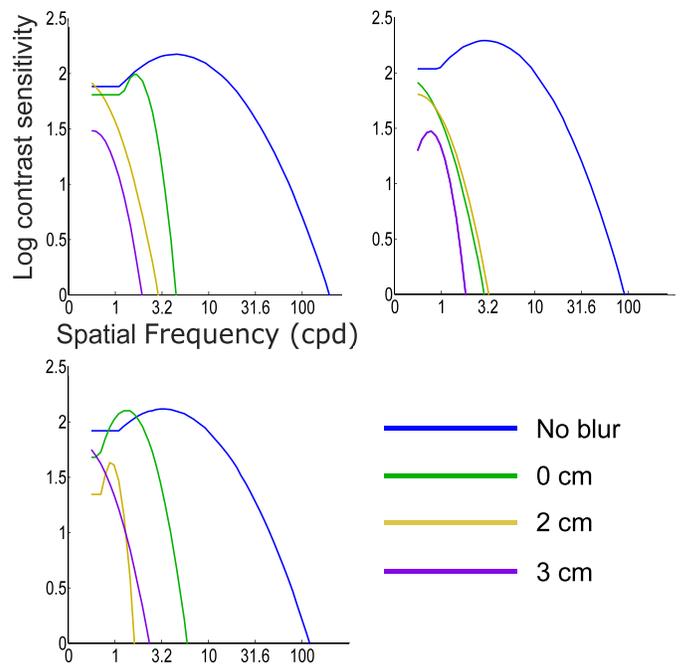

Figure 3. Contrast sensitivity functions for three individuals under the different blur levels. All three participants were at ceiling (13.5 c/°) in the no blur condition, so data above this value were derived from the fitted contrast sensitivity function.

Acuities for each blur level are reported in Table 1. Participants also had their acuity measured with no blur; however, due to limitations of the monitor, all results were at ceiling with the highest recordable acuity being 0.26 LogMAR.

In order to further assess the impact of blur on acuity and contrast sensitivity, the same three participants had their contrast sensitivity function measured at each blur level using the qCSF method (Lesmes, Lu, Baek, & Albright, 2010). Participants had to judge the side of the screen containing a 5.8° × 5.8° Gabor, which varied from trial to trial in both contrast and spatial frequency based on the qCSF staircase. Participants completed 100 trials at a distance of 60 cm, from which their contrast sensitivity function was plotted. Figure 3 shows contrast sensitivity functions for the three participants at each blur level. This demonstrates that there was a marked loss of contrast sensitivity at higher spatial frequencies, confirming that the diffuser was acting as a low-pass filter.

Results

Behavioral Tests

Both form and motion thresholds increased with increasing blur, indicating a worsening in performance
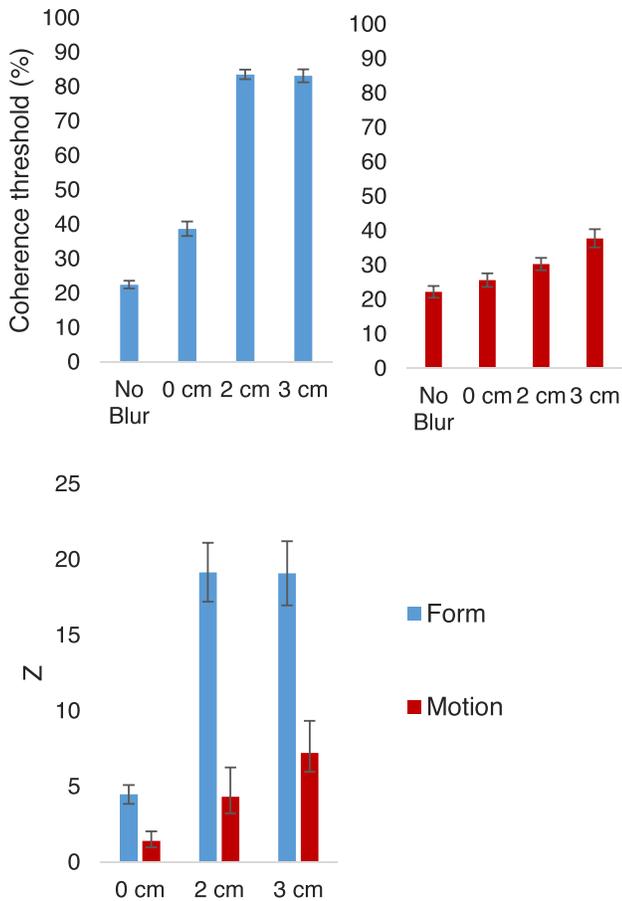
Figure 4. Global form (blue) and motion (red) coherence thresholds under four levels of blur as well as *z*-scores for the two tests. Error bars represent the standard error of the mean.

Figure 5. Group analysis of motion and form for each level of blur. These maps represent statistically significant T^2_{circ} values across scalp electrodes. These are projected onto a two-dimensional surface, interpolated onto a Cartesian grid, and mapped onto different colors according to the given scales representing the T^2_{circ} value. Areas plotted in green did not produce a significant T^2_{circ} response ($p > 0.05$). T^2_{circ} values above 5.65 were highly significant ($p < 0.001$). Views are given as from the top of the head.

as shown in Figure 4. Performance on both tasks was significantly reduced as a function of blur: motion, $F(3, 57) = 28.530$, $p < 0.001$; form, $F(3, 57) = 390.989$, $p < 0.001$. *Z*-scores were calculated for each level of blur against the baseline condition of no blur to allow comparison between form and motion results. These demonstrate that motion was relatively unaffected by blur in comparison to form (Figure 4). A two-way repeated-measures ANOVA on the *z*-scores showed a significant main effect of both blur, $F(2, 38) = 239.527$, $p < 0.001$, and test, $F(1,19) = 891.992$, $p < 0.001$, as well as a significant interaction between the two, $F(2, 38) = 124.366$, $p < 0.001$. This further confirms that blur had a differential effect on the two tests.

SSVEP

VEP topography

Figure 5 shows topographic plots of group-level T^2_{circ} values for the F1 and F2 responses to form and motion stimuli. The plots are thresholded at $p = 0.05$ corrected for false discovery rate (Benjamini & Hochberg, 1995)
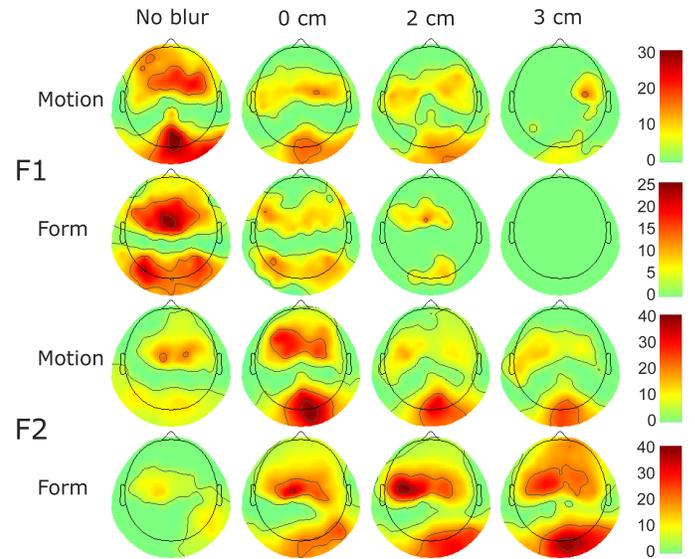
with nonsignificant values plotted in green (equivalent of $T^2_{circ} > 3.25$). T^2_{circ} values above 5.65 were highly significant ($p < 0.001$). Motion F1 responses showed peak activation over the occipital midline, and the form stimulus produced a lateralized F1 response. This pattern is consistent with previous findings with these stimuli (Wattam-Bell et al., 2010). Increasing blur led to an overall reduction in activation. This effect was greater for the form stimuli than the motion with the two highest levels of blur leading to a loss of the lateralized form response. F2 responses, which reflect local processing, at least in part, differed somewhat in their spatial patterning compared to F1. F2 activation was localized to the occipital midline for both form and motion at all blur levels. F2 T^2_{circ} values were lowest in the no blur condition for form and motion, indicating a low signal-to-noise ratio in the response. Form F2 T^2_{circ} values increased with blur, indicating a higher signal-to-noise ratio, and motion F2 T^2_{circ} values peaked in the 0-cm blur condition.

VEP amplitude

Regions of interest (ROIs) were selected for further analysis at both F1 and F2 as shown in Figure 6. The motion F1 ROI was located over the central occipital pole, and the form F1 ROI consisted of two regions located laterally over the occipital cortex. The F2 ROI
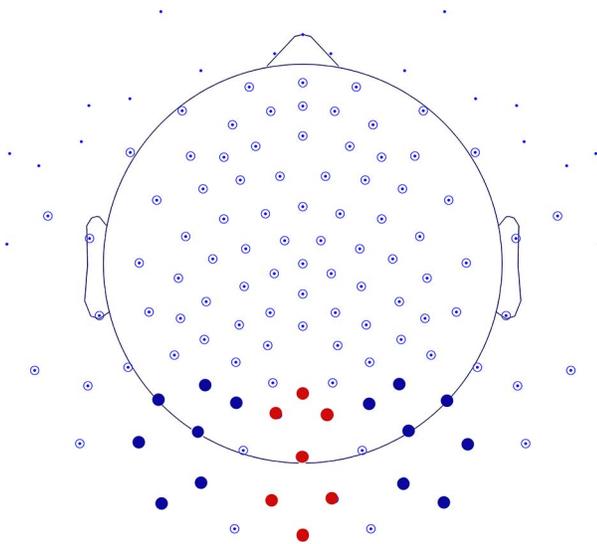
Figure 6. ROIs analyzed for the F1 motion data, shown in red, and F1 form data, shown in blue. The F2 ROI is also represented by the region shown in red.

for both motion and form was located over the central occipital pole. ROIs were selected based on the posterior channels showing the highest overall activation in Wattam-Bell et al. (2010). For each ROI, overall amplitude was calculated by vector-averaging the Fourier coefficients across all the channels comprising the ROI and then taking the absolute value of the average.

As described in the Methods and materials section, channels were excluded if their variance exceeded 800 μV. As a result, the form ROI included data from 279 channels out of a total of 280 (20 participants $\times$ 14 channels), and the motion ROI included data from 137 channels out of a total of 140 (20 participants $\times$ seven channels).

Mirroring the results seen in the topographic plots, F1 amplitude decreased in both form and motion ROIs with increasing blur (see Figure 7). A repeated-measures ANOVA with a Greenhouse-Geisser correction confirmed that amplitudes significantly varied between blur levels: $F(2.219, 42.162) = 6.790$, $p = 0.002$ (form); $F(2.203, 41.856) = 7.422$, $p = 0.001$ (motion). Plotting F1 amplitudes for both stimuli together using log axes (Figure 7) results in two near-parallel curves. This is consistent with an overall lower response to the form stimulus and with blur acting as a constant multiplicative factor for both stimuli.

There was no overall significant effect of blur on F2 amplitude: form, $F(2.103, 40.479) = 0.321$, $p = 0.741$; motion, $F(2.381, 45.233) = 1.147$, $p = 0.338$. Although there is some indication of blur-related changes in the topographic plots of significant T^2_{circ} (signal-to-noise ratio) in Figure 5, the amplitude measure showed no effect of blur on mean amplitudes in ROIs. In the
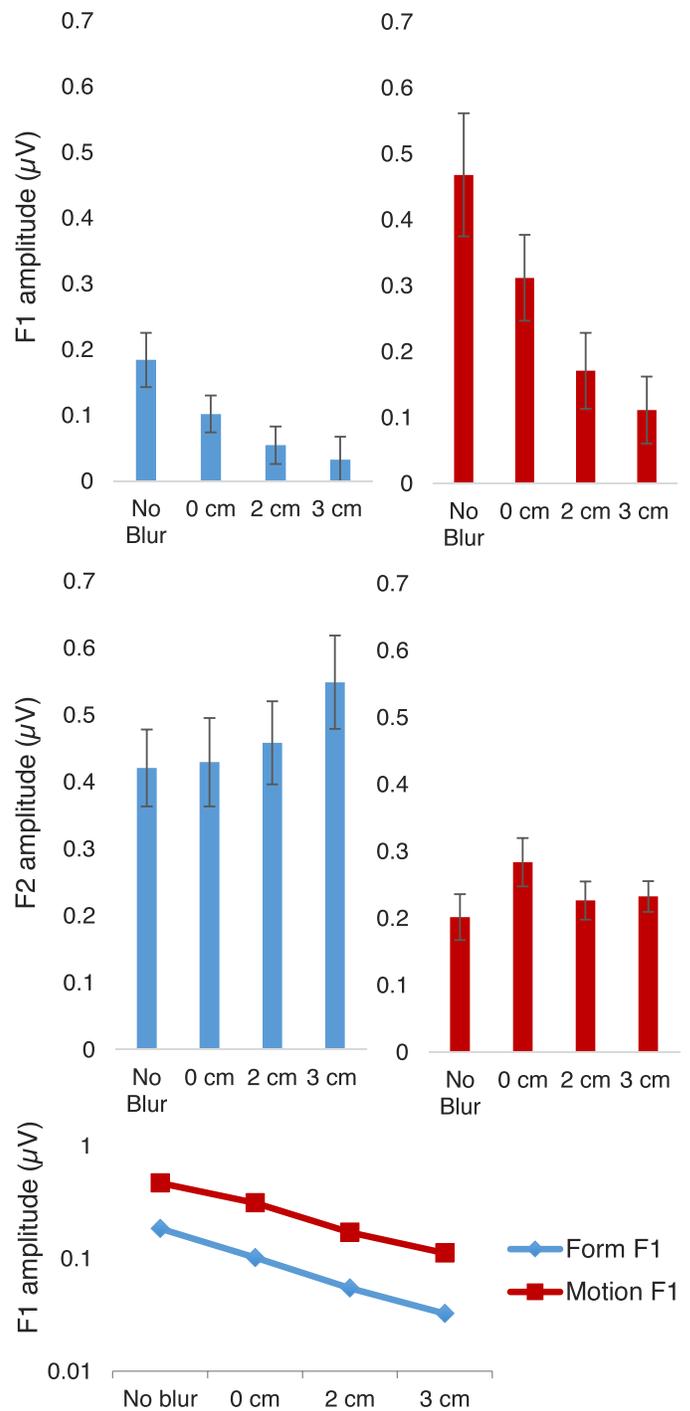

Figure 7. Group averaged F1 (top row) and F2 (middle row) ROI amplitudes (μV) for form (blue) and motion (red). The lower plot represents form and motion F1 amplitudes replotted on log axes. Error bars represent the standard error of the mean.

amplitude data plotted in Figure 7, the no blur conditions are not significantly reduced compared to the other blur conditions, which departs somewhat from the signal-to-noise T^2_{circ} pattern in Figure 5. Some deviations of this kind may arise because the amplitude and signal-to-noise measures are not identical. The T^2_{circ}

statistic depends not only on mean amplitude but also on the variability of phase and of amplitude across participants, and these kinds of variability can lead to differences between amplitude and signal-to-noise measures.

A control experiment including a condition in which all stimuli were 0% coherent (see Supplementary Material) found no evidence that global organization contributed to the amplitude of the F2 response. This supports the interpretation of the F2 amplitude as a measure of responses to local changes only.

Discussion

The results of the study show that blur decreases both behavioral and cortical responses to global form and motion but not to an equivalent degree.

Global form and motion discrimination thresholds were on average very similar (~22%) with no blur and became elevated with increasing blur. This indicates that high spatial frequencies contribute to both form and motion perception. However, form and motion were not equally affected. With increasing blur, form perception thresholds rose to more than 80%, approaching the measurement limit of a "100%" threshold. The loss of global form perception at mid and high blur levels indicates that high spatial frequencies are necessary for detecting coherent form in the current stimuli. Motion perception, however, remained functional, albeit impaired, suggesting that high spatial frequencies contribute but are not essential for detecting global motion in these stimuli. A comparison of z-scores confirms this differential effect on perceptual sensitivity.

The reason for these differences may lie in the pathways that process form and motion. Form perception has been argued to be processed predominantly by the ventral stream, which receives input from the parvocellular system, and motion perception is processed via the dorsal stream, which receives input from the magnocellular system (Livingstone & Hubel, 1988; Merigan & Maunsell, 1993). The parvo- and magnocellular systems differ in their relative contribution from high and low spatial frequencies with the parvocellular system favoring high and the magnocellular low spatial frequencies. Our results support this view in that form perception was more affected by the loss of high spatial frequencies than motion perception.

The finding of a reduction in F1 amplitude for both form and motion indicates that blur reduces the information used by the visual system in order to detect global organization within the stimuli. As high spatial frequency information is lost, neurons tuned to higher frequencies will be excluded from the analysis of the

image. As a result, the processing of increasingly blurred stimuli is likely to be carried out by increasingly smaller subpopulations of neurons. T^2_{circ} results show that statistically significant form VEP responses are lost at high levels of blur but maintained for motion (see Figure 5, Motion vs. Form F1 at 3 cm). This suggests that as blur increased there was reduced processing of global form patterns in associated brain regions. The fact that the motion system receives a greater input from lower spatial frequencies than the form system may explain why some neural activation was recorded even at high levels of blur.

F1 amplitudes were lower for form than for motion even with no blur. A comparison of these on log axes (Figure 7) suggests that blur-related amplitude changes for neural responses in the ROIs could be explained by blur having similar multiplicative effects for both kinds of stimuli. This would suggest that the form stimulus is distinctive only in having an overall lower neural response. However, this conclusion is at odds with the behavioral findings, in which discrimination thresholds with no blur were closely matched. This discrepancy may be due to a number of factors, including non-linearities in the mapping from ROI F1 amplitude to behavioral discrimination threshold and, crucially, the fact that VEP measures relate only to the case of 100% coherence, and threshold measures come from low-coherence stimuli. In summary, our behavioral results support the conclusion that sensitivity to coherent form versus motion in these stimuli is differentially affected by blur, and our EEG results suggest that at 100% coherence differences in amplitudes of cortical responses may be well explained simply by an overall lower response to form.

Although loss of information would explain reductions in F1 amplitude with blur, it would also predict reductions in F2 amplitude, related to processing of the local elements in primary visual cortex. Surprisingly, we found that F2 amplitudes were not significantly affected by blur. Because the F2 is a response to the broadband spatiotemporal transients occurring each time the stimulus switches between coherence levels, it is likely to involve magnocellular mechanisms. The magnocellular system's preference for low spatial frequencies could therefore explain why F2 was not strongly affected by removal of high spatial frequencies.

The results found are broadly consistent with the psychophysical data of Zwicker et al. (2006). They found global form coherence thresholds worsened rapidly with lenses stronger than +2D and +2.25D. This mirrors our finding as global form thresholds became impaired at blur levels comparable to those in our 2- and 3-cm conditions. Motion results were less affected by blur in Zwicker et al.'s study; however, some decrease was seen at the very highest level of blur tested

(+3.5D and +4D). This is similar to our findings in that motion thresholds were less affected than form thresholds by blur but showed some degree of impairment at high levels of blur. The present results are also broadly consistent with the psychophysical data of Braddick et al. (2007) on the effect of blur on form and motion coherence thresholds. They only found significant effects on form and motion thresholds with high levels of blur, +7D and +10D lenses, respectively, as did the current study in the 2- and 3-cm conditions.

Our results support previous findings into the interaction between spatial frequencies and dot displacement. Cleary and Braddick (1990) found that d_{max} increased when high spatial frequencies were filtered out of the stimulus. Blur producing a visual acuity of 3.56 c/° and below led to progressively higher d_{max}, indicating increased sensitivity. Similar results have been reported by Barton et al. (1996), who found reductions in motion coherence sensitivity for low dot displacement (<16′) under blur but not for higher dot displacement, concluding that high spatial frequencies are important for motion discrimination within this range. The current study used a dot displacement of 8.6′, falling within the low displacement range. These results have been attributed to multiple motion processing channels selective for specific spatial frequencies. At high dot displacements, high spatial frequency channels exceed their d_{max} and, as a result, begin to mask low spatial frequency channels. When these high spatial frequency channels are excluded, the masking does not occur, allowing low spatial frequency channels to function efficiently (Cleary & Braddick, 1990). This suggests that with larger dot displacements, thresholds may begin to improve with increasing blur in the current study.

Although stimuli were matched across the VEP and behavioral tests, the location of the stimuli on the display was not the same across the two tests. VEPs were presented centrally, and behavioral tests were presented to the left or right of fixation. Because the coherent pattern subtended 16°, when either the center was fixated (VEP) or a region near the edge was fixated (behavior), some of the stimulus was in the periphery. However, in behavioral tests, a greater proportion of the coherent stimulus was in the periphery. This difference might be expected to bias the behavioral measure to show a greater relative advantage for motion versus form than the VEP measure. Consistent with this, the behavioral but not the VEP measure shows a form advantage that could not be explained by a mismatch in initial (unblurred) response. However, conclusions from direct comparisons of VEP and behavioral measures are also limited because all VEP measures were at 100% coherence.

One of the aims of the study was to establish whether poor sensitivity at high spatial frequencies could account for reduced form or motion perception in developmental and clinical groups. Acuity and contrast sensitivity develop rapidly over the first year of life as reported by both behavioral and VEP data (Atkinson & Braddick, 1981; Atkinson et al., 1977a, b; Norcia & Tyler, 1985). Behavioral studies report acuity reaching ~12 c/° by 12 months (Atkinson, 2000), and sweep VEP demonstrates acuities up to 20 c/° (Norcia & Tyler, 1985) with differences in results likely due to variations in stimuli and methodology. Form and motion perception also show rapid development over the first year with motion perception emerging first around 6–8 weeks of age (Wattam-Bell, 1996) followed by form from 12 weeks (Atkinson et al., 2004). VEP results (Wattam-Bell et al., 2010) show that at age 5 months global motion processing is advanced over that for global form. The earlier development of motion over form perception in early infancy is consistent with our finding that blurred conditions in which high spatial frequency content is reduced favored motion perception. However, the developmental trajectory of form and motion perception throughout childhood diverges from that of acuity and contrast sensitivity, suggesting other factors have a greater bearing on their development.

Visual acuity and contrast sensitivity progress to adult-like levels during the preschool years. For example, Atkinson et al. (1981) tested 30 preschool children (aged 3–5 years) using a grating detection task and found all but three had vision comparable to 6/6 or 30 c/°. In contrast to acuity, global form and motion show a slower rate of development (Atkinson & Braddick, 2005; Gunn et al., 2002; Hadad et al., 2011). Gunn et al. (2002) tested typically developing 4-year-olds with close to adult-level acuity using a 2AFC paradigm and found form and motion coherence thresholds were 23% and 34.2%, respectively, compared to 15.6% (form) and 23.5% (motion) in adults. Form thresholds became adult-like at 6 years of age, and motion thresholds were not adult-like until 10–11 years of age. If the contrast sensitivity function was the limiting factor in the development of global form and motion, then the maturation of maximum acuity would be expected to coincide with the maturation of these other skills, which is not the case. Loss of high spatial frequencies, although clearly impacting on form and motion perception, is insufficient to explain their developmental trajectories. In particular, the development of global motion sensitivity is more prolonged than for global form although our results show that the latter is more dependent on high spatial frequencies.

The differences between form and motion perception observed in the current study diverge from what is seen in both developmental and clinical populations. Our

study found form perception was more impaired by blur than motion perception. In clinical populations, it is overwhelmingly motion perception that shows the greater impairment, indicating a selective vulnerability of the dorsal stream (Atkinson et al., 2003; Atkinson et al., 1997; Braddick et al., 2003; Gunn et al., 2002; Spencer et al., 2000). This suggests that factors other than spatial frequency sensitivity are the key to constraining form and motion coherence thresholds in development.

The results suggest that when working with developmental and low vision groups, global form and motion sensitivity are unlikely to be directly influenced by acuity unless acuity is reduced significantly (<1 LogMAR). This is supported by results from low vision patients with congenital achromatopsia who show reduced global form and motion sensitivity independent of acuity and contrast sensitivity results (Burton et al., 2013). For groups with very low vision, stimuli should be carefully controlled to ensure that they are suitably designed for the group being studied. This may involve, for example, increasing the contrast of stimuli presented and/or the size of stimuli to ensure they are effectively resolved. However, it is unlikely that poor acuity and contrast sensitivity are primarily responsible for the effects that have been reported in either typical or atypical development.

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References

Atkinson, J. (2000). Newborn vision. In *The developing visual brain* (pp. 43–57). Oxford, UK: Oxford University Press.

Atkinson, J., & Braddick, O. (1981). Acuity, contrast sensitivity and accommodation in infancy. In R. N. Aslin, J. R. Alberts, M. R. Petersen (Eds.), *The development of perception* (Vol. 2, pp. 245–278). New York: The Academic Press.

Atkinson, J., & Braddick, O. (2005). Dorsal stream vulnerability and autistic disorders: The importance of comparative studies of form and motion coherence in typically developing children and children with developmental disorders. *Cahiers de Psychologie Cognitive, 23*(1–2), 49–58.

Atkinson, J., & Braddick, O. (2007). Visual and visuocognitive development in children born very prematurely. *Progress in Brain Research, 164*, 123. [PubMed]

Atkinson, J., & Braddick, O. (2011). From genes to brain development to phenotypic behavior: "Dorsal-stream vulnerability" in relation to spatial cognition, attention, and planning of actions in Williams syndrome (WS) and other developmental disorders. *Progress in Brain Research, 189*, 261, doi:10.1016/B978-0-444-53884-0.00029-4. [PubMed]

Atkinson, J., Braddick, O., Anker, S., Curran, W., Andrew, R., Wattam-Bell, J., & Braddick, F. (2003). Neurobiological models of visuospatial cognition in children with Williams syndrome: Measures of dorsal-stream and frontal function. *Developmental Neuropsychology, 23*(1–2), 139–172. [PubMed]

Atkinson, J., Braddick, O., & Moar, K. (1977a). Development of contrast sensitivity over the first 3 months of life in the human infant. *Vision Research, 17*(9), 1037–1044. [PubMed]

Atkinson, J., Braddick, O., & Moar, K. (1977b). Infants' detection of image defocus. *Vision Research, 17*, 1125–1126. [PubMed]

Atkinson, J., French, J., & Braddick, O. (1981). Contrast sensitivity function of preschool children. *British Journal of Ophthalmology, 65*(8), 525–529. [PubMed]

Atkinson, J., King, J., Braddick, O., Nokes, L., Anker, S., & Braddick, F. (1997). A specific deficit of dorsal stream function in Williams' syndrome. *Neuroreport, 8*(8), 1919–1922. [PubMed]

Atkinson, J., Wattam-Bell, J., Braddick, O., Birtles, D., Barnett, A., & Cowie, D. (2004). Form vs motion coherence sensitivity in infants: The dorsal/ventral developmental debate continues. *Journal of Vision, 4*(8):32, doi:10.1167/4.8.32. [Abstract]

Barton, J. J. S., Rizzo, M., Nawtrot, M., & Simpson, T. (1996). Optical blur and the perception of global coherent motion in random dot cinematograms. *Vision Research, 36*(19), 3051–3059, doi:10.1016/0042-6989(96)00063-6. [PubMed]

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, *57*(1), 289–300.

Birch, E. E., & Stager, D. R. (1988). Prevalence of good visual acuity following surgery for congenital unilateral cataract. *Archives of Ophthalmology*, *106*(1), 40. [PubMed]

Braddick, O., Akthar, F., Anker, S., & Atkinson, J. (2007). Global form and global motion sensitivity are equally resistant to blur [Abstract]. *Perception*, *36*, 58.

Braddick, O., Atkinson, J., & Wattam-Bell, J. (2003). Normal and anomalous development of visual motion processing: Motion coherence and "dorsal-stream vulnerability". *Neuropsychologia, 41*(13), 1769–1784. [PubMed]

Braddick, O., Birtles, D., Mills, S., Warshafsky, J., Wattam-Bell, J., & Atkinson, J. (2006). Brain responses to global perceptual coherence. *Journal of Vision, 6*(6):426, doi:10.1167/6.6.426. [Abstract]

Braddick, O., O'Brien, J. M., Wattam-Bell, J., Atkinson, J., Hartley, T., & Turner, R. (2001). Brain areas sensitive to coherent visual motion. *Perception, 30*(1), 61–72. [PubMed]

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10*, 433–436.

Burton, E., Wattam-Bell, J., Nishiguchi, K., Sundaram, V., Aboshiha, J., Webster, A., . . . Nardini, M. (2013). Cortical visual processing in patients with congenital achromatopsia: Coherent form, motion and biological motion perception. *Journal of Vision, 13*(9):21, doi:10.1167/13.9.21. [Abstract]

Cleary, R., & Braddick, O. J. (1990). Masking of low frequency information in short-range apparent motion. *Vision Research, 30*(2), 317–327. doi:10.1016/0042-6989(90)90046-N. [PubMed]

Ellemberg, 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*(2), 169–180.

Ellemberg, D., Lewis, T. L., Maurer, D., & Brent, H. P. (2000). Influence of monocular deprivation during infancy on the later development of spatial and temporal vision. *Vision Research, 40*(23), 3283–3295, doi:10.1016/S0042-6989(00)00165-6.

Ellemberg, D., Lewis, T. L., Maurer, D., Lui, C. H., & Brent, H. P. (1999). Spatial and temporal vision in patients treated for bilateral congenital cataracts. *Vision Research, 39*(20), 3480–3489, doi:10.1016/S0042-6989(99)00078-4.

Enoch, J. M., & Williams, R. A. (1983). Development of clinical tests of vision: Initial data on two hyperacuity paradigms. *Perception & Psychophysics, 33*(4), 314–322, doi:10.3758/BF03205878. [PubMed]

Essock, E. A., Williams, R. A., Enoch, J. M., & Raphael, S. (1984). The effects of image degradation by cataract on vernier acuity. *Investigative Ophthalmology & Visual Science, 25*(9), 1043–1050. [PubMed] [Article]

Gallant, J. L., Shoup, R. E., & Mazer, J. A. (2000). A human extrastriate area functionally homologous to macaque V4. *Neuron, 27*(2), 227–235, doi:10.1016/S0896-6273(00)00032-5.

Golarai, G., Liberman, A., Yoon, J. M. D., & Grill-Spector, K. (2010). Differential development of the ventral visual cortex extends through adolescence. *Frontiers in Human Neuroscience, 3*(80), 1–19, doi:10.3389/neuro.09.080.2009.

Gunn, A., Cory, E., Atkinson, J., Braddick, O., Wattam-Bell, J., Guzzetta, A., & Cioni, G. (2002). Dorsal and ventral stream sensitivity in normal development and hemiplegia. *Neuroreport, 13*(6), 843–847. [PubMed]

Hadad, B.-S., Maurer, D., & Lewis, T. L. (2011). Long trajectory for the development of sensitivity to global and biological motion. *Developmental Science, 14*(6), 1330–1339, doi:10.1111/j.1467-7687.2011.01078.x. [PubMed]

Harvey, B. M., Braddick, O. J., & Cowey, A. (2010). Similar effects of repetitive transcranial magnetic stimulation of MT+ and a dorsomedial extrastriate site including V3A on pattern detection and position discrimination of rotating and radial motion patterns. *Journal of Vision, 10*(5):21, 1–15, doi:10.1167/10.5.21. [PubMed] [Article]

Hou, C., Gilmore, R. O., Pettet, M. W., & Norcia, A. M. (2009). Spatio-temporal tuning of coherent motion evoked responses in 4-6 month old infants and adults. *Vision Research, 49*(20), 2509–2517, doi:0.1016/j.visres.2009.08.007.

Jacobson, S. G., Mohindra, I., & Held, R. (1981). Development of visual acuity in infants with congenital cataracts. *The British Journal of Ophthalmology, 65*(10), 727–735.

Kogan, C. S., Bertone, A., Cornish, K., Boutet, I., Kaloustian, V. M. D., Andermann, E., . . . Chaudhuri, A. (2004). Integrative cortical dysfunction and pervasive motion perception deficit in fragile X syndrome. *Neurology, 63*(9), 1634–1639, doi:10.1212/01.WNL.0000142987.44035.3B. [PubMed]

Kontsevich, L. L., & Tyler, C. W. (1999). Bayesian adaptive estimation of psychometric slope and

threshold. *Vision Research, 39*(16), 2729–2737, doi: 10.1016/S0042-6989(98)00285-5.

Kovács, I., Kozma, P., Fehér, Á., & Benedek, G. (1999). Late maturation of visual spatial integration in humans. *Proceedings of the National Academy of Sciences, USA, 96*(21), 12204–12209, doi:10.1073/pnas.96.21.12204.

Kugelberg, U. (1992). Visual acuity following treatment of bilateral congenital cataracts. *Documenta Ophthalmologica. Advances in Ophthalmology, 82*(3), 211–215. [PubMed]

Legge, G. E., Pelli, D. G., Rubin, G. S., & Schleske, M. M. (1985). Psychophysics of reading—I. Normal vision. *Vision Research, 25*(2), 239–252, doi:10.1016/0042-6989(85)90117-8. [PubMed]

Lesmes, L. A., Lu, Z.-L., Baek, J., & Albright, T. D. (2010). Bayesian adaptive estimation of the contrast sensitivity function: The quick CSF method. *Journal of Vision, 10*(3):17, 1–21, doi:10.1167/10.3.17. [PubMed] [Article]

Lewis, T. L., Ellemberg, D., Maurer, D., Wilkinson, F., Wilson, H. R., Dirks, M., & Brent, H. P. (2002). Sensitivity to global form in glass patterns after early visual deprivation in humans. *Vision Research, 42*(8), 939–948, doi:10.1016/S0042-6989(02)00041-X.

Lewis, T. L., Maurer, D., & Brent, H. P. (1995). Development of grating acuity in children treated for unilateral or bilateral congenital cataract. *Investigative Ophthalmology & Visual Science, 36*(10), 2080–2095. [PubMed] [Article]

Livingstone, M., & Hubel, D. (1988, May 6). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science, 240,* 740–749. [PubMed]

Maurer, D., & Lewis, T. L. (2001). Visual acuity: The role of visual input in inducing postnatal change. *Clinical Neuroscience Research, 1*(4), 239–247.

Merigan, W. H., & Maunsell, J. H. R. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience, 16*(1), 369–402, doi:10.1146/annurev.ne.16.030193.002101. [PubMed]

Norcia, A. M., Pei, F., Bonneh, Y., Hou, C., Sampath, V., & Pettet, M. W. (2005). Development of sensitivity to texture and contour information in the human infant. *Journal of Cognitive Neuroscience, 17*(4), 569–579, doi:10.1162/0898929053467596. [PubMed]

Norcia, A. M., & Tyler, C. W. (1985). Spatial frequency sweep VEP: Visual acuity during the first year of life. *Vision Research, 25*(10), 1399–1408. [PubMed]

Norcia, A. M., Tyler, C. W., & Hamer, R. D. (1990).

Development of contrast sensitivity in the human infant. *Vision Research, 30*(10), 1475–1486. [PubMed]

Odom, J. V., Bach, M., Brigell, M., Holder, G. E., McCulloch, D. L., & Tormene, A. P. (2010). ISCEV standard for clinical visual evoked potentials (2009 update). *Documenta Ophthalmologica, 120*(1), 111–119. [PubMed]

Ostwald, D., Lam, J. M., Li, S., & Kourtzi, Z. (2008). Neural coding of global form in the human visual cortex. *Journal of Neurophysiology, 99*(5), 2456–2469, doi:10.1152/jn.01307.2007. [PubMed]

Palomares, M., Pettet, M., Vildavski, V., Hou, C., & Norcia, A. (2009). Connecting the dots: How local structure affects global integration in infants. *Journal of Cognitive Neuroscience, 22*(7), 1557–1569, doi:10.1162/jocn.2009.21323.

Pelli, D. G., Robson, J. G., & Wilkinson, A. J. (1988). The design of a new letter chart for measuring contrast sensitivity. *Clinical Vision Sciences, 2*(3), 187–199, doi:10.1.1.321.5971.

Picton, T. W., Bentin, S., Berg, P., Donchin, E., Hillyard, S. A., Johnson, R., Jr., . . . Taylor, M. J. (2000). Guidelines for using human event-related potentials to study cognition: Recording standards and publication criteria. *Psychophysiology, 37*(2), 127–152. [PubMed]

Rees, G., Friston, K., & Koch, C. (2000). A direct quantitative relationship between the functional properties of human and macaque V5. *Nature Neuroscience, 3*(7), 716–723, doi:10.1038/76673. [PubMed]

Spencer, J., O'Brien, J., Riggs, K., Braddick, O., Atkinson, J., & Wattam-Bell, J. (2000). Motion processing in autism: Evidence for a dorsal stream deficiency. *Neuroreport, 11*(12), 2765–2767. [PubMed]

Taylor, N. M., Jakobson, L. S., Maurer, D., & Lewis, T. L. (2009). Differential vulnerability of global motion, global form, and biological motion processing in full-term and preterm children. *Neuropsychologia, 47*(13), 2766–2778. [PubMed]

Victor, J. D., & Mast, J. (1991). A new statistic for steady-state evoked potentials. *Electroencephalography and Clinical Neurophysiology, 78*(5), 378–388.

Wattam-Bell, J. (1996). Visual motion processing in one-month-old infants: Habituation experiments. *Vision Research, 36*(11), 1679–1685, doi:10.1016/0042-6989(95)00237-5.

Wattam-Bell, J., Birtles, D., Nyström, P., von Hofsten, C., Rosander, K., Anker, S., . . . Braddick, O. (2010). Reorganization of global form and motion processing during human visual development.

Current Biology, 20(5), 411–415, doi:10.1016/j.cub.2009.12.020.

Weinstein, J. M., Gilmore, R. O., Shaikh, S. M., Kunselman, A. R., Trescher, W. V., Tashima, L. M., . . . Fesi, J. D. (2012). Defective motion processing in children with cerebral visual impairment due to periventricular white matter damage. *Developmental Medicine & Child Neurology, 54*(7), e1–e8, doi:10.1111/j.1469-8749.2010.03874.x.

Westheimer, G., & McKee, S. P. (1980). Stereoscopic acuity with defocused and spatially filtered retinal images. *Journal of the Optical Society of America, 70*(7), 772–778, doi:10.1364/JOSA.70.000772.

Wilkinson, F., James, T. W., Wilson, H. R., Gati, J. S., Menon, R. S., & Goodale, M. A. (2000). An fMRI study of the selective activation of human extrastriate form vision areas by radial and concentric gratings. *Current Biology, 10*(22), 1455–1458, doi:10.1016/S0960-9822(00)00800-9. [PubMed]

Williams, R. A., Enoch, J. M., & Essock, E. A. (1984). The resistance of selected hyperacuity configurations to retinal image degradation. *Investigative Ophthalmology & Visual Science, 25*(4), 389–399. [PubMed] [Article]

Zwicker, A. E., Hoag, R. A., Edwards, V. T., Boden, C., & Giaschi, D. E. (2006). The effects of optical blur on motion and texture perception. *Optometry and Vision Science, 83*(6), 382–390, doi:10.1097/01.opx.0000222919.21909.1e. [PubMed]