



Deposited via The University of York.

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/id/eprint/136110/>

Version: Published Version

Article:

Maloney, Ryan Thomas, Kaestner, Milena, Bruce, Alison et al. (2018) Sensitivity to velocity- and disparity-based cues to motion-in-depth with and without spared stereopsis in binocular visual impairment. *Investigative ophthalmology & visual science*. pp. 4375-4383. ISSN: 0146-0404

<https://doi.org/10.1167/iovs.17-23692>

Reuse

This article is distributed under the terms of the Creative Commons Attribution (CC BY) licence. This licence allows you to distribute, remix, tweak, and build upon the work, even commercially, as long as you credit the authors for the original work. More information and the full terms of the licence here:

<https://creativecommons.org/licenses/>

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.

Sensitivity to Velocity- and Disparity-Based Cues to Motion-In-Depth With and Without Spared Stereopsis in Binocular Visual Impairment

Ryan T. Maloney,¹ Milena Kaestner,¹ Alison Bruce,² Marina Bloj,³ Julie M. Harris,⁴ and Alex R. Wade¹

¹Department of Psychology, The University of York, York, United Kingdom

²Bradford Institute for Health Research, Bradford Teaching Hospitals NHS Foundation Trust, Bradford, United Kingdom

³School of Optometry and Vision Science, University of Bradford, Bradford, United Kingdom

⁴School of Psychology and Neuroscience, University of St. Andrews, St. Andrews, United Kingdom

Correspondence: Alex R. Wade, Department of Psychology, University of York, York YO10 5DD, UK; wade@wadelab.net.

Submitted: February 13, 2018

Accepted: July 31, 2018

Citation: Maloney RT, Kaestner M, Bruce A, Bloj M, Harris JM, Wade AR. Sensitivity to velocity- and disparity-based cues to motion-in-depth with and without spared stereopsis in binocular visual impairment. *Invest Ophthalmol Vis Sci.* 2018;59:4375-4383. <https://doi.org/10.1167/iovs.17-23692>

PURPOSE. Two binocular sources of information serve motion-in-depth (MID) perception: changes in disparity over time (CD), and interocular velocity differences (IOVD). While CD requires the computation of small spatial disparities, IOVD could be computed from a much lower-resolution signal. IOVD signals therefore might still be available under conditions of binocular vision impairment (BVI) with limited or no stereopsis, for example, amblyopia.

METHODS. Sensitivity to CD and IOVD was measured in adults who had undergone therapy to correct optical misalignment or amblyopia in childhood ($n = 16$), as well as normal vision controls with good stereoacuity ($n = 8$). Observers discriminated the interval containing a smoothly oscillating MID “test” stimulus from a “control” stimulus in a two-interval forced choice paradigm.

RESULTS. Of the BVI observers with no static stereoacuity ($n = 9$), one displayed evidence for sensitivity to IOVD only, while there was otherwise no sensitivity for either CD or IOVD in the group. Generally, BVI observers with measurable stereoacuity ($n = 7$) displayed a pattern resembling the control group: showing a similar sensitivity for both cues. A neutral density filter placed in front of the fixing eye in a subset of BVI observers did not improve performance.

CONCLUSIONS. In one BVI observer there was preserved sensitivity to IOVD but not CD, though overall only those BVI observers with at least gross stereopsis were able to detect disparity- or velocity-based cues to MID. The results imply that these logically distinct information sources are somehow coupled, and in some cases BVI observers with no stereopsis may still retain sensitivity to IOVD.

Keywords: 3D motion, strabismus, binocular vision, amblyopia, motion perception

Two binocular sources of information can, in principle, be used to perceive motion-in-depth (MID): the change in disparity (CD) between the two retinae over time and the relative motion velocities on the two retinae (interocular velocity differences, or IOVD). The study of binocular motion perception has been relatively neglected in favor of 2D or frontoparallel motion, and consequently the mechanisms of MID perception remain poorly understood.^{1,2}

A recent series of studies have shown that cells in area V5/MT of the macaque encode MID on the basis of CD and IOVD cues,^{3,4} while functional neuroimaging in humans indicates a similar selectivity in extrastriate area V5/MT.⁵⁻⁷ Psychophysical investigations suggest that CD and IOVD have distinct spatiotemporal properties,⁸⁻¹² and individual observers appear to weigh the two cues differently in MID perception, with some favoring one cue over the other.¹³⁻¹⁵

While both CD and IOVD can result in a perception of MID, they are computationally distinct in theoretically important ways. For CD, MID is computed by first detecting binocular disparities and then comparing their change over time.^{16,17}

Thus, CD requires the accurate spatial matching of the two eyes' views in the primary visual cortex (V1) or beyond. Binocular vision impairment (BVI) such as strabismic amblyopia is linked to dysfunction in V1 and disruption to stereoscopic processing,^{18,19} and therefore CD should be abolished in such conditions.²⁰ Alternatively, an IOVD-based mechanism contributes to MID perception by first detecting the velocities of motion signals separately at a monocular level and then compares these interocular velocity differences. Therefore, IOVD does not necessarily require the fine spatial matches demanded by a CD-based mechanism and could conceivably survive in amblyopia.

Interestingly, the resurgence of stereoscopic films in mainstream cinema has led to increasing reports of three-dimensional (3D) effects in individuals with otherwise no measurable static stereopsis in clinical tests.²¹ This has been attributed to the dynamic nature of the 3D films: dynamic disparity information facilitates lower disparity thresholds than does static disparity.^{13,22} Latent stereopsis has also been demonstrated in subsets of stereo-deficient patients with



strabismus and/or amblyopia when tested with dynamic stereomotion displays.^{23,24} Furthermore, in their measurements of static stereopsis and MID sensitivity in a large sample of normal vision observers, Allen et al.¹³ found that a significant proportion could be classified as “stereoanomalous”: possessing static sensitivity no greater than chance, yet reasonable sensitivity to CD or IOVD (or sometimes both). Moving stereoscopic images also contain IOVD information, and some preliminary work has hinted that binocular motion processing may be spared in strabismic and/or amblyopic populations with poor or no measurable stereopsis. Maeda et al.²⁵ reported that almost half of their sample of patients with infantile or late-onset esotropia were able to discriminate MID based on IOVD information in a simple four-alternative forced choice task, despite a lack of fine stereopsis, whereas Watanabe et al.²⁶ reported that a handful of strabismic patients with no measurable static stereopsis were still able to detect MID signals, although it is not clear whether they were relying on CD, IOVD, or both cues (the authors suggest it was primarily IOVD). While CD requires the accurate computation of small spatial disparities, IOVD could, in principle, be computed from a much lower-resolution signal and be responsible for such experiences of MID in populations with impaired binocular vision and poor stereopsis.^{22,25}

Overall, in this study we measured the perceptual sensitivity (defined as the inverse of the motion coherence threshold) to both the CD and IOVD cues in a sample of 16 adult observers who had all received treatment for BVI as children, as well as in eight age-matched controls with no history of visual problems and demonstrable stereoacuity. In particular, we did so using a powerful two-interval forced choice (2IFC) psychophysical paradigm with carefully controlled and balanced stimuli that provided excellent theoretical isolation of the two cues. In our BVI sample, we found that observers with no measurable static stereopsis generally displayed no sensitivity for either CD or IOVD cues, except for one observer who showed greater than chance sensitivity to IOVD, but not CD. This one interesting case provides anecdotal support for the hypothesis that sensitivity to IOVD might be preserved even in the absence of stereopsis. Sensitivity to CD and IOVD in the remaining BVI observers who did possess some measurable static stereopsis was similar to the control group.

While the amblyopic visual cortex was previously thought to result from a failure in the development of binocular neurons during the critical period of visual development,²⁷⁻²⁹ recent evidence suggests that in adult amblyopes intact binocular mechanisms may still exist that are in fact obscured by interocular suppression during binocular viewing that favors the fellow/fixing (or nonamblyopic) eye (see Ref. 30 for review). Baker et al.,³¹ for example, found that binocular summation in adult amblyopes could reach normal levels by adjusting the contrast of the stimulus presented to the amblyopic eye so that it was as strong as that in the fellow eye (in terms of multiples of the detection threshold). Furthermore, such interocular suppression effects in amblyopia have also been shown at the cellular level, whereby increasing the contrast presented to the amblyopic eye decreased responses at binocular cortical sites in macaque V1 and V2.³² Accordingly, Hess et al.²³ also measured MID sensitivity in four of their amblyopic observers with a neutral density (ND) filter placed in front of the fellow/fixing eye, their rationale being that it would introduce some temporal delay in processing and/or decrease luminance reaching the fellow eye, releasing the amblyopic eye from interocular suppression and potentially improving perceptual performance.²³ They found that doing so improved performance on MID conditions but not on tests of static stereopsis for these observers, nor did it

alter performance for normal control observers. As such, we followed Hess et al.²³ by running a follow-up experiment where a subset of BVI and control observers repeated the experiment but with a ND filter placed in front of the fellow or dominant eye, respectively. Unlike Hess et al.,²³ however, we did not find any overall change in sensitivity for either group of observers when comparing performance with the ND filter to that without. The approach adopted here helps resolve some of the ambiguity surrounding MID perception in BVI populations through the examination of CD and IOVD cues separately. In general, it largely strengthens the existing view that IOVD and CD detection depends on brain mechanisms that are separate yet complementary,^{1,5,33} though it also suggests that sensitivity to MID cues in adults with BVI is even more complicated than with normal vision controls. It seems that some BVI observers with no static stereopsis may still retain sensitivity to IOVD information, but as with normal vision observers, sensitivity to CD or IOVD seems to have a large individual differences component.^{13,15}

METHODS

Participants

All experimental procedures were approved by the Human Research Ethics Committee of the Department of Psychology at the University of York and conformed to the precepts of the Declaration of Helsinki. Observers (all adults) provided written informed consent and were recruited via advertisements and participant pools from the local community in and around the University of York. The advertisement was titled “Did you ever need to wear an eye patch as a child?” and asked whether individuals met any (or all) of the following criteria: that they have, or have had, amblyopia (“lazy eye”); that they have, or have had, strabismus (“squint”); or whether they have problems seeing 3D films at the cinema. Initially, 17 observers in total were tested, although one declined to continue the study due to discomfort in viewing the IOVD stimulus. The resulting final sample of observers ($n = 16$, mean age = 24.3, range 18–47 years, three male) represented a heterogeneous mix of clinical characteristics (summarized in the Table), although all had at some point received a clinical diagnosis of amblyopia during childhood and had received occlusion therapy. The type of BVI was based on observer history, and the type of strabismus was confirmed with a cover test. Several observers had also undergone strabismus surgery as children. All reported difficulty or discomfort in viewing 3D films at the cinema. In addition, eight control observers (mean age = 25.5 years, three male) with no history of any visual or neurologic impairment were also tested in the same way as the clinical group.

All BVI observers were tested while wearing their refractive prescription spectacles, except for some who either had no refractive correction or did not routinely wear them in their day-to-day interactions with video displays (e.g., observer 3). Visual acuity for all observers was measured monocularly with the aid of a lorgnette occluder at 3 m using the Early Treatment Diabetic Retinopathy Study logMAR acuity chart (National Vision Research Institute, Melbourne, Australia). Static stereoscopic acuity thresholds were also measured for all observers according to the TNO test³⁴ and another stereopsis test (Frisby Near Stereotest; Stereotest Ltd., Sheffield, UK) at 40 cm with spectacles if worn. Nine of the 16 BVI observers had no measurable static stereopsis on either test, while in the remaining seven BVI observers some degree of stereopsis was measurable in one or both of these tests. Accordingly, we divided the BVI group along these lines in our subsequent

TABLE. Demographic and Clinical Details of BVI and Control Observers

ID	Age, y/Sex	VA, logMAR		Static Stereoacuity, Arcsec		Binocularity Description
		Right	Left	TNO Test, 40 cm	Frisby Near Stereotest, 40 cm	
1	21.4/F	0.04	0.04	None	None	Bilateral exotropia from 15 months of age. Occlusion therapy of left eye until strabismus surgery at age 3.
2	20.5/F	0.1	0.2	60	340	Left exotropia manifested at age 4 and again age 13; prism therapy as teenager.
3	20.4/F	-0.16	-0.16	60	85	Left intermittent exotropia from age 2. Occlusion therapy until age 5.
4*	21.8/F	-0.06	0.24	None	None	Left exotropia. Prism therapy from age 5; occlusion from ages 7-9. Strabismus surgery suggested at age 9 but declined.
5	21/F	0.94	1.06	None	None	Septo-optic dysplasia, optic nerve hypoplasia, nystagmus, astigmatism, amblyopia, and left exotropia manifested from birth. Hypopituitarism, though no growth problems. Occlusion therapy of right eye from late infancy.
6	23/F	-0.08	-0.08	60	340	Left exotropia. Brief occlusion therapy prior to strabismus surgery at age 4.
7	20.1/M	-0.1	0.12	None	None	Left exotropia. Occlusion therapy from age 2 until strabismus surgery at age 3.
8*	46.8/F	0.34	0.22	None	None	Right exotropia. Occlusion therapy ages 5-6.
9	24.2/M	0.44	0.44	60	85	Right vertical heterophoria at age 3; diplopia inducing head tilt. Occlusion therapy over right eye prior to successful strabismus surgery.
10	47.3/F	-0.04	-0.08	90	85	Right exotropia. Occlusion therapy ages 4-5.
11	18.9/F	0.5	0.52	None	None	Left exotropia. Occlusion therapy ages 9-10.
12	21.3/F	-0.04	0.04	None	None	Left esotropia. Occlusion therapy ages 1.5-3.
13*	21.6/F	0.22	0.3	None	None	Mild left exotropia and astigmatism. Occlusion therapy ages 5-6.
14*	19.1/F	0.5	0.42	60	85	Right exotropia. Brief occlusion therapy age 6 months.
15*	22/M	0.34	0.5	None	None	Left exotropia and astigmatism. Occlusion therapy ages 1.5-3. Prism therapy until age 8.
16*	18.3/F	0.04	0.12	90	170	Amblyopia of left eye and occlusion therapy ages 5-8; bilateral astigmatism.
Controls	22.3 to 34	-0.18 to 0.1	-0.18 to 0.1	60	85	Normal vision, no history of visual impairment, binocular or otherwise.

VA, visual acuity, measured at 3 m with Early Treatment Diabetic Retinopathy Study (ETDRS) logMAR chart. Values for control observers are ranges ($n = 8$).

* Indicates observers who took part in the ND filter experiment.

analyses: nine BVI (no static stereopsis: BVI-n) and seven BVI (static stereopsis: BVI-ss). All control observers had measurable static stereoscopic acuity with thresholds of at least 60 arcseconds (arcsec) (TNO test) or at least 85 arcsec (Frisby Near Stereotest). Eye dominance information was also collected using the hole-in-card test and two variations of the sighting test.³⁵

A subset of six observers also took part in the follow-up experiment using a ND filter, as indicated in the Table. Of these, four were of the BVI-n subgroup and the remaining two were of the BVI-ss subgroup. Four control observers also took part.

Apparatus

Stereoscopic stimuli were presented using a liquid crystal display (LCD) system (VIEWpixx/3D LCD; VPixx Technologies, Saint-Bruno, Quebec, Canada) combined with wireless LCD vision shutter goggles and an infrared emitter (NVIDIA GeForce 3D; NVIDIA, Santa Clara, CA, USA). The display (resolution 1920×1080 pixels; 120-Hz refresh rate) was gamma corrected using a photospectrometer (Jaz; Ocean Optics, Largo, FL, USA). Because we were using stereoscopic stimuli, we calibrated each eye separately through the LCD shutter goggles. We did not attempt to align the eyes (e.g., using prisms) of BVI observers; rather, the stimuli were presented as they would be

viewed under (relatively) natural viewing conditions. Stimuli were generated with software (Matlab 64-bit 8.5.0, R2015a; Mathworks, Natick, MA, USA) and the Psychophysics Toolbox 3.0^{36,37} and the DatapixxToolbox (VPixx Technologies) subroutines for precise control of the VIEWpixx/3D. The VIEWpixx/3D was driven by a PC computer (Shuttle XPC PC; Shuttle Computer Group, City of Industry, CA, USA) with an Intel Core i7-4790K processor (Intel, Santa Clara, CA, US) and NVIDIA GeForce GTX970 graphics card (NVIDIA) running Windows 7 64-bit (Microsoft Corp., Redmond, WA, USA). The Viewpixx3D has been independently demonstrated to have good temporal properties and limited cross talk for the presentation of stereoscopic stimuli, especially for the high-contrast, dynamic, and transient dot stimuli (see below) used here.^{38,39}

MID Stimuli

All MID stimuli were based on variants of cyclopean dynamic random dot stereograms (DRDSS)^{40,41} and were specially designed to target the CD and IOVD cues. In this type of stimulus, information about MID is carried either in changes in the disparity of pairs of dots presented to the left and right eye (CD) or in the relative velocities of populations of dots presented to the left and right eye (IOVD). Our stimuli were conceptually similar to those used by Czuba et al.,⁹ but

because we did not present a combined “full cue” stimulus, each condition used only a single dot lifetime. Within this framework, the concept of motion coherence describes the proportion of dots that carry a consistent MID signal and varies somewhere between 0 (all dots randomly positioned) and 1.0 (100% coherent motion). At one extreme, the dots in both the left and right eyes can be randomly positioned. For CD, this corresponds to the absence of a single surface moving through depth, although random correspondence between left and right eye patterns could lead to the perception of a dynamic 3D cloud. In the case of IOVD, a coherence of 0 corresponds to a case in which each eye contains, on average, an equal number of leftward- and rightward-moving dots. Under both these conditions, subjects should perform at chance. At the other extreme (coherence = 1.0), all dots either pair with a fellow dot in the other eye (CD) or move in the same direction within a single eye (IOVD), and the potential MID signal is maximized. Coherence therefore provides a unit-free way of defining signal-to-noise in both CD and IOVD and permits us to make normalized comparisons between the two types of stimulus.

The antialiased dots that made up the DRDSs had a Gaussian profile ($\sigma = 0.075^\circ$), were positioned at a density of 0.75 dots/deg², and were assigned to be either 100% contrast black or white (against a mean luminance gray background) with a probability of 0.5. The dot positions for each frame of the 2-second stimulus interval were pregenerated and loaded prior to being displayed during the experiment. Dots were pseudorandomly positioned with the constraint that all dot centers were separated by at least 0.5° in any direction. Thirty examples of both cue types were pregenerated, and one was selected at random for each stimulus interval. CD and IOVD stimuli had similarities to those described in prior studies.^{11,15,17} The stimulus parameters of both cue types were determined in pilot testing with four normal-sighted observers prior to the main experiment reported here.⁴² These pilot experiments were conducted using identical stimuli, apparatus, and procedure as that described here, except the motion parameters of the MID stimuli (the temporal frequency and the amplitude of the MID excursion) were varied over a wide range, and observers provided many threshold measurements over many testing sessions. The motion parameters for CD and IOVD (given below) that were, on average, optimal in these four normal-sighted observers were found to align closely with values measured in complementary prior studies.^{9,11} Schematics of the MID stimuli and their associated control versions are given in Figure 1.

CD stimuli were temporally uncorrelated DRDSs, where each video frame consisted of a new set of randomly positioned dots (Fig. 1a). These dots were paired across the eyes and differed only in a lateral shift that determined the disparity for that given point in time. Because the dots were randomly repositioned on each frame, there was no net continuous motion across the retina, and hence no consistent IOVD information. The sensation of motion-through-depth was provided by only the smooth change in the disparity of the images across time. Thus, the dots had a binocular correlation, but no temporal correlation. The disparity oscillated sinusoidally at 1.4 Hz for the duration of each stimulus interval (2 seconds; see below) to an amplitude extending to ± 12 arcmin (monocular) or ± 24 arcmin (binocular) disparity.

IOVD stimuli consisted of decorrelated random dot stereograms (Fig. 1c), meaning that the lateral shift of a given dot was consistent across time, though there was no binocular pairing of dots across the left and right eyes. Individual dots had a maximum lifetime of 50 milliseconds, and they maintained a consistent horizontal trajectory while visible. This lateral shift was always in opposite directions in the two eyes. Equal numbers of dots reached the end of their lifetime

and were “reborn” at a new position on each frame of the stimulus in order to maintain dot density and the number of visual transients throughout the stimulus. Based on preliminary testing, we found normal observers were maximally sensitive to an oscillation frequency of 1.1 Hz⁴² with a lateral shift of ± 200 arcmin between the eyes, meaning that the maximum lateral shift of the dots at the peak of the oscillation was 100 arcmin in a single eye. Note that such a large amplitude shift is possible in the IOVD stimulus because dots were never paired binocularly (compared to CD, where binocular disparities greater than about ± 32 arcmin tend to result in a break in binocular fusion).⁴³

While it is straightforward to eliminate velocity cues in a dynamic random dot stereogram to isolate CD information, it is more difficult to isolate IOVD without some disparity information leaking through in the form of spurious binocular correlations of dots.⁴⁴ To avoid this as much as possible, dots were positioned within narrow horizontal strips (two dot widths wide) that alternated across the eyes in a manner similar to that of Shioiri et al.,^{11,17} such that they never coincided on the two retinæ. Furthermore, we sorted the dots according to their positions and determined whenever a dot near the border of a left eye strip was close to a dot near the border of a right eye strip. On the rare occasions where this occurred, the border-dwelling dots in opposite eyes were assigned opposite contrast polarity, which is known to disrupt disparity signals in a way similar to the anticorrelated random dot stereograms used by some researchers to target IOVD signals.^{7,9,45}

For both CD and IOVD stimuli, we also developed matching “control” versions. These were designed to match all the statistical, low-level, and temporal characteristics of the MID stimuli while at the same time nulling the smooth motion-through-depth signal. In this way we could target the sensitivity to MID from either cue specifically from that of the low-level characteristics. For CD, we used a similar approach to Rokers and colleagues⁷ by simply taking the CD stimulus and temporally shuffling the frames (Fig. 1b). This meant that the distribution of disparities across time was identical to the MID CD stimulus, but there was no smooth or consistent oscillation in depth. Subjectively, these resembled a noisy 3D cloud of dots. IOVD control stimuli (Fig. 1d) were constructed in exactly the same manner as their MID counterparts, except that the lateral motion shift of the dots was in the same direction in each eye, and they were still in nonoverlapping retinal locations across the eyes. Subjectively, this produced a “flat” version of the IOVD stimulus that cancelled the oscillating “wobble” in depth experienced with the decorrelated random dot stereogram while retaining the same overall amount of motion energy.

All stimuli were presented in an annular arrangement with an inner radius of 1° and an outer radius of 6° . The edges of the annulus were smoothed by ramping dot contrast up and down along a cosine of length equivalent to one dot width. A small fixation lock consisting of a ring of radius 0.4° (width 0.2°) was centered on the display surrounding the fixation cross. A similar ring was also presented at the edge of the display (radius 11.75°). Taken together, the rings were colored black or white in alternating quadrants and were designed to help stabilize gaze and the fusion of the two eyes' images in the manner of nonius lines.

Procedure

Dot motion coherence thresholds were determined in all observers in a 2IFC task similar to the one used by Cumming and Parker,¹⁶ whereby observers chose which stimulus presentation interval contained the smoothly oscillating MID stimulus from the interval containing only the control

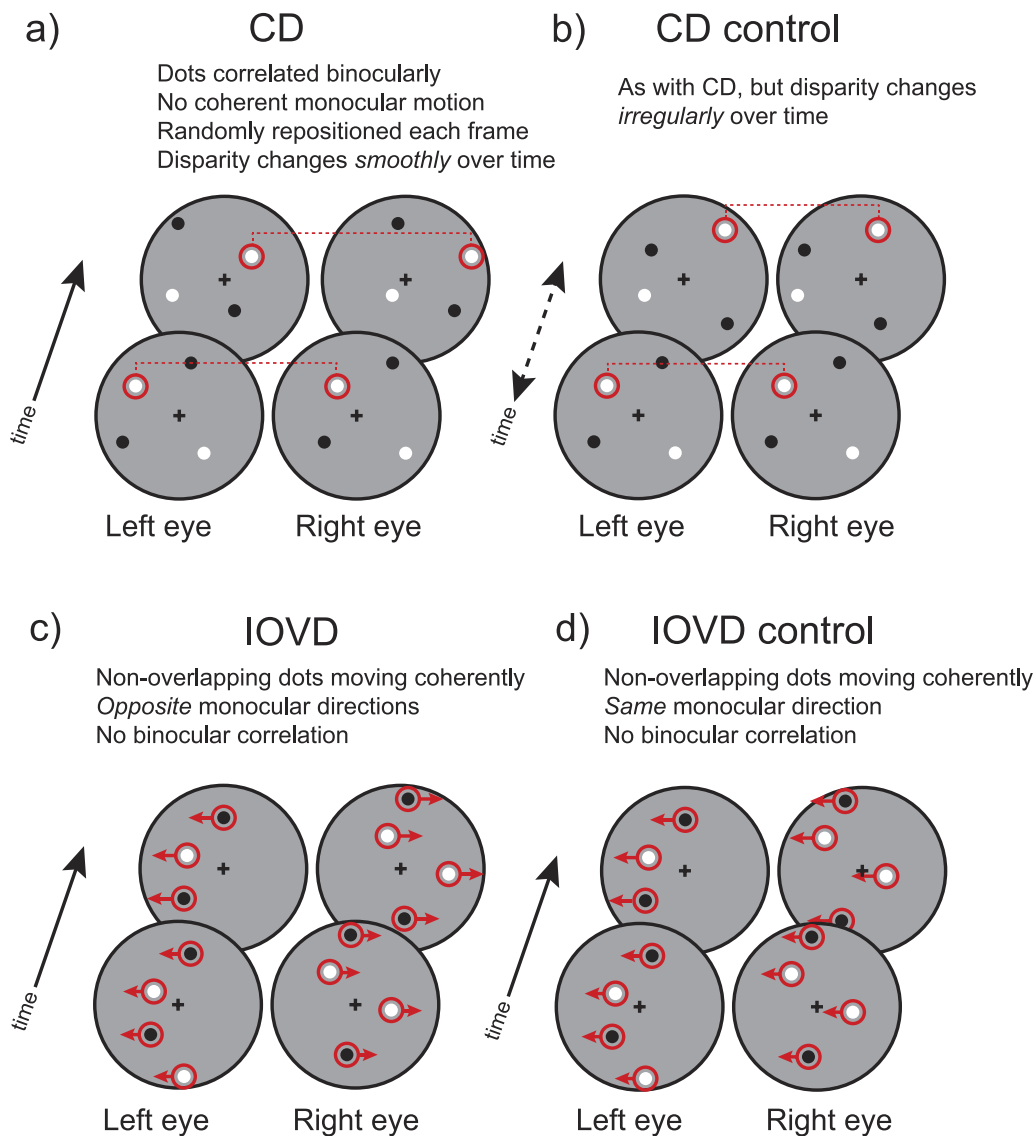


FIGURE 1. Schematic illustrations of the MID stimuli, illustrating the images presented to each eye and how they change across two consecutive motion frames. Only the stimuli on the left provide the ingredients for binocular MID; the control stimuli on the right contained identical low-level properties but could not be perceived as MID. Each set of left and right eye images are stereograms that can be fused. Note that these images are not to scale, and *red circles* or *arrows* were not present on the actual stimulus.

counterpart. By dot motion coherence, we mean the proportion (0–1.0) of total dots in the display adhering to the predefined positions that make up the MID (and control) stimuli (see above). Coherence thresholds were determined within a Bayesian Psi staircase paradigm⁴⁶ that estimated the threshold (and slope) of the Weibull psychometric function. Two interleaved staircases of 30 trials each were used, and observers performed three repeat runs, yielding six threshold estimates for both CD and IOVD. We took the inverse of the mean threshold across the six estimates to provide an estimate of perceptual sensitivity to the MID signals.⁹ In the staircase, motion coherence could vary anywhere between 0.01 and 1.0 in steps of 0.01. Because in principle the maximum coherence threshold possible is 1.0 (effectively the inability to measure a threshold), the lowest possible sensitivity is 1.0 (i.e., 1/1) and this indicates zero sensitivity to the MID signal.

Observers performed the 2IFC task in blocks of either CD or IOVD runs (in an order interleaved across observers). They were instructed to choose which of the two intervals (1 or 2)

contained the smooth backward and forward motion and to simply pick one or the other if they could not perceive any difference. Before beginning the task, they were shown demonstration versions of the MID stimuli to illustrate their target and were free to examine the demonstration for as long as they wished. They were positioned at a viewing distance of 57 cm, wearing the NVIDIA shutter goggles (over their prescription spectacles, if used). Responses were nonsped, and no feedback was provided, although each observer performed at least 10 practice trials for each condition to allow familiarization with the task. Each interval was 2 seconds in duration, during which the stimulus oscillated in depth, from a random starting phase within the cycle. To avoid luminance transients, the stimulus (Michelson) contrast was ramped from 0% to 100% with a cosine profile over 250 milliseconds. Intervals and trials were separated by a 500-millisecond and 1-second pause, respectively.

One very important feature of our 2IFC task was that it could not be performed on the basis of any binocular static

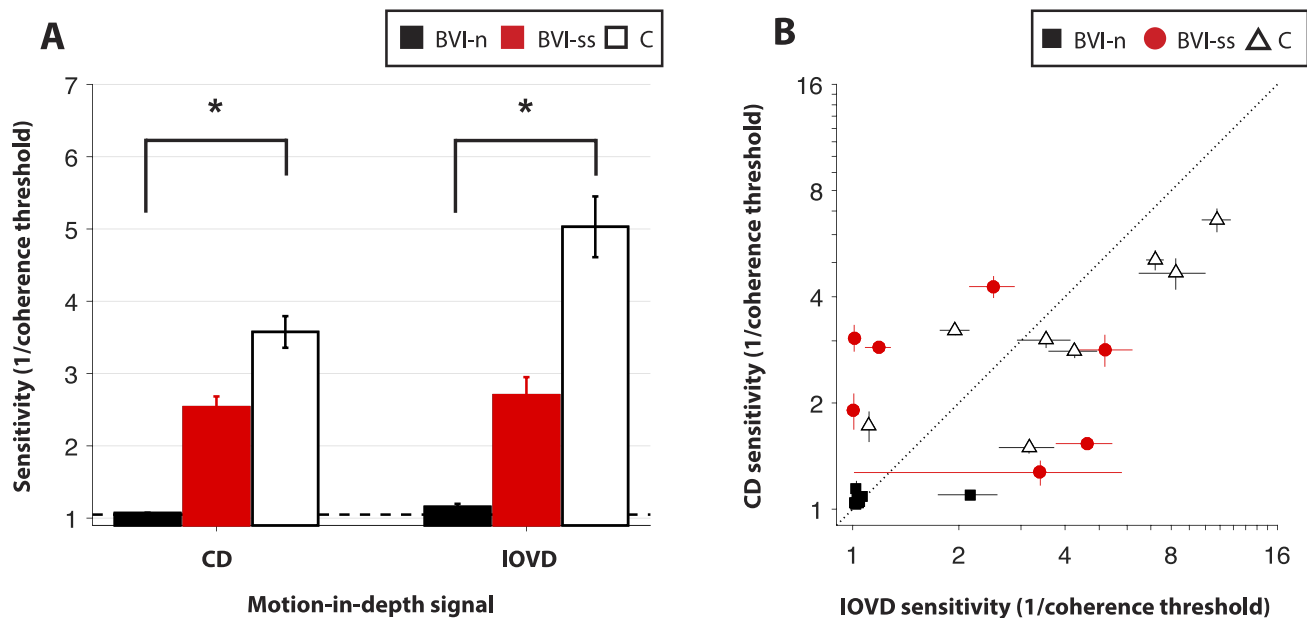


FIGURE 2. Motion coherence sensitivities (given as 1/coherence threshold) obtained in the 2IFC task. (A) Mean sensitivity for CD and IOVD cues across observers for each group. Error bars show standard error of the mean. * $P < 0.05$, according to post hoc tests in the factorial ANOVA (Bonferroni corrected). Dashed line indicates chance performance level. (B) Scatterplot of all individual observers' sensitivities for CD (ordinate) plotted against IOVD (abscissa). Horizontal error bars for IOVD and vertical error bars for CD give standard error of the mean across the six staircase estimates for each observer at each MID cue type. (C) Control group.

information (such as static disparities within the oscillation): crucially, we were interested in sensitivity to the oscillating MID signals, not the static components that are integrated to achieve the percept of MID. This is important in particular for any of our BVI volunteers that might have latent stereopsis²³ and therefore be sensitive to gross static binocular depth information within the stimulus, but not necessarily binocular dynamic depth information. Furthermore, the task was impossible to perform on the basis of inputs from one eye only.

Follow-up Experiment With ND Filter

We also ran an additional follow-up experiment following Hess et al.,²³ whereby an ND filter (ND 0.6) was placed over the fellow eye for our BVI observers or the dominant eye for the control observers. As described above, this was to test the hypothesis in the BVI observers that the ND filter might have the effect of introducing a temporal delay and/or reducing luminance entering the fellow eye and release the non-fellow eye from suppression, potentially improving performance on the MID task as was observed in Hess et al.²³ This experiment was conducted in exactly the same manner as the primary experiment, apart from the presence of the ND filter. Observers always performed the ND filter follow-up experiment after completing the primary experiment.

RESULTS

Figure 2A shows the mean sensitivity (defined as the inverse of the coherence threshold) measured for three types of observer: BVI observers with no static stereopsis (BVI-n), BVI observers with preserved static stereopsis (BVI-ss), and control observers. Figure 2A shows mean sensitivities. A value of 1.0 corresponds to a failure to detect motion even at 100% coherence and therefore represents the lowest possible value we could measure in our dataset since motion coherence cannot be higher than 1.0. The dashed horizontal line in Figure

2A shows theoretical chance performance on the 2IFC task on the basis of the mean of 1000 simulated staircases with purely random responses.

The most salient feature of the data in Figure 2 is that while C and BVI-ss observers were generally able to perform the staircase task and produce similar sensitivities (detecting MID when around one-third of the dots carried a coherent motion signal), we were unable to measure sensitivity for our BVI-n group for CD or IOVD, even at the highest coherences, except for one observer who showed a reasonable degree of sensitivity to IOVD. The data are replotted in Figure 2B to demonstrate this difference. All but one (observer 13 in the Table) of the BVI-n observers are clustered at the lower left of the graph with little interobserver variation and no evidence of sparing of either IOVD or CD sensitivity. Also worth noting in Figure 2B is that both the C and BVI-ss observers are scattered on either side of the identity line (the dashed diagonal line), indicating that some show a higher sensitivity to CD than IOVD and others a higher sensitivity to IOVD than CD. This is consistent with studies in large samples of normal vision observers that have shown that sensitivity to either cue varies quite markedly across the population.^{15,15} Nevertheless, CD and IOVD sensitivity was strongly positively correlated for the control observer group, $r_6 = 0.92$, $P = 0.001$. There was no significant correlation between CD and IOVD sensitivity for either the BVI-ss group: $r_5 = -0.25$, $P = 0.59$, or (not surprisingly) the BVI-n group: $r_7 = 0.28$, $P = 0.46$.

A 2-way (three group \times two MID cue) mixed-effects factorial ANOVA revealed a main effect of group: $F_{2,42} = 14.28$, $P < 0.0001$. There was no main effect of MID cue: $F_{1,42} = 1.27$, $P = 0.27$; and there was no interaction between cue type and group: $F_{2,42} = 0.79$, $P = 0.46$. Planned Bonferroni-corrected post hoc tests indicated that overall, sensitivities for the control group were significantly greater than both BVI subgroups, which themselves did not differ. The main effect of observer group was explored further with two separate 1-way ANOVAs on the CD and IOVD data. Both were significant; CD, $F_{2,21} = 10.12$, $P = 0.0008$; IOVD, $F_{2,21} = 6.8$, $P = 0.005$.

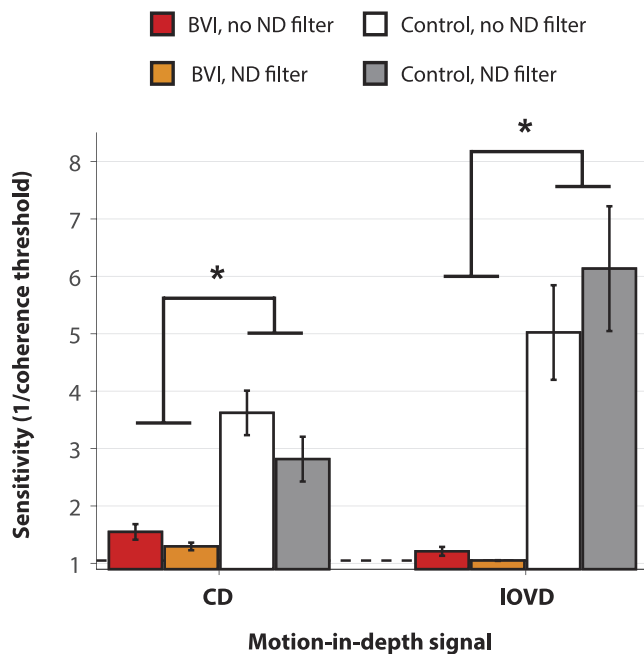


FIGURE 3. Mean coherence sensitivities (given as 1/coherence threshold) across observers in the 2IFC task with ND filter placement over the dominant (for control observers) or fellow (for BVI observers) eyes. Error bars show standard errors of the mean. * $P < 0.05$, according to post hoc tests in the factorial ANOVA (Bonferroni corrected). Dashed horizontal line indicates simulated chance performance level.

Bonferroni-corrected multiple comparisons indicated that only the difference in sensitivity between the control and BVI-n groups was significant ($P < 0.05$ for both CD and IOVD).

In a follow-up experiment, a subset of our observers performed the 2IFC task again, this time with a ND filter placed in front of the fellow eye for BVI observers ($n = 6$), or the dominant eye for controls ($n = 4$). We did not analyze data from the two BVI subgroups separately. Mean sensitivities for this experiment are plotted in Figure 3, along with the data for these same observers from the primary experiment where no ND filter was used. These results were submitted to a 3-way (two group \times two MID cue \times two ND filter state) mixed-effects factorial ANOVA, including in the model all 2-way and the 3-way interactions. As with the primary experiment, there was a simple main effect of group, $F_{1,32} = 27.48$, $P < 0.0001$, reflecting the gross differences in sensitivity between the BVI and control groups. The 2-way group \times cue interaction was also significant, $F_{1,32} = 4.95$, $P = 0.03$, reflecting that overall, control observers had higher sensitivity than BVI observers, and this was more markedly so for IOVD, as in the primary experiment. No other effects in the ANOVA were significant. In general, the results follow the same trends as in the primary experiment without the ND filter and show that placing the ND filter over the fellow eye for the BVI observers or the dominant eye for control observers has no effect: neither improving nor reducing sensitivity to either CD or IOVD.

DISCUSSION

We examined the psychophysical sensitivity to binocular motion cues in adults who had been treated for BVI as children. Most of our sample of observers diagnosed with strabismus and/or amblyopia as children and with no measurable static stereopsis according to widely available

commercial clinical stereo tests showed no sensitivity to either CD or IOVD cues. One observer from this group, however, did demonstrate sensitivity to IOVD but not CD (observer 13 from the Table). This special “Black Swan”⁴⁷ case is intriguing and provides some support for our original hypothesis that sensitivity to the lower-resolution IOVD signal might be spared in such populations. It is notable, however, that this effect is absent in the vast majority of our BVI observers who lack static stereo, while most individuals with demonstrable static stereoacuity were sensitive to IOVD to some degree.

Maeda et al.²⁵ found that the presence of gross stereopsis (as measured by the Titmus fly test) was correlated with the ability to detect IOVD in a handful of their patients, as was having a smaller angle of strabismus (less than about 15 prism diopters), according to the simultaneous prism cover test (in agreement with Watanabe et al.²⁶) and fusion of the Worth four-dot test. In general, small-angled strabismus is likely to be associated with some peripheral fusion, which would also be predictive of gross stereopsis and perhaps sensitivity to IOVD. Unfortunately, we cannot compare our results with Maeda et al.²⁵ because we did not measure fusion or angle of strabismus in our BVI observers; thus, it is possible that overall our sample had larger angles and poorer fusion, which may explain the general lack of sensitivity to IOVD in our BVI-n sample. Kitaoji and Toyama²⁰ also found that the strabismus angle was important in the preservation of stereomotion perception. Watanabe et al.²⁶ used the method of limits to determine disparity (or the equivalent lateral motion amplitude for IOVD) thresholds for CD, IOVD, and the two cues combined within a fixed range of 100 to 1200 arcsec (1.67–20 arcmin), for which many of their observers abutted the maximum and hence were unable to discern MID even at the highest values tested.²⁶ They do not report the number of trials used and the correlations between static disparity thresholds (as measured with the Titmus stereotest), and the IOVD or CD (disparity/lateral motion amplitude) thresholds were weak (–0.1 and 0.11, respectively). It is not clear whether these correlations were statistically reliable. The key commonality in these studies as well as ours is the presence of some degree of static stereopsis. In Hess et al.²³ and Maeda et al.,²⁵ those observers who demonstrated some sensitivity to MID conditions containing IOVD information also had some degree of gross static stereo.^{23,25}

Both Maeda et al.²⁵ and Watanabe et al.²⁶ used red/green anaglyphs, which have been demonstrated to be prone to cross talk.³⁸ Cross talk is a particular issue for IOVD stimuli where even small amounts of interocular leakage can permit an observer to solve the MID task almost perfectly. Maeda et al.²⁵ report that observers received feedback on the correctness of each trial,²⁵ though Watanabe et al.²⁶ do not mention whether feedback was used. One issue with providing feedback with such difficult stereoscopic stimuli in nonnormal or nonexpert psychophysical observers is that they allow observers to use stimulus or display artifacts (such as interocular cross talk) that might permit solutions to the psychophysical task that bypass the physiological mechanism under investigation.

Vision in the amblyopic eye is sometimes modeled as a reduction in effective contrast, and interocular suppression will act to reduce the strength of signals in the amblyopic eye still further under binocular conditions.⁴⁸ Hess et al.²³ examined this to some degree: performance on a stereomotion task improved when ND filters were placed over the fellow eye. Although this is not reflective of normal viewing conditions, it does suggest that further experiments are required to completely rule out the existence of latent stereomotion systems in deficient observers. They attributed the improvement in MID sensitivity in their stereo-deficient observers to the effect of reducing the fixing eye’s suppressive

influence via a reduction in contrast, mean luminance, or both. In our experiment, the use of the ND filter did not make any difference to the results. We used a filter of ND = 0.6 (approximately a four-fold reduction in luminance) while Hess et al.²³ used a full log unit of reduction (ND = 1.0). Most observers did report that the ND filter made the task significantly more difficult, although overall we saw no change in sensitivity for either control or BVI observers.

The suppression of inputs from the amblyopic eye can render amblyopic visual cortex almost functionally monocular.³⁰ As noted in the Methods, we followed Cumming and Parker¹⁶ by using a 2IFC task with oscillating (cyclical, bidirectional) MID stimuli to measure observer sensitivity, rather than a two-alternative forced choice (2AFC) signed direction of MID judgment (i.e., toward or away). We were very careful in implementing the 2IFC design here because it meant that it was impossible to deduce the direction of IOVD based on monocular motion direction information only. Basing decisions on monocular information rather than the smooth, binocular MID signal could earn the BVI observers an unfair advantage in IOVD sensitivity in a 2AFC (toward/away) task. Indeed, the 2IFC task adopted here prevents any observer from “cheating” on the task by simply closing one eye. It is worth noting that an IOVD sensitivity of 1.0 (or close to it) for any observer implies that he or she was unable to consistently discriminate lateral motion in one direction in both eyes (our IOVD control) from lateral motion in opposite directions in the two eyes (the IOVD stimulus). The issue of whether an observer can extract a functionally useful, signed MID signal would require a 2AFC discrimination judgment, something that was not compatible with the 2IFC task employed here. We suspect that inputs from the nonfixing (amblyopic) eye are being suppressed in many of our BVI observers. It may be that motion is suppressed more than static information because motion is largely carried through the magnocellular pathway, which is far more sensitive to gain control.⁴⁹ Furthermore, Baker and Wade⁵⁰ have recently shown that if one input is particularly noisy, it will be suppressed (via a gain control mechanism) in a nonlinear manner.

Finally, it has been suggested that static disparity measures do not fully characterize an observer's ability to perceive stereoscopic motion stimuli.^{13,22} Sensitivity to both CD and IOVD cues were indistinguishable from normal for the BVI-ss group with measurable stereopsis for all but one observer. Here, we were interested in the nature of the underlying binocular cues, not the potential clinical implications, and thus our results are agnostic toward calls for use of more advanced tools for the clinical testing of stereopsis using dynamic stimuli.^{13,22,25,26} Nevertheless, new tablet-based technologies such as column-interleaved digital autostereoscopic displays⁵¹ offer the exciting promise of allowing for the measurement of dynamic stereopsis and stereomotion thresholds in a clinical setting, while obviating the need for bulky or expensive stereoscopic displays, goggles, or special optics. Given the presence of the IOVD-sensitive outlier in our BVI-n group and the overall preponderance of individual differences in sensitivity to MID stimuli,¹³⁻¹⁵ such developments can only lead to more discoveries about sensitivity to IOVD in BVI and normal populations.

Acknowledgments

The authors thank Daniel Baker, Suzanne McKee, Andrew Logan, Freya Lygo, and Bruno Richard for valuable practical and theoretical input and for help in recruiting BVI volunteers.

Supported by grants provided by the UK Biotechnology and Biological Sciences Research Council: BB/M002543/1 (ARW); BB/M001660/1 (JMH); and BB/M001210/1 (MB).

Disclosure: **R.T. Maloney**, None; **M. Kaestner**, None; **A. Bruce**, None; **M. Bloj**, None; **J.M. Harris**, None; **A.R. Wade**, None

References

- Harris JM, Nefs HT, Grafton CE. Binocular vision and motion-in-depth. *Spat Vis*. 2008;21:531-547.
- Regan D, Gray R. Binocular processing of motion: some unresolved questions. *Spat Vis*. 2009;22:1-43.
- Czuba TB, Huk AC, Cormack LK, Kohn A. Area MT encodes three-dimensional motion. *J Neurosci*. 2014;34:15522-15533.
- Sanada TM, DeAngelis GC. Neural representation of motion-in-depth in area MT. *J Neurosci*. 2014;34:15508-15521.
- Joo SJ, Czuba TB, Cormack LK, Huk AC. Separate perceptual and neural processing of velocity- and disparity-based 3D motion signals. *J Neurosci*. 2016;36:10791-10802.
- Likova IT, Tyler CW. Stereomotion processing in the human occipital cortex. *Neuroimage*. 2007;38:293-305.
- Rokers B, Cormack LK, Huk AC. Disparity- and velocity-based signals for three-dimensional motion perception in human MT+. *Nat Neurosci*. 2009;12:1050-1055.
- Brooks KR, Stone LS. Stereomotion speed perception: contributions from both changing disparity and interocular velocity difference over a range of relative disparities. *J Vis*. 2004;4(12):1061-1079.
- Czuba TB, Rokers B, Huk AC, Cormack LK. Speed and eccentricity tuning reveal a central role for the velocity-based cue to 3D visual motion. *J Neurophysiol*. 2010;104:2886-2899.
- Sakano Y, Allison RS. Aftereffect of motion-in-depth based on binocular cues: effects of adaptation duration, interocular correlation, and temporal correlation. *J Vis*. 2014;14(8):21.
- Shioiri S, Nakajima T, Kakehi D, Yaguchi H. Differences in temporal frequency tuning between the two binocular mechanisms for seeing motion in depth. *J Opt Soc Am A Opt Image Sci Vis*. 2008;25:1574-1585.
- Wardle SG, Alais D. Evidence for speed sensitivity to motion in depth from binocular cues. *J Vis*. 2013;13(1):17.
- Allen B, Haun AM, Hanley T, Green CS, Rokers B. Optimal combination of the binocular cues to 3D motion. *Invest Ophthalmol Vis Sci*. 2015;56:7589-7596.
- Barendregt M, Dumoulin SO, Rokers B. Impaired velocity processing reveals an agnosia for motion in depth. *Psychol Sci*. 2016;27:1474-1485.
- Nefs HT, O'Hare L, Harris JM. Two independent mechanisms for motion-in-depth perception: evidence from individual differences. *Front Psychol*. 2010;1:155.
- Cumming BG, Parker AJ. Binocular mechanisms for detecting motion-in-depth. *Vis Res*. 1994;34:483-495.
- Shioiri S, Saisho H, Yaguchi H. Motion in depth based on interocular velocity differences. *Vis Res*. 2000;40:2565-2572.
- Hess RF, Thompson B, Gole GA, Mullen KT. The amblyopic deficit and its relationship to geniculocortical processing streams. *J Neurophysiol*. 2010;104:475-483.
- Tao X, Zhang B, Shen G, et al. Early monocular defocus disrupts the normal development of receptive-field structure in V2 neurons of macaque monkeys. *J Neurosci*. 2014;34:13840-13854.
- Kitaoji H, Toyama K. Preservation of position and motion stereopsis in strabismic subjects. *Invest Ophthalmol Vis Sci*. 1987;28:1260-1267.
- Tidbury LP, Black RH, O'Connor AR. Perceiving 3D in the absence of measurable stereo-acuity. *Br Ir Orthopt J*. 2014;11:34-38.
- Tidbury LP, Brooks KR, O'Connor AR, Wuerger SM. A systematic comparison of static and dynamic cues for depth perception. *Invest Ophthalmol Vis Sci*. 2016;57:3545-3553.

23. Hess RF, Mansouri B, Thompson B, Gheorghiu E. Latent stereopsis for motion in depth in strabismic amblyopia. *Invest Ophthalmol Vis Sci.* 2009;50:5006-5016.
24. Rouse MW, Tittle JS, Braunstein ML. Stereoscopic depth perception by static stereo-deficient observers in dynamic displays with constant and changing disparity. *Optom Vis Sci.* 1989;66:355-362.
25. Maeda M, Sato M, Ohmura T, Miyazaki Y, Wang AH, Awaya S. Binocular depth-from-motion in infantile and late-onset esotropia patients with poor stereopsis. *Invest Ophthalmol Vis Sci.* 1999;40:3031-3036.
26. Watanabe Y, Kezuka T, Harasawa K, Usui M, Yaguchi H, Shioiri S. A new method for assessing motion-in-depth perception in strabismic patients. *Br J Ophthalmol.* 2008;92:47-50.
27. Eggers HM, Blakemore C. Physiological basis of anisometropic amblyopia. *Science.* 1978;201:264-267.
28. Hubel DH, Wiesel TN. Binocular interaction in striate cortex of kittens reared with artificial squint. *J Neurophysiol.* 1965; 28:1041-1059.
29. Swindale NV, Mitchell DE. Comparison of receptive field properties of neurons in area 17 of normal and bilaterally amblyopic cats. *Exp Brain Res.* 1994;99:399-410.
30. Hess RF, Thompson B, Baker DH. Binocular vision in amblyopia: structure, suppression and plasticity. *Ophthalmic Physiol Opt.* 2014;34:146-162.
31. Baker DH, Meese TS, Mansouri B, Hess RF. Binocular summation of contrast remains intact in strabismic amblyopia. *Invest Ophthalmol Vis Sci.* 2007;48:5332-5338.
32. Hallum LE, Shoener C, Kumbhani RD, et al. Altered balance of receptive field excitation and suppression in visual cortex of amblyopic macaque monkeys. *J Neurosci.* 2017;37:8216-8226.
33. Huk AC. Multiplexing in the primate motion pathway. *Vis Res.* 2012;62:173-180.
34. TNO. *TNO Test for Stereoscopic Vision.* Vol 19. Ede, The Netherlands: Laméris Ootech BV; 1972.
35. Porac C, Coren S. The dominant eye. *Psychol Bull.* 1976;83: 880-897.
36. Brainard DH. The Psychophysics Toolbox. *Spat Vis.* 1997;10: 433-436.
37. Pelli DG. The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spat Vis.* 1997;10: 437-442.
38. Baker DH, Kaestner M, Gouws AD. Measurement of crosstalk in stereoscopic display systems used for vision research. *J Vis.* 2016;16(15):14.
39. Ghodrati M, Morris AP, Price NS. The (un)suitability of modern liquid crystal displays (LCDs) for vision research. *Front Psychol.* 2015;6:303.
40. Julesz B. *Foundations of Cyclopean Perception.* Chicago: University of Chicago Press; 1971.
41. Julesz B, Payne RA. Differences between monocular and binocular stroboscopic movement perception. *Vision Res.* 1968;8:433-444.
42. Maloney RT, Kaestner M, Ansell J, Bloj M, Harris JM, Wade AR. Mapping the temporal and neural properties of binocular mechanisms for motion-in-depth perception. *Perception.* 2016;45(suppl 2):201.
43. Howard IP, Rogers BJ. *Seeing in Depth.* Vol 2. Toronto: I. Porteous; 2002.
44. Peng Q, Shi BE. Neural population models for perception of motion in depth. *Vis Res.* 2014;101:11-31.
45. Rokers B, Cormack LK, Huk AC. Strong percepts of motion through depth without strong percepts of position in depth. *J Vis.* 2008;8(4):6.
46. Kontsevich LL, Tyler CW. Bayesian adaptive estimation of psychometric slope and threshold. *Vis Res.* 1999;39:2729-2737.
47. Taleb NN. *The Black Swan: The Impact of the Highly Improbable.* New York: Random House; 2007.
48. Huang P-C, Baker DH, Hess RF. Interocular suppression in normal and amblyopic vision: spatio-temporal properties. *J Vis.* 2012;12(11):29.
49. Solomon SG, Lee BB, Sun H. Suppressive surrounds and contrast gain in magnocellular-pathway retinal ganglion cells of macaque. *J Neurosci.* 2006;26:8715-8726.
50. Baker DH, Wade AR. Evidence for an optimal algorithm underlying signal combination in human visual cortex. *Cereb Cortex.* 2017;27:254-264.
51. Serrano-Pedraza I, Vancleef K, Read JC. Avoiding monocular artifacts in clinical stereotests presented on column-interleaved digital stereoscopic displays. *J Vis.* 2016;16(14):13.