Adaptation to interocular difference

Frederick A. A. Kingdom
McGill Vision Research, Department of Ophthalmology, Montréal General Hospital, Montréal, Canada

Ben J. Jennings
Centre for Cognitive Science, Department of Psychology, College of Health and Life Sciences, Brunel University, London, UK

Mark A. Georgeson
School of Life & Health Sciences, Aston University, Birmingham, UK

Patterns in the two eyes’ views that are not identical in hue or contrast often elicit an impression of luster, providing a cue for discriminating them from perfectly matched patterns. Here we ask whether the mechanism for detecting interocular differences (IDs) is adaptable. Our stimuli were horizontally oriented multispatial-frequency grating patterns that could be subject to varying degrees of ID through the introduction of interocular phase differences in the grating components. Subjects adapted to patterns that were either correlated, uncorrelated, monocular (one eye only), or anticorrelated. Following adaptation, thresholds for detecting IDs were measured using a staircase procedure. It was found that ID thresholds were elevated following adaptation to uncorrelated, monocular, and anticorrelated but not correlated patterns. Threshold elevation was found to be maximal when the orientations of the adaptor and test gratings were the same, and when their spatial frequencies were similar. The results support the existence of a specialized mechanism for detecting IDs, the most likely candidate being the binocular differencing channel proposed in previous studies.

Introduction

Humans and animals are said to have binocular vision if they possess two spatially separated eyes, but with overlapping visual fields that together provide a coherent view of the external world. Two eyes offer a range of advantages over one—for example, a wider field of view, stereopsis, and binocular summation. To achieve stereopsis, the visual system detects disparities in the positions of objects in the two eyes. However, humans are also sensitive to interocular (between-eye) differences in dimensions other than position—for example, in contrast or hue (Cohn, Leong, & Lasley, 1981; Cormack, Stevenson, & Schor, 1991; Stevenson, Cormack, Schor, & Tyler, 1992; Yoonessi & Kingdom, 2009; Formankiewicz & Mollon, 2009; Malkoc & Kingdom, 2012; Jennings & Kingdom, 2016; Georgeson, Wallis, Meese, & Baker, 2016). Such differences have been termed interocular (de)correlations (Cormack et al., 1991; Stevenson et al., 1992), dichoptic differences (e.g., Yoonessi & Kingdom, 2009; Malkoc & Kingdom, 2012), and binocular luminance disparities (Formankiewicz & Mollon, 2009). Here we term them interocular differences (IDs). An ID in contrast or hue can generate an impression of luster, and several previous studies have argued that a luster cue enables the ID to be detected (Formankiewicz & Mollon, 2009; Yoonessi & Kingdom, 2009; Malkoc & Kingdom, 2012; Jennings & Kingdom, 2016). Some recent studies have suggested models for the detection of IDs in hue and in contrast, based on luster (Georgeson et al., 2016; Jennings & Kingdom, 2016).

Those studies that explicitly measured thresholds for detecting IDs used conventional forced-choice “Type 1” procedures (i.e., procedures with a correct/incorrect response on each trial). An ID threshold is thus different from the threshold for perceiving binocular rivalry; this is an appearance measure based on the criterion that the stimuli in the two eyes are perceived to alternate (Alais & Blake, 2005). In general the ID required for detection is smaller than that for eliciting binocular rivalry—for example, Malkoc and Kingdom (2012), using isoluminant colored (chromatic) patches, found that the threshold for detecting an ID in hue was about 3 times lower than that for perceiving hue rivalry.

In this communication we ask whether the detection of IDs is adaptable. Our motivation is based on the widely held premise that if something is selectively...
adaptable it is likely to be processed by a dedicated channel. At present, though, there is no compelling evidence for the existence of a channel for detecting IDs in contrast and hue. Support for a binocular differencing channel comes not from studies of ID detection but from studies of contrast detection (Cohn et al., 1981), motion perception (May, Zhaoping, & Hibbard, 2012; and see Kingdom, 2012), orientation perception (May & Zhaoping, 2016), stereopsis (Goncalves & Welchman, 2017; Kingdom, May, & Hibbard, 2017), binocular rivalry (Said & Heeger, 2013), and visual-evoked potentials (Katyal, Vergeer, He, He, & Engel, 2018). Thus evidence that IDs are adaptable would suggest that ID detection should be added to the list of likely functional roles for a differencing channel.

The stimuli we have employed to test for ID adaptation are horizontally oriented multi-spatial–frequency, as well as single-spatial–frequency sine-wave gratings. Examples of the former variety are shown in Figure 1. These stimuli possess varying degrees of ID in the phases of the component sine waves, and hence varying degrees of ID in local luminance contrasts in the pattern. As with interocular contrast differences, our informal observations suggest that interocular phase differences generate an impression of luster, and it is reasonable to assume that the luster in both types of stimulus manipulation is mediated by a common mechanism.

There are two advantages to measuring ID thresholds using interocular phase rather than contrast differences. First, it minimizes the possibility that contrast can be used as a cue to the presence of an ID. Why so? Consider the alternative. If one were to present a forced-choice pair in which one alternative was a grating with an interocular contrast difference of, say 0.4 to one eye and 0.6 to the other, while the other alternative was a grating with the average of those two contrasts (0.5) in both eyes, the former alternative would appear to have a higher contrast because of the well-known “winner-take-all” rule that mediates suprathreshold binocular contrast summation (Meese, Georgeson, & Baker, 2006; Baker, Wallis, Georgeson, & Meese, 2012; Ding, Klein, & Levi, 2013; Kingdom & Libenson, 2015). Thus the subject could learn that the alternative with the higher perceived contrast contained the ID. There are ways around this confound—for example, by adding contrast distractors (Formaniewicz & Mollon, 2009; Jennings & Kingdom, 2016), or contrast jitter—but an arguably elegant solution lies in the use of phase, since the introduction of interocular phase differences has no apparent effect on perceived contrast at high contrasts (≥30%) and for medium interocular phase offsets (≤90°; Huang, Zhou, Zhou, & Lu, 2010; Baker et al., 2012; Ding et al., 2013). The other advantage of using interocular phase differences is that there is a simple mathematical relationship between interocular correlation and interocular phase difference: The correlation between two sinusoids is given by \( \cos \varphi \), where \( \varphi \) is the phase difference. This relation also holds for a multicomponent grating where each sinewave component has a disparity of \( \pm \varphi \) in phase.

Why horizontally oriented gratings? This should minimize stereo-depth cues to the stimulus containing the ID difference, because horizontally oriented gratings have only vertical disparities, and these appear to play no role in depth perception, at least in central vision.

**General methods**

**Observers**

Four observers took part in the experiments. Two were authors and two were naive undergraduate volunteers. All observers had normal or corrected-to-
normal visual acuity. Prior to experimental testing, informed consent was obtained from each observer. All experiments were conducted in accordance with the Declaration of Helsinki and the Research Institute of the McGill University Health Centre Ethics Board. Observer initials on graphs have been anonymized in accordance with requirements of the Ethics Board.

**Stimulus display**

All experiments were conducted using a Dell Precision T1650 PC with a VISeGe graphics card (Cambridge Research Systems, Cambridge, UK). The visual stimuli were displayed on a gamma-corrected Sony Trinitron Multiscan F500 flat-screen CRT Monitor. Stimulus generation and experimental control employed custom software written in C. Participants viewed the dichoptic pairs through a custom-built eight-mirror Wheatstone stereoscope with an aperture of $10^\circ \times 10^\circ$ and a viewing distance along the light path of 55 cm. A chin rest was employed to minimize rotational head movements in the second experiment, in which adaptor orientation was manipulated. During the experiments observers were seated in a darkened room and their responses were recorded via a keypad.

**Stimuli**

The stimuli in all experiments were dichoptic pairs of circular patches, one pair above and one below fixation. Each patch had a diameter of 4.35°, and a center-to-center vertical separation of 5.8°. The horizontal separation of the two members of each dichoptic pair on the monitor was adjusted so that the dichoptic pair appeared fused in the center of the aperture. In the first two experiments each patch comprised eight sine-wave luminance gratings of equal contrast, with spatial frequencies (SFs) one, two, three, four, five, six, seven, and eight cycles per patch, corresponding to SFs ranging from 0.23–1.84 cpd. The base spatial phase $\phi_0$ of each grating component was randomized across SFs, but the magnitude of phase disparity $\varphi$ was the same for each SF, with the sign of this disparity randomized across SF. Thus the component phase for the left eye was $(\phi_0 + a \cdot \varphi/2)$ and for the right eye was $(\phi_0 - a \cdot \varphi/2)$, where $a$ was randomly 1 or −1 across SFs. In the third experiment only one SF of grating was displayed. The adaptors and test stimuli contained varying degrees of interocular phase difference $\varphi$, and hence interocular correlation, as detailed for each experiment.

**Procedure**

We employed a conventional sequence of stimuli: adaptation followed by test followed by top-up adaptation followed by test etc., in conjunction with a staircase procedure that adjusted the test IDs according to previous responses. During the adaptation period, the patches were refreshed by re-randomizing the base phases $\phi_0$ every 250 ms for subjects BB and FF, and 500 ms for subjects KK and NN. The adaptation sequence lasted 45 s. Each test pattern was a single presentation with the same exposure duration as the adaptation refreshes (250/500 ms). It was preceded by and followed by a spatially uniform interstimulus interval at mean luminance for 100 ms. The test patterns were interspersed with 6 s of top-up adaptation. After 30 test presentations, the session was terminated. The task on each trial was to identify which of the two patches, top or bottom, contained the ID. The presence of the test stimulus was signaled by a green spot filling the fixation circle. Feedback was given as a red spot in the fixation circle for an incorrect response. The initial test interocular phase difference was randomly selected from a range whose average was approximately double the expected threshold phase difference as determined in pilot runs. A three-up-one-down staircase method was employed in which the interocular phase difference was either increased or decreased by a factor of 2.5 for the first five trials and 1.3 thereafter. An upper limit of interocular phase difference of $180^\circ$ was imposed, to prevent any wraparound in ID. There were six sessions for each condition, resulting in a total of 150 test trials per condition per observer, with the exception of BB’s one, two, and four cycles per patch conditions where there were nine sessions, resulting in 270 trials per condition. Condition order was randomized with the constraint that observers conducted three consecutive sessions of the same condition in order to maximize any effects of adaptation, followed by a 5-min break between conditions.

**Analysis**

Test interocular phase differences were first transformed into a metric of ID based on the degree of interocular correlation. For this purpose we defined ID as $[1 - \cos \varphi]/2$, where $\varphi$ is the interocular phase difference. This metric transforms the correlation $\cos \varphi$, which ranges from 1 to −1 to the range 0 to 1, making more tractable the fitting of psychometric functions. According to this metric a stimulus with perfect interocular correlation ($\varphi = 0$) has an ID of 0, an uncorrelated stimulus ($\varphi = 90$) has an ID of 0.5, and an anticorrelated stimulus ($\varphi = 180$) has an ID of 1. Psychometric functions plotting proportion correct against ID were fitted with a Quick function using a
maximum likelihood criterion, using routines from the Palamedes toolbox (Prins & Kingdom, 2009). Thresholds at the 75% correct level and associated bootstrap errors were estimated from the fits.

**Experiment 1: Type of adaptor**

In this experiment we measured ID thresholds following adaptation to the four types of adaptor shown in Figure 1 plus a no-adaptor condition. The adaptors were therefore no-adaptor, correlated, anti-correlated, and monocular. The no-adaptor condition was a (midgray) blank screen. The correlated adaptors were identical in each eye. The anticorrelated adaptors comprised SF components that were of opposite phase (i.e., a 180° phase difference in the two eyes). The uncorrelated adaptors comprised SF components with a phase difference of ±90°, with the sign of the phase difference randomised for each component. For the monocular adaptor the stimulus was presented to just one eye, with eye selection randomized for each refresh (250/500 ms) during the adaptation period(s). Note that for each stimulus presentation the absolute phases of all SF components were randomized. The root-mean-square (RMS) contrasts of the adaptors were 0.31, and we used two RMS contrasts for the test stimuli: 0.096 and 0.29.

Psychometric functions for the 0.29 RMS contrast test stimuli obtained using the correlated and anticorrelated adaptors are shown in Figure 2, together with their Quick fits. The functions are clearly separated showing that the type of adaptor significantly affected ID detection. Figure 3 shows ID thresholds and bootstrap errors as a function of adaptor ID, for the no-adaptor (dashed lines), correlated (ID = 0), uncorrelated (ID = 0.5) and anticorrelated (ID = 1) adaptors, for both test contrasts. One can see that while thresholds for the correlated adaptors were not significantly above baseline, thresholds increased systematically with adaptor ID.

The two types of uncorrelated adaptor—uncorrelated versus monocular—are compared in Figure 4, this time with ID thresholds plotted as a function of test RMS contrast. As can be seen, threshold IDs were around twice as high following adaptation to the uncorrelated compared with the monocular adaptors.

**Experiment 2: Adaptor orientation tuning**

The aim of this experiment was to determine whether the elevation in ID thresholds following adaptation to anticorrelated versus correlated adaptors was selective for adaptor orientation. For this purpose we varied the orientation of the adaptor gratings while holding the test adaptor gratings constant at 90° (horizontal). We used four orientations of adaptor: 0° (vertical), 45° (right oblique), 90° (horizontal), and 135° (left-oblique). If adaptation to IDs is orientation tuned, we would expect the differential effect of adapting to correlated versus anticorrelated adaptor to be maximal when the adaptor and test orientations were of the same orientation. As in the previous experiment the adaptor stimuli had an RMS contrast of 0.31. Here the test RMS contrast was 0.19.

The results in Figure 5 show that changing the orientation of the correlated adaptors had little effect on thresholds, whereas thresholds following the anticorrelated adaptors were in all cases highest for the 90° adaptor condition (i.e., when the orientations of adaptor and test were the same).

**Experiment 3: Adaptor SF tuning**

To examine adaptor SF tuning we used single-SF–component stimuli. Three subjects participated. Our adaptors were one, two, four, eight, and 16 cycles per patch, corresponding to SFs of 0.23, 0.46, 0.92, 1.84, and 3.68 cpd. The test was four cycles per patch (0.92 cpd). The contrasts of the adaptor and test were set to the same as the contrasts of any one SF component in Experiment 2, namely 0.156 for the adaptor and 0.096 for the test, corresponding to RMS contrasts of 0.11 and 0.068 (the RMS of a sinusoid with no DC offset, i.e., modulated around zero, and amplitude $a$ equals $a/\sqrt{2}$).

Results are shown in Figure 6. The biggest differential effect of the anticorrelated versus correlated adaptors was for the adaptor at two cycles per patch (0.46 cpd), with the difference falling away on either side of this peak, and no differential effect for the 16 cycle per patch adaptor (3.68 cpd).

**Discussion**

The following summarises the results of the study.

1. Thresholds for detecting the presence of interocular phase differences in horizontally oriented multi-SF grating patterns were found to be elevated following adaptation to uncorrelated, monocular, and anticorrelated patterns, but not with perfectly correlated adapting patterns.
Relation to interocular contrast differences

In these experiments, the two eyes were always presented with the same global contrast. The Fourier component contrasts at each SF were the same across eyes, and so it follows that the contrast energy and RMS contrasts were also the same. We envisaged, however, that the perception of interocular phase differences and the perception of local interocular contrast differences might be intimately related. We now show that, by recasting our data in terms of local interocular contrast differences, we can account for a key finding in the first experiment—namely that ID thresholds were higher for the uncorrelated than for the monocular adaptors (see Figure 4).

Let the spatial luminance waveforms for the left and right eyes be \( I_L(x) \) and \( I_R(x) \) with mean luminance \( I_0 \). Subtracting and normalizing by the mean luminance defines two local contrast signals, \( L(x) = [I_L(x) - I_0]/I_0 \) and \( R(x) = [I_R(x) - I_0]/I_0 \). We can then define an interocular contrast difference signal \( (R[x] - L[x]) \); Figure 7) whose RMS value is \( C_{DIFF} \). The relationship between this interocular RMS contrast difference and interocular correlation/phase difference is neatly captured by the variance sum law (which expresses the variance of the sum [or difference] of two correlated variables, in terms of the individual variances and the correlation between them). Here the correlation term is expressed as \( \cos \phi \). If \( C_{DIFF} \) is the RMS value of the contrast difference signal, defined above, then

\[
C_{DIFF}^2 = C_L^2 + C_R^2 - 2C_L C_R \cos \phi \quad (1)
\]

where \( C_L \) and \( C_R \) are the left and right eye RMS contrasts, \( \phi \) is the interocular phase difference, and \( \cos \phi \) the interocular correlation. Since for all except our monocular stimuli \( C_L = C_R = C \), Equation 1 simplifies to:

\[
C_{DIFF} = C \sqrt{2(1 - \cos \phi)} \quad (2)
\]

The contrast of the difference signal is not negligible, even for very small levels of ID (Figure 7). If the RMS contrast of the monocular adaptor is given by \( c \), it follows from Equation 2 that the values of \( C_{DIFF} \) for our four types of adaptor (correlated, monocular, uncorrelated, anticorrelated) are \( [0, c, c\sqrt{2}, 2c] \) respectively. Figure 8a plots the normalized ID thresholds averaged across-subsjects as a function of \( C_{DIFF} \) expressed in units of \( c \). There is a nearly linear relationship between the two when plotted on log-linear coordinates, and, importantly, the relationship predicts the observed difference between the thresholds after monocular and uncorrelated adaptors. This simple exercise reinforces the idea that interocular ID thresholds are mediated by a mechanism that assesses local interocular contrast differences.

Figure 8b plots the data from the first experiment separately for the two test contrasts but this time with the test threshold IDs recalculated as \( C_{DIFF} \), expressed in % contrast. The figure reveals that these interocular contrast difference thresholds are higher for the higher test contrast, unlike the ID values seen in Figure 3. That the thresholds are higher when expressed in terms of RMS contrast differences is perhaps expected given the well-known finding that contrast increment thresholds increase with pedestal contrast, at least for suprathreshold pedestals (e.g., in the context of binocular vision see Meese et al., 2006; Georgeson et al., 2016).
Tuning to orientation and SF

Our results show that adaptation to IDs is selective for the orientation and SF relationship between the adaptor and test. Let us take the orientation results first. In their study of Li and Atick’s (1994) efficient coding theory in relation to orientation perception, May et al. (2016) also probed the orientation relationships between adaptor and test. Their test patterns consisted of different images presented to the two eyes such that the binocular summation and binocular difference signals were gratings tilted in opposite directions to give ambiguous information about tilt. They found that correlated and anticorrelated noise...
adaptation shifted the perceived tilt of the gratings in opposite directions, consistent with the idea that the summing and differencing signals were independently adaptable. They also found, across 16 test subjects, when the adaptor and test orientations were orthogonal, the magnitude of the shifts was reduced by about half, but not eliminated. In the present study, the differential effect of correlated versus anticorrelated adaptation on ID thresholds was eliminated when adaptor and test orientations were orthogonal in three out of the four subjects tested (see left-most data points in Figure 5). Our subject pool is arguably too small to draw any firm conclusions about the exact size of the reduction of the effects in the orthogonal orientation case, but it may be that the detection of IDs is more sharply tuned to orientation than are other manifestations of binocular differencing. This would suggest different binocular differencing channels for different functions.

Figure 4. Data from Experiment 1. Thresholds IDs as a function of test RMS contrast for uncorrelated (Uncorr.), monocular (Monoc.), and no-adaptor conditions. Error bars are bootstrap errors. Bottom graph shows the normalized (geometric) mean threshold across observers, with standard errors calculated across observers.
A reviewer also pointed out that it is possible that the nonhorizontal adaptors evoked greater vergence eye movements due to their relative depth uncertainty, which may have made them less effective as adaptors.

While the orientation as well as SF tuning results are consistent with the idea that there are multiple channels for detecting IDs, each selective to a narrow range of orientations and SFs, our results do not prove this. We cannot rule out the possibility that there exists a single channel for detecting IDs that is maximally sensitive to horizontal orientations and a SF of around 0.5 cpd, with sensitivity declining at other orientations/SFs. However, a single channel optimally sensitive to horizontal and 0.5 cpd seems unlikely to us given that the visual world naturally generates IDs at all orientations and SFs.

Figure 5. Results from Experiment 2. Threshold IDs are plotted against adaptor orientation, for a test orientation of 90° (arrow) and for correlated and anticorrelated adaptors. Error bars are bootstrap errors. The bottom graph shows the across-subjects’ average ratio of anticorrelated to correlated adaptor thresholds. Error bars are standard errors across observers.
To address the single- versus multiple-channel issue, further experiments using adaptors and tests with a range of orientation relationships will be needed.

**Binocular differencing channel**

In the Introduction we mentioned a number of studies providing support for the existence of a binocular differencing channel. Some of these studies were motivated by a recent theory of binocular vision advanced by Li and Atick (1994) and Zhaoping (2014; Li and Zhaoping are the same person: Zhaoping Li) that suggests that early in vision the retinal images of the two eyes are processed by two binocular channels, $B_+$ that sums their signals, and $B_-$ that differences them. Crucially, the two channels are subject to separate gain controls, with the gain being adjustable by, among other things, adaptation. Underpinning the idea of the $B_+$ and $B_-$ channels is that they constitute an efficient code for representing binocular information, since they serve to decorrelate the highly correlated left and right eye signals. As mentioned in the Introduction, there is evidence for involvement of the $B_-$ (and $B_+$) channel in a variety of visual tasks, such as contrast detection, motion perception, orientation processing, binocular rivalry, and stereopsis. From our finding that the detection of IDs is highly adaptable, and that the degree of adaptation increases with the strength of the interocular contrast difference signal (Figure 8), we suggest that the proposed $B_-$ channel also mediates the detection of IDs.

**Detecting interocular correlation, via the summing channel?**

Our findings complement those of Stevenson et al. (1992) who used dynamic random-dot stereograms to quantify the ability to detect small amounts of interocular correlation (i.e., departures from zero correlation). In their study, correlation thresholds were elevated by adapting to perfectly correlated images, while in complementary fashion we found that adapting to uncorrelated and anticorrelated images.

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Figure 6. Results for Experiment 3. Threshold ID as a function of adaptor SF in cycles per patch (cpp), for correlated versus anticorrelated adaptors. The test SF was 4 cpp (arrow). Asterisk shows the one condition for which bootstrap errors were unobtainable.
raised thresholds for detecting departures from correlation. The impairment of correlation detection (Stevenson et al., 1992) was disparity-specific: The largest effect was obtained when the test correlation (embedded in uncorrelated noise) had the same disparity as the adaptor. They interpreted these results as due to adaptation of disparity-tuned neurons within the stereovision system. This seems very likely but also suggests that, in our paradigm, we may be able to tap into the B+ channel (in addition to the B−/C0 channel), even while silencing the stereo system by the use of horizontal gratings. In future experiments, we plan to adapt to perfect correlation (without stereo disparity) but then test for the impairment of correlation detection (i.e., the detection of small increases in correlation from an uncorrelated or anticorrelated baseline). We predict the converse of our present findings—that this task will be impaired by adapting to perfect correlation via the B+ channel, but unaffected by adapting to de-correlation via the B− channel.

Keywords: adaptation, interocular correlation, interocular differences, interocular phase differences, binocular differencing channel

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Corresponding author: Frederick A. A. Kingdom.
Email: fred.kingdom@mcgill.ca.
Address: McGill Vision Research, Department of Ophthalmology, Montréal General Hospital, Montréal, Canada.

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