



Evidence for strictly monocular processing in visual motion opponency and Glass pattern perception

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ABSTRACT

When presented with locally paired dots moving in opposite directions, motion selective neurons in the middle temporal cortex (MT) reduce firing while neurons in V1 are unaffected. This physiological effect is known as motion opponency. The current study used psychophysics to investigate the neural circuit underlying motion opponency. We asked whether opposing motion signals could arrive from different eyes into the receptive field of a binocular neuron while still maintaining motion opponency. We took advantage of prior findings that orientation discrimination of the motion axis (along which paired dots oscillate) is harder when dots move counter-phase than in-phase, an effect associated with motion opponency. We found that such an effect disappeared when paired dots originated from different eyes. This suggests that motion opponency, at some point, involves strictly monocular processing. This does not mean that motion opponency is entirely monocular. Further, we found that the effect of a Glass pattern disappeared under similar viewing conditions, suggesting that Glass pattern perception also involves some strictly monocular processing.

1. Introduction

When participants observe stimuli wherein opposing motion signals are locally balanced (i.e., signals for one direction appear near signals for the opposing direction with one-to-one pairing), researchers observe suppression in visual area V5/MT (Qian & Andersen, 1994b; Heeger et al., 1999; Thompson, Tjan, & Liu, 2013). Area V5/MT is well understood as being selective for motion direction, and the suppression of activity in this area under such stimulation is called *motion opponency* (but see Garcia & Grossman, 2009, who suggested opponency also at V2, V3, and V4). During motion opponency, participants exhibit reduced motion sensitivity (Thompson & Liu, 2006; Silva & Liu, 2015) and fail to learn motion discrimination tasks (Lu, Qian, & Liu, 2004). By comparison, when a display contains signals for two opposite vectors of motion, but these signals are locally *unbalanced* (i.e., signals for one direction do not appear near signals for the opposing direction), participants perceive two coherent surfaces moving transparently through one another (Qian, Andersen, & Adelson, 1994a) and are able to learn motion discrimination tasks (Thompson & Liu, 2006).

Although superimposed sine-wave and square-wave gratings can activate motion opponency, random fields of paired dots (“random dot kinematograms,” or “RDKs”) are commonly used. Opponency-activating RDKs consist of dots that move parallel to a single axis of motion. These dots are locally paired and typically oriented such that paired dots move collinearly² toward or away from each other (the “counter-phase,” or “CP,” condition). During motion opponency with such paired dots, a participant will perceive mostly nontransparent flicker motion. However, when the same participant is presented with a similar RDK that is animated such that paired dots instead move collinearly in the same direction with each pair moving in either of two opposing directions (the “in-phase,” or “IP,” condition), the participant will weakly perceive the transparent motion of two sheets of dots.

When asked to identify the axis of motion of an RDK, the participant will perform worse under the CP condition as compared to the IP condition, and this difference in response accuracy between the two conditions is a behavioral effect used to index motion opponency (Lu et al., 2004; Thompson & Liu, 2006; Silva & Liu, 2015). Of course, there are many physiological factors that might lead to variation in performance

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² We should note that Qian et al. (1994a) showed that collinearity is not strictly necessary: paired dots with orthogonal offsets less than 0.2° elicit motion opponency (with diminishing effects at larger offsets).

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(e.g., changes in neural synchrony), so it is important to clarify that motion opponency is the reduction in *average* firing of MT neurons (i.e., all other factors being equal), a reduction that is attributed to the locally balanced motion stimulus (Qian & Andersen, 1994b; Hibbard & Bradshaw, 1999; Thompson et al., 2013). Behavioral measures are used to index specifically this effect and not absolute MT suppression or other physiological effects that may occur in tandem.

Although the ecological function of motion opponency is open to debate, many vision scientists believe it is an important mechanism for noise reduction in motion processing whereby an overall motion direction may be extracted from a noisy or sparse velocity field (Snowden, Treue, Erickson, & Andersen, 1991; Born & Bradley, 2005).

1.1. Do locally opposing motion signals need to come from the same eye?

Despite what we know about motion opponency, there remains an important outstanding question: to what extent is motion opponency monocular versus binocular? Specifically, do opposing motion signals need to originate from the same eye to elicit motion opponency, or can they come from different eyes? This paper aims to answer this question. An answer could have important implications for our understanding of motion processing. Standard models of motion processing generally do not address this kind of issue. They operate on single images, so they can only account for the monocular or cyclopean aspects of motion processing (van Santen & Sperling, 1984, 1985; Adelson & Bergen, 1985; Qian et al., 1994c; Simoncelli & Heeger, 1998; Bowns, 2018). The three-motion-systems theory (as originally formulated by Lu & Sperling, 1995) considered the integration of two eye images, but it posited first-order motion detection only *within* eye channels. Lu and Sperling (2001) amended this by including *interocular* first-order motion detection in their theory, prompted by the findings of Carney & Shadlen (1992,1993) and Carney (1997). In spite of such findings, our review of the literature suggests that the topic of early interocular motion integration has not received much attention and deserves further investigation.

Some studies have attempted to answer our question (“do opposing motion signals need to originate from the same eye to elicit motion opponency?”) using a different class of stimuli: drifting gratings. For two superimposed gratings moving in opposite directions, Stromeyer, Kronauer, Madsen, and Klein (1984) found that contrast changes were easier to detect when the gratings changed with opposite polarity (i.e., one increased in contrast while the other decreased) than with the same polarity (i.e., both increased or decreased in contrast). This effect has been attributed to motion opponency, and Gorea, Conway, and Blake (2001) found that this effect did not persist under dichoptic viewing conditions. They interpreted this result as evidence of monocular motion opponency, answering our question in the affirmative. However, motion perception is not necessary to detect changes in contrast, so it is not clear how much of their observed effect may be attributed to motion opponency versus motion-agnostic contrast change detection mechanisms. Using a similar set of stimuli, Maehara, Hess, and Georgeson (2017) asked participants to discriminate the motion direction of target gratings (treating a contrast increment as a target grating superimposed on a pedestal). They used their data to compare monocular and binocular opponency models and found that their data were consistent with either possibility. They performed the same comparison using the data of Gorea et al. (2001), ruling in favor of the monocular model but noting the limitations of the earlier study’s design.

Although Maehara et al. tested competing monocular and binocular models, motion opponency need not be only monocular or only binocular. Qian et al. (1994a) used RDKs to investigate whether motion opponency is *disparity tuned* and found that motion opponency was released as binocular disparity increased (i.e., as paired dots appeared to be separated in depth). Others have found that motion transparency of RDKs improved when depth cues were used to separate the motion signals (Snowden & Rossiter, 1999; Hibbard & Bradshaw, 1999; Greenwood & Edwards, 2006). These results show that there is some

aspect of motion opponency that is strictly binocular: they find that motion opponency is sensitive to stimulus features such as disparity that are defined only for two eyes. The designs of Gorea et al. and Maehara et al. considered a separate question: is there an aspect of motion opponency that is strictly monocular? This is the question we seek to answer. The disparity-based studies cited above do not preclude this possibility, and we believe that the results of Gorea et al. and Maehara et al. leave the question open.

We also believe that the RDKs used in the present study improve upon the stimulus gratings used in the earlier studies in a number of ways. They (1) allow us to directly control local pairing, (2) allow us to balance single-eye motion signals (thereby mitigating vergence issues due to tracking), and (3) provide a stimulus that unambiguously exhibits directional movement under monocular conditions (note that counter-phase gratings presented monocularly are equivalent to a single amplitude-modulated grating). To our knowledge, no study has used such stimuli to directly test the monocularly of motion opponency. In the present study, we used dichoptic RDKs that had no definable disparity: every dot was presented to only one eye, with pairs defined monocularly (both to the same eye) or interocularly (one to each eye). Thus, we tested the monocularly of motion opponency by isolating the effect of paired dots’ eye-of-origin (i.e., pair ocularity).

We know of three other studies that have used stimuli like those of the present study: two concerning binocular rivalry (Matthews, Geesaman, & Qian, 2000; Meng, Chen, & Qian, 2004) and one concerning steady-state visually evoked potentials (SSVEPs) (Kohler, Meredith, & Norcia, 2018). Binocular motion rivalry and SSVEPs may have a complex relationship with motion opponency, so it is not clear what implications these studies have for our present question.

2. Experiment 1

2.1. Design

The present study measured participants’ response accuracy on a two-alternative discrimination task using RDKs uniquely generated for each condition under a $2 \times 2 \times 3$ within-subjects factorial design. The three factors manipulated in this experiment were (1) phase of motion, (2) dot pair ocularity, and (3) orientation of the motion axis. (1) As done in standard motion opponency experiments, we manipulated the phase of motion of locally paired dots between two levels: counter-phase (CP) and in-phase (IP). (2) Since our goal was to determine whether opposing motion signals must originate from the same eye to elicit motion opponency, we manipulated the eye-of-origin of locally paired dots. This manipulation involved two levels: monocular pairing (MO) and interocular pairing (IO). Anaglyph glasses were used to achieve binocular separation, so under MO, locally paired dots were identically colored (red-red or blue-blue). Under IO, locally paired dots were differently colored (red-blue or blue-red). (3) Lastly, we manipulated the angle of offset from vertical of the axis of motion. The discrimination task used in this study required participants to identify the direction of this offset, so manipulating angle modulated the difficulty of the task parametrically. The offset angles tested were $\pm 5^\circ$, $\pm 15^\circ$, and $\pm 25^\circ$. Fig. 1 provides a schematic illustration of the stimulus under the four “primary conditions” (each combination of phase of motion and pair ocularity).

Since dots needed to be paired to create locally opposing motion signals, and since pairings were made parallel to the motion axis on which the behavioral task was defined, each static frame of the stimulus necessarily generated a Glass pattern (Glass, 1969) that provided a static (as opposed to motion-defined) cue for the motion axis orientation. To prevent participants from exploiting such static orientation cues, the present study used the “twin pairs” paradigm of Lu et al. (2004) to reduce the salience of Glass patterns; however, this design does not completely destroy the static orientation cue. Thus, IP conditions served as a control. Except for the relative phase of motion between paired dots, the control stimuli were identical to CP stimuli. Such controls worked

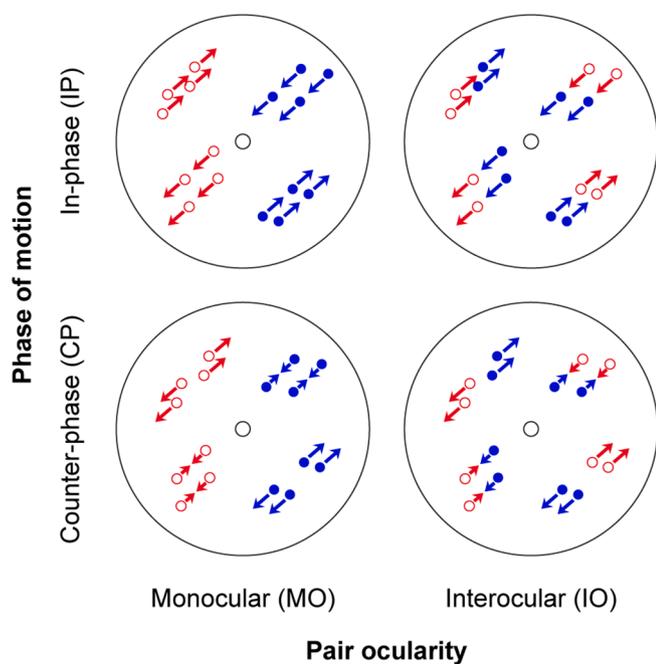


Fig. 1. Schematic illustrations of stimuli under different levels of pair ocularity and phase of motion, all presented at a clockwise offset from vertical with a fixed angle. In each cell, four reference dot pairs and their corresponding twin pairs are visible (in truth, more pairs were present in each stimulus). Dots of one color (red or blue) were visible to only one eye. Arrows indicate a dot's direction of motion. Note that in every condition, the dot field animation presented to a single eye contained opposite motion signals in equal amounts. A black fixation circle was visible at the center of each frame. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

adequately in prior studies since paired dots were always presented to the same eye.

2.2. Participants

One hundred and five UCLA undergraduate students participated in Experiment 1 for extra credit toward a psychology course. All had normal or corrected-to-normal vision by self-report. Informed consent was obtained from all participants, and the experiment was subject to ethical approval by the UCLA Institutional Review Board.

This experiment was run in two versions: one in which the distance between paired dots followed a sawtooth wave (Version 1, $n = 37$); and one in which dot pairs, upon reaching maximum separation, were replaced by new pairs, drawn elsewhere (Version 2, $n = 68$). See the Stimuli section for further details.

2.3. Apparatus

The experiment was conducted with Matlab R2014a (Math Works Inc., Natick, MA) using Psychophysics Toolbox Version 3 (Brainard, 1997; Pelli, 1997; Kleiner, Brainard, & Pelli, 2007), and was run on a standard desktop PC running Windows XP and equipped with an ATi Radeon X300/X550/X1050 Series GPU. Instructions and experimental stimuli were presented on a ViewSonic Graphics Series G75f monitor using the built-in settings for maximum contrast and minimum brightness. This display was the only active light source in the testing room. Its refresh rate was set to 85 Hz. Participants used a chin rest that was placed at a viewing distance of 100 cm from the display. Over the duration of the experiment, participants wore red-blue anaglyph glasses and used a standard QWERTY keyboard.

2.4. Stimuli

Stimuli consisted of randomly generated dot field animations. Each animation lasted 350 ms (500 ms during practice) and consisted of a field of 400 dots moving in opposite directions, parallel to a single orientation (i.e., axis of motion). Dots were drawn in pairs with a maximum within-pair distance of 0.3° , and the dots within each pair were oriented such that an imagined segment connecting them would be parallel to the axis of motion. Paired dots thus moved collinearly.

The relative motion of paired dots was experimentally manipulated. In the IP condition, paired dots moved along their shared line in the same direction. In the CP condition, paired dots moved along their shared line in opposite directions (paired dots moving toward one another did not overlap: upon collision, paired dots swapped positions and continued moving in their original directions). Dots moved at an average velocity of $2.5^\circ/s$, exhibiting coherent motion for a maximum lifetime of 120 ms (the amount of time required for a dot to traverse the maximum within-pair distance of 0.3°). Thus, under CP, paired dots moved as to exchange positions, whereas under IP, paired dots maintained a constant distance (between 0.06° and 0.3° , determined randomly). Pairs were “aged” randomly such that by the first frame of an animation, dots in a pair had less than 120 ms to reach their final positions and subsequently disappeared (“died”). As stated earlier, Experiment 1 was run under two slightly different versions. The difference between versions was this: if a dot pair died before the end of a stimulus presentation, it was either reset, resulting in a sawtooth wave motion (Version 1), or a new dot pair was drawn in a different location (Version 2).

Dot pairs were positioned following the “twin pairs” paradigm of Lu et al. (2004). The 200 dot pairs in every frame of an animation consisted of 100 “reference” pairs and 100 “twin” pairs. To make the dot pairings unambiguous, the centroid of each reference pair was drawn at least 1.2° away from the centroid of any neighboring reference pair. Twin pairs were drawn near reference pairs, one-to-one, as to disrupt any emergent Glass pattern. Each twin pair and its reference pair differed only in the position of their centroids: the centroid of each twin pair was determined randomly to be between 0.06° and 0.15° from the centroid of its reference pair in a random direction. The distance between a reference dot and its twin dot was thus, on average, shorter than the distance between the reference dot and its paired reference dot. Each resultant cluster of four dots (one reference pair and its twin pair) appeared like the vertices of a parallelogram. Presuming that the shorter sides of each implicit parallelogram determined the prevailing orientation of the four-dot cluster, the prevailing orientation of each parallelogram was thus, on average, the direction of the random offset between the twin and reference pairs. Any Glass pattern along the true pair orientation (and thus the axis of motion) was thereby disrupted.

All dots were identical except in color, and the relative color of paired dots was experimentally manipulated. Each dot was drawn with a diameter of 0.06° . Of the 400 dots total in any given frame, exactly 200 dots were red and the remaining 200 dots were blue. Dots were presented against a gray background, and the specific shades of red and blue were tuned such that when viewed through the red lens of the anaglyph glasses, only blue dots were visible (red dots were invisible against the background) and inversely so through the blue lens. Half of the dots were thus visible only to one eye, and the other half were visible only to the other eye when filtered through the anaglyph glasses. A photometer was used to verify that the invisible dots were approximately equiluminant to the background when viewed through the corresponding lens. The photometer was also used to verify that the contrast between visible dots and the background was supra-threshold and roughly equal between eyes. When viewed through the red lens, the red dots had a luminance of 8.7 cd/m^2 , the blue dots had a luminance of 6.7 cd/m^2 , and the background had a luminance of 8.9 cd/m^2 ; when viewed through the blue lens, the red dots had a luminance of 7.8 cd/m^2 , the blue dots had a luminance of 9.4 cd/m^2 , and the background

had a luminance of 9.5 cd/m^2 . In the MO condition, paired dots were of the same color (red-red/blue-blue). In the IO condition, paired dots were of different colors (red-blue/blue-red). Motion signals to each eye were balanced such that the net directional signal was zero: half of the dots of any one color moved in one direction while the remaining half of the same color moved in the opposite direction.

Dot field animations were presented through a circular aperture on screen with a radius of 7° and a gray background. A black circular fixation was presented at the center of this aperture to minimize any misalignment of the eyes. The display area outside the aperture was black and contained no visual information.

2.5. A single trial

Participants identified whether the angular offset of the motion axis from vertical on each trial was clockwise or counterclockwise. After each stimulus presentation, all 400 dots disappeared, and participants pressed the ‘/’ key to respond “clockwise” or the ‘z’ key to respond “counterclockwise.” As feedback, a short beep sounded after an incorrect response. The subsequent stimulus was presented 500 ms after each response. The stimulus presentation for each test trial lasted 350 ms, but practice presentations lasted 500 ms to provide participants additional time to familiarize with the task. If a participant did not respond within 10 s of the stimulus presentation, the lack of response was recorded, and the experiment resumed as though the participant had responded incorrectly.

2.6. Practice

Each participant completed 80 practice trials before beginning the experiment proper. The offset angle of each practice trial became incrementally smaller (i.e., more difficult) during practice: the first trial used 45° , and the last trial used 5° with each subsequent trial using an angle 0.5° smaller than the preceding trial. The direction of the offset was random and counterbalanced. All four combinations of phase of motion and pair ocularity (the four “primary conditions”) were interleaved such that every four consecutive trials belonged to the same combination of the two variables. Such ordering was used to facilitate understanding of the task. Participants were free to respond at their own pace.

2.7. Testing

After practice, participants completed 960 trials in the experiment proper. These trials were divided evenly into six blocks. The first three blocks tested each of the three angular offsets in a random order. The last three blocks followed the reverse order of the first three. Forty trials in each block were dedicated to each of the four primary conditions, with random interleaving. The direction of offset of the motion axis was determined randomly and counterbalanced within conditions within blocks. After the 2nd and 4th blocks, an open-ended break was provided, allowing participants to resume whenever ready.

2.8. Results

Of the 37 participants run on Version 1, one participant did not complete the experiment and was excluded from the analysis. Of the remaining 36 participants, 15 achieved an overall accuracy of 55% or greater. Of the 68 participants run on Version 2, 50 achieved an overall accuracy of 55% or greater. Secondary analyses found that the effects of interest were not modulated by experimental version.

For Version 2, we fit a cumulative Gaussian function to each participant’s data in each condition, setting angle ($-25, -15, -5, +5, +15, +25$) as the independent variable and $P(\text{respond counterclockwise})$ as the dependent variable. Thus, for each participant, we estimated eight parameters: the biases $\mu_{IP,MO}$, $\mu_{CP,MO}$, $\mu_{IP,IO}$, and $\mu_{CP,IO}$, and the standard

deviations $\sigma_{IP,MO}$, $\sigma_{CP,MO}$, $\sigma_{IP,IO}$, and $\sigma_{CP,IO}$ (from which discrimination sensitivity was derived as the reciprocal). Note that the data for Version 1 were only recorded in a summarized format (percent correct) and were thus not amenable to this analysis. Fig. 2 shows the individual data and fits for three participants, one randomly chosen from each of three groups: (1) those who performed below 55% correct overall, (2) those who performed at or above 55% but below 75% correct overall, and (3) those who achieved at least 75% correct overall. Fig. 3 plots the individual discrimination sensitivities in each condition against each other, using the same color coding as Fig. 2 to distinguish the groups. The biases were not systematically different than zero: accuracy was monotonically related to discrimination sensitivity (Fig. 4). Importantly, under IO, discrimination sensitivity was roughly equal comparing CP to IP (i.e., individuals fell along the $y = x$ line in Fig. 3, right) whereas, under MO, discrimination sensitivity was higher for IP than CP (i.e., most individuals fell above the $y = x$ line in Fig. 3, left). A Wilcoxon rank sum test provided evidence ($p = 3.3 \times 10^{-11}$) that the median IP-CP difference under MO diverged from the median IP-CP difference under IO. This suggests an interaction between phase of motion and pair ocularity such that the difference between IP-CP (associated with motion opponency) was greater under MO viewing conditions.

It should be noted, however, that the psychometric function fit poorly for low-performing individuals, so to avoid issues related to the poor fit and to aggregate data across both versions of the experiment, we also analyzed the data using percent correct as the dependent variable. Percent correct is a model-free measure that serves as a proxy for discrimination performance (Fig. 4). As part of this analysis, we also excluded any participants who did not achieve at least 55% correct overall. This gave us an aggregate sample of 65 participants (15 from Version 1 and 50 from Version 2).

A $2 \times 2 \times 3$ within-subjects ANOVA model was fit to this aggregate sample. Table 1 summarizes the test results. Figs. 5 and 6 summarize the average performance across conditions (note the relative boost in accuracy in the IP, MO condition with respect to the other three conditions). Tests yielded significant evidence for effects across all factors. As with the Wilcoxon test on the discrimination sensitivities summarized above, the interaction between phase of motion and pair ocularity was the effect of interest. We found strong evidence for this interaction ($p = 2.6 \times 10^{-10}$): the IP-CP difference observed under MO was not observed under IO (a direct comparison of IP, IO and CP, IO is described below). This pattern in performance suggests that pair ocularity modulated motion opponency, and it provides the main piece of evidence in this study that motion opponency involves some strictly monocular processing.

To gain a better understanding of how the IP-CP performance difference was modulated by IO, we fit a 2×3 within-subjects ANOVA model to the aggregate sample using accuracy data for IO only, for both phases of motion, and for all three angles. The effect of interest in this model was that of phase of motion, and we found no evidence for this effect ($F(1, 64) = 1.29, p = 0.26$). This result suggests that paired dots needed to originate from the same eye to elicit motion opponency, and it provides the second piece of evidence for a monocular component of motion opponency. The lack of an interaction between phase of motion and angle ($F(2, 128) = 0.33, p = 0.72$) reinforces this conclusion. Moreover, it is unlikely that a floor effect was responsible for these results given the modulation of response accuracy by offset angle ($F(1, 64) = 134.8, p = 3.1 \times 10^{-32}$). Such modulation would not be observed if the task were too difficult to perform under IO.

It should be noted that, in Fig. 6, in the CP condition when motion opponency was presumably released from MO to IO, an increase in accuracy was expected but not observed. In the IP condition, going from MO to IO, the accuracy decreased even though no motion opponency was expected. What might this drop in performance from MO to IO be due to? We noticed that a monocular Glass pattern ceased to exist from MO to IO and wondered whether the removal of the monocular Glass pattern was responsible. Experiment 2 tested this possibility.

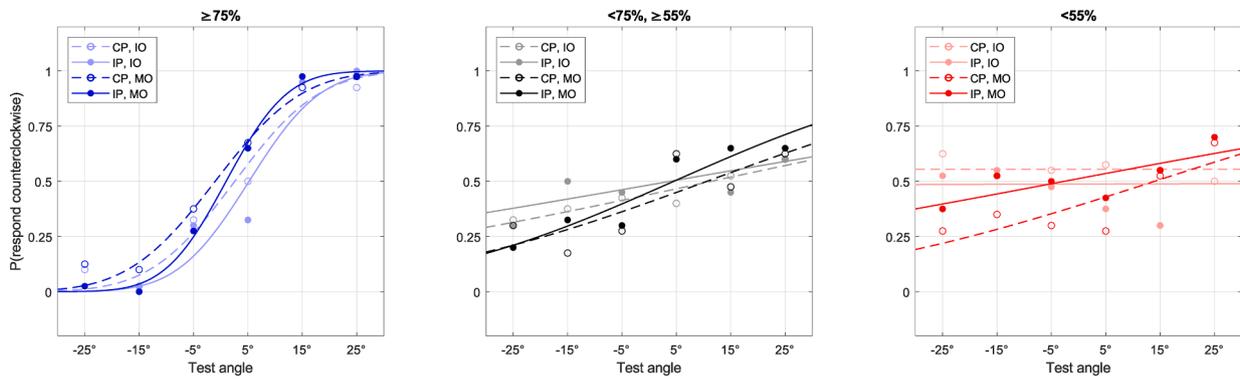


Fig. 2. The individual data and psychometric function fits for three participants, one randomly chosen from each performance group in Version 2. The range of overall accuracy from which each participant was drawn is indicated above each plot. The color coding of groups matches that in Fig. 3.

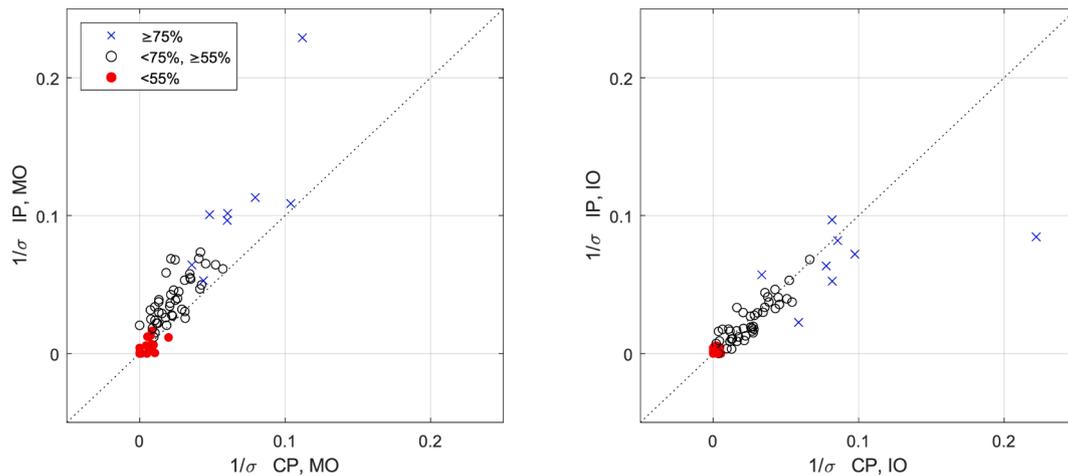


Fig. 3. Scatterplot comparing CP to IP discrimination sensitivity under MO (left) and under IO (right). The dotted line represents equality between CP and IP. Data come from all participants in Version 2 ($n = 68$), with the individuals represented by filled circles falling below the 55% performance criterion. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

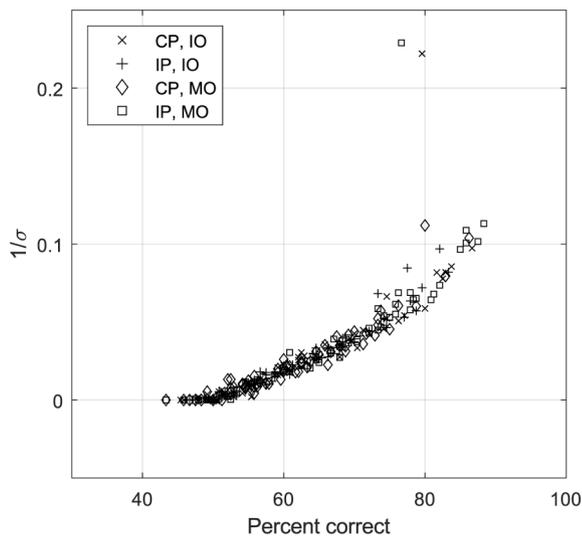


Fig. 4. Scatterplot comparing percent correct to discrimination sensitivity. One symbol represents one participant on one condition. Data come from all participants in Version 2 ($n = 68$). The monotonic relationship between accuracy and discrimination sensitivity justified the use of accuracy as a proxy for discrimination performance. This is because, in a clockwise- or counterclockwise-from-vertical discrimination, systematic bias was not expected and not found (data not shown).

Table 1

Summary of the $2 \times 2 \times 3$ within-subjects ANOVA, fit to the aggregate sample ($n = 65$). The phase \times ocularity interaction was the effect of interest in this model.

Effect	df (residual df)	F	p-value
Phase	1 (64)	32.28	3.5×10^{-7}
Ocularity	1 (64)	21.35	1.9×10^{-5}
Angle	2 (128)	183.0	2.9×10^{-38}
phase \times ocularity	1 (64)	56.01	2.6×10^{-10}
phase \times angle	2 (128)	4.25	0.016
ocularity \times angle	2 (128)	4.33	0.015
phase \times ocularity \times angle	2 (128)	7.60	7.6×10^{-4}

3. Experiment 2

In Experiment 1, we used the “twin pairs” paradigm of Lu et al. (2004) to reduce the salience of Glass patterns; however, we manipulated the eye-of-origin of paired dots (i.e., pair ocularity), and this created a new problem. In the IO condition, neither single-eye image contained a Glass pattern, but in the MO condition, a Glass pattern was present in both. As a result, Glass pattern salience (though reduced by the “twin pairs” design) became confounded with pair ocularity. Albeit worthy of investigation, this potential confound would not affect our interpretation of Experiment 1 since our effect of interest was the interaction between pair ocularity and phase of motion (which is independent of pair ocularity alone).

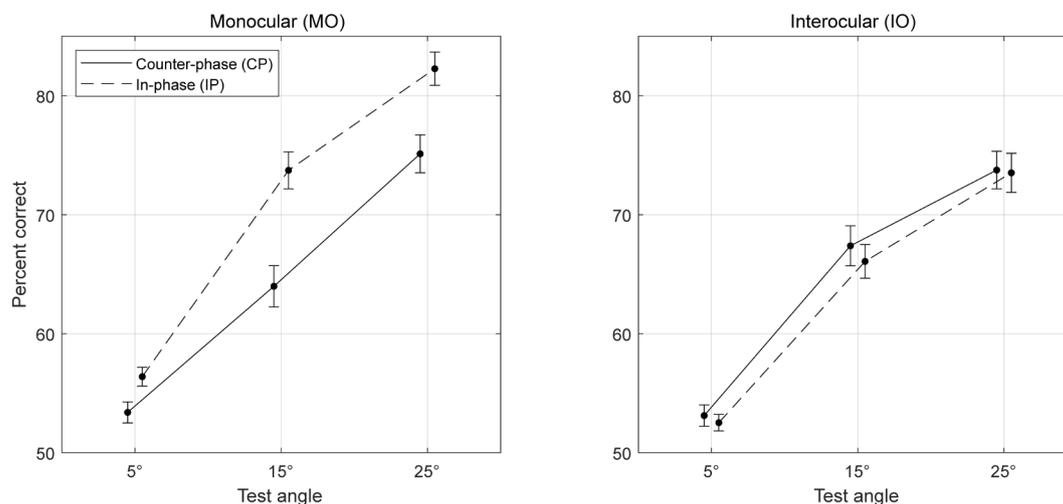


Fig. 5. These line graphs describe the average performance of participants in the aggregate sample ($n = 65$). Left compares performance between CP (solid line) and IP (dotted line) for monocular pairs (MO). Right compares performance between CP and IP for interocular pairs (IO). Bars indicate one standard error from the mean in this and subsequent figures.

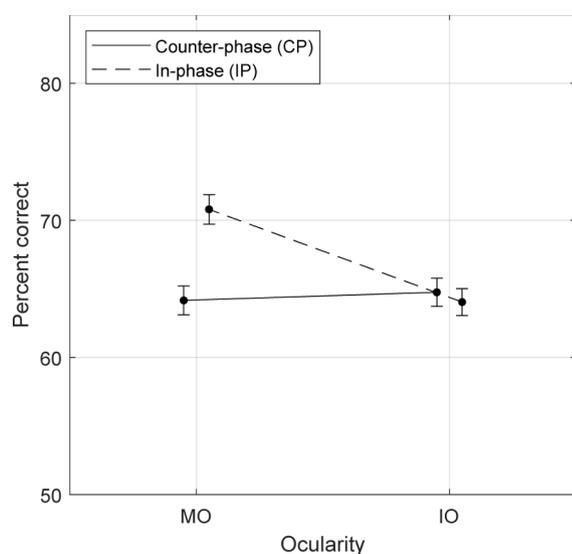


Fig. 6. This graph plots the interaction between phase of motion and pair ocularity. There is a noticeable difference in performance between CP (solid line) and IP (dotted line) under MO, but no such difference under IO.

As it turned out, it was largely unknown whether a Glass pattern was as salient monocularly as interocularly. The only study that we could find that examined this effect directly was published by Glass & Perez (1973), and it relied entirely on self-report. A number of other studies have examined the relationship between Glass pattern perception and binocular depth cues (Earle, 1985; Prazdny, 1986; Khuu & Hayes, 2005), showing that depth can be used to both reveal and destroy Glass patterns. Again, we cannot gain insight into the interocular presentation of dot pairs from such studies: although they involve stimuli that present different images to each eye, every dot is represented in both eyes (unlike in the current study). Interestingly, some work has shown that *adaptation* to a Glass pattern can transfer interocularly (Clifford & Weston, 2005; Vreven & Berge, 2007). However, the interocular transfer (IOT) of adaptation does not imply that Glass patterns themselves are detected interocularly. The current theory of Glass pattern perception involves two stages of processing: (1) early local orientation detection, and (2) late global orientation integration (Wilson, Wilkinson, & Asaad, 1997; Dakin & Bex, 2001; Wilson, Switkes, & De Valois, 2004; Mandelli

& Kiper, 2005). The IOT effect cited above fits within the second stage and thus does not help characterize the early detection stage (at which interocular pairing in Glass pattern perception would presumably need to occur). Of course, there has also been much work regarding Glass pattern perception with respect to contrast (Glass & Switkes, 1976; Kovačs & Julesz, 1992), color (Cardinal & Kiper, 2003; Mandelli & Kiper, 2005), coherence of the global pattern (McGraw, Badcock, & Khuu, 2004; Badcock, Clifford, & Khuu, 2005), and masking (Maloney, Mitchison, & Barlow, 1987; Chen, 2009). But again, these studies do not have much to say about the relationship between Glass pattern perception and pair ocularity.

3.1. Design

Being unable to rely on earlier work to assess the confounding role of Glass pattern salience in Experiment 1, we designed Experiment 2 to directly measure the Glass pattern effect under dichoptic viewing conditions. Stimuli were generated exactly as in Experiment 1 with some simple modifications. Foremost, there was no manipulation of phase of motion: all stimuli were IP. Instead of phase of motion, we manipulated Glass pattern salience. We used five levels (L2, L1, NT, H1, and H2, described below), which were designed to provide a quasi-parametric manipulation of Glass pattern salience.

Experiment 2 used a $2 \times 3 \times 5$ within-subjects factorial design. There were 10 primary conditions each corresponding to a combination of Glass pattern salience (L2, L1, NT, H1, or H2) and pair ocularity (MO/IO). All 10 conditions were tested at three different angles from vertical (± 5 , ± 15 , and $\pm 25^\circ$).

3.2. Participants and apparatus

Forty-eight UCLA students who had not participated in Experiment 1 participated in Experiment 2. The same recruitment procedures, selection criteria, and experimental setup were used as in Experiment 1.

3.3. Modifications to Experiment 1 stimuli

Instead of phase of motion (as manipulated in Experiment 1), we manipulated Glass pattern salience, using five levels (L2, L1, NT, H1, and H2). At the neutral level (NT), the stimuli were identical to those of Experiment 1. At the lower two levels (L1 and L2) paired dots were placed exactly as in Experiment 1 except one dot in each pair was offset horizontally. The direction of this offset was randomly leftward or

rightward with equally many offset in each direction in each eye. The same offset was applied to each reference pair and its twin pair, and the magnitude of this offset was 0.075° under L1 and 0.15° under L2. The overall effect of L1 and L2 was to reduce Glass pattern salience relative to NT by making the pairing axis inconsistent with the axis of motion. At the higher two levels (H1 and H2), the centroid of each twin pair was initially determined exactly as in Experiment 1 then offset horizontally away from its corresponding reference pair. The magnitude of this offset was 0.075° under H1 and 0.15° under H2. Paired dots remained collinear under H1 and H2, and the overall effect of these conditions was to enhance Glass pattern salience relative to NT by making the pairing of dots unambiguous. Fig. 7 illustrates the placement of a reference pair and its twin pair under such manipulations.

3.4. Practice

As in Experiment 1, all participants first received practice. The structure of the practice phase was exactly as before. However, due to the greater number of primary conditions, each kind of stimulus appeared fewer times altogether (80 trials total). Moreover, a completely random order was used, i.e., two consecutive stimuli were not necessarily of the same primary condition.

3.5. Testing

Participants completed 1560 trials over the duration of the test phase, in six blocks, each testing a single angle of 5, 15, or 25° . The six blocks were counterbalanced similarly as in Experiment 1. Each block was evenly subdivided among the 10 primary conditions, with trials randomly interleaved. After the 2nd and 4th block, a break of 30 s was provided.

3.6. Results

As in Experiment 1, we fit cumulative Gaussian functions to participants' data. For each combination of ocularity and Glass pattern level (2×5), we estimated one bias μ and one standard deviation σ per participant. Discrimination sensitivity was taken to be σ^{-1} . The mean discrimination sensitivities are plotted in Fig. 8.

A 2×5 within-subjects ANOVA was used to analyze the discrimination sensitivity data. The purpose of Experiment 2 was to determine

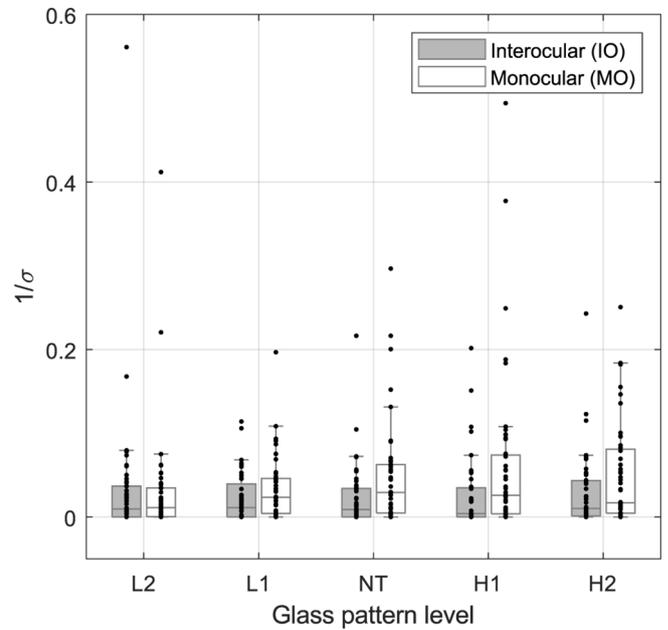


Fig. 8. Discrimination sensitivities estimated for participants in Experiment 2 ($n = 48$) for each combination of ocularity and Glass pattern level. Points represent individual data. The lower and upper bounds of the box represent the first and third quartiles, respectively. The interior horizontal line represents the median, and the whiskers extend to the most extreme non-outlier observation. Outliers were defined using the standard $1.5 \times \text{IQR}$ rule.

Table 2

Summary of the 2×5 within-subjects ANOVA, fit to the Experiment 2 sample ($n = 48$). The Glass \times ocularity interaction was the effect of interest in this model.

Effect	df (residual df)	F	p-value
Glass	4 (188)	2.26	0.064
ocularity	1 (47)	35.85	2.8×10^{-7}
Glass \times ocularity	4 (188)	8.14	4.5×10^{-6}

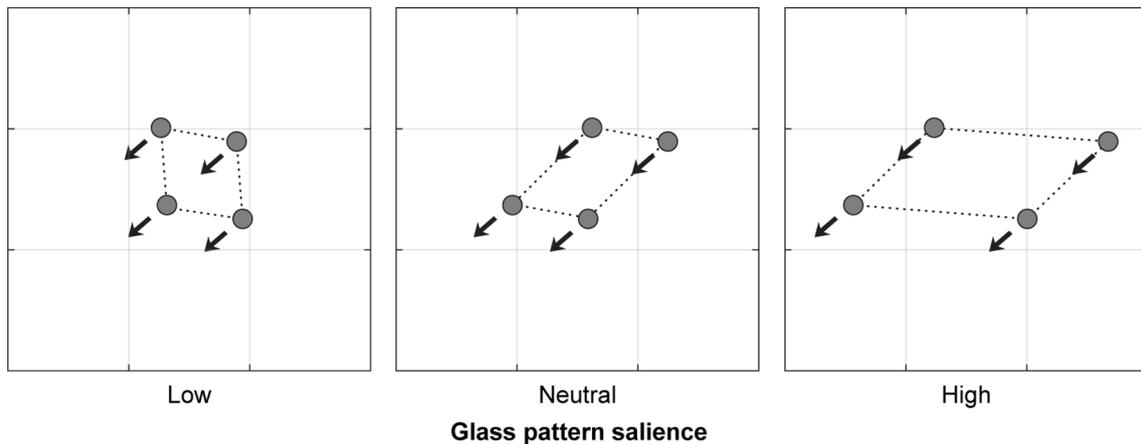


Fig. 7. Schematic illustration of the Glass pattern salience manipulation. Each column contains one reference pair and its twin pair. Arrows indicate a dot's direction of motion. Dotted lines indicate the possible pairings which a participant may perceive as a Glass pattern. At the neutral level (NT), two different Glass pattern orientations may be perceived. The orientation consistent with the motion axis became more legible when we increased the distance between reference and twin pairs (high salience, H1 and H2). Any Glass pattern perceived at low salience (L1 and L2) could not assist in the discrimination task because neither orientation was consistent with the motion axis. In Experiment 2, we also manipulated pair ocularity; this figure assumes MO. Phase of motion was always IP in Experiment 2. Thus, a schematic representation of a complete Experiment 2 stimulus under MO and IO conditions would be analogous to the top-left and top-right cells of Fig. 1, respectively.

whether Glass pattern salience interacted with pair ocularity in Experiment 1. An F-test provided significant evidence of an interaction between ocularity and Glass pattern level, as summarized in Table 2. This result suggests that a Glass pattern can be destroyed by separating paired dots interocularly. Thus, the effect of ocularity observed in Experiment 1 may be explained by a Glass pattern that boosted performance under MO but was not available under IO.

As noted in the Experiment 1 analysis, the psychometric function fit poorly for low-performing individuals, so a $2 \times 3 \times 5$ within-subjects ANOVA was performed, using percent correct instead as the dependent variable (and treating angle as an additional factor). This model, like that above, found significant evidence of an interaction between ocularity and Glass pattern level ($F(4, 188) = 13.24, p = 1.6 \times 10^{-9}$).

4. Discussion

Despite the presumed importance of motion opponency, neither its function nor circuitry is completely understood. The current study attempted to better understand the circuitry question by teasing apart whether two opposing moving dots, each from a different eye, still gave rise to behavioral markers of opponency. In essence, this manipulation probed at the circuitry question from the perspective of eye-of-origin, which has never been studied as far as we know. Eye-of-origin information is critical for other visual processes. Stereoscopic depth perception, for example, depends on how input signals are received by the two eyes, making use of binocular disparity as a depth cue; visual area MT (where motion opponency is most commonly observed) is known to be involved in stereoscopic depth perception and has disparity-selective neurons (DeAngelis, Cumming, & Newsome, 1998). With respect to motion opponency, it has been found that MT cells' responses to opposingly moving dots depended on binocular disparity between the relative depth of the opposing dots (Snowden et al., 1991; Qian & Andersen, 1994b; Bradley, Qian, & Andersen, 1995). Such results indicate that motion opponency involves some strictly binocular processing. After all, sensitivity to binocular disparity is only possible when two eye images are available as input. However, these results do not imply that motion opponency is *entirely* binocular. In RDKs exhibiting binocular disparity, all dots are visible to each eye. Therefore, the possibility of monocular motion opponency is always available and never directly tested. By manipulating eye-of-origin, we examined the possibility that motion opponency involves some strictly monocular processing.

We also studied the contribution of a Glass pattern to task performance under such viewing conditions. Although this pattern provided a static orientation cue, its contribution was likely independent of opponency. Glass pattern perception is generally attributed to visual areas earlier than MT, e.g., V1 and V4 (Wilson et al., 1997). The suppressed responses at MT to opponent paired dots appear to be due only to motion signals and not to any Glass pattern formed by the dot pairs along a common axis; for example, Silva, Thompson, and Liu (2021) used static dot pairs (without the “twin pairs” control as in the current study) with the axis either along the vertical or horizontal orientations. Discrimination between two such cardinal orientations from fMRI BOLD signals collected at the human MT/MST + complex was at chance by machine learning algorithms, indicating that the apparent use of such Glass pattern information by the human participants in the current study was likely outside MT.

We found that motion opponency was elicited by dots originating from the same eye but not by dots originating from different eyes. In Experiment 1, we found significant evidence of an interaction between phase of motion and ocularity such that the typical motion opponency effect (i.e., diminished performance under CP as compared to IP) was observed for monocular dot pairs, but not for interocular dot pairs. This result shows that the eye-of-origin of two paired dots modulates the effect of motion opponency. Further, we found no difference in discrimination accuracy between CP and IP under IO. This suggests that

interocular pairing completely neutralized motion opponency; that is, locally paired counter-phase motions induced no opponency when they originated from different eyes. Taken together, these results provide evidence that, at some point, motion opponency involves strictly monocular processing. This finding agrees with some earlier results using sinusoidal gratings (Gorea et al., 2001; Maehara et al., 2017). Moreover, we suppose that standard models of motion processing (e.g., van Santen & Sperling, 1984, 1985; Adelson & Bergen, 1985; Qian et al., 1994c; Simoncelli & Heeger, 1998) can adequately account for our results given an additional stipulation that their inputs originate from a single eye. It is important to note, however, that the current study used behavior to index a physiological effect. While there is strong evidence that stimuli such as ours modulate opponency (Lu et al., 2004; Thompson & Liu, 2006; Silva & Liu, 2015), we cannot make guarantees without reproducing this study with neuroimaging.

It might be argued that the similarity in performance between CP and IP under IO may be due to issues of binocular vergence rather than monocularly in motion opponency; that is, participants may not have achieved perfect binocular vergence at all times of the experiment, and the resultant offset between paired dots may have released motion opponency. If imperfect binocular vergence had such an influence on our results, we believe that the influence was minimal. It seems unlikely that small deviations from proper vergence would have modulated the motion opponency effect: Qian et al. (1994a) found relatively strong motion opponency with an orthogonal separation of 0.112° between paired dots (the size of this separation is about twice the diameter of a single dot in the present study). It also seems unlikely that a participant performing the task would have experienced larger misalignments, for a number of reasons. (1) The edge of the aperture and the black circle in the middle provided cues for proper fixation that were present at all times of the experiment. (2) The net motion in each single-eye image was zero, so there was no global motion (monocular or binocular) for participants' eyes to track. (3) The correspondence between interocularly paired dots was not horizontal. Thus, no arrangement of the eyes would have made the two single-eye images cohere, and by the same token, participants' eyes had no fixation toward which to reflexively accommodate, other than the intended one.

In Experiment 1, we also found evidence for an effect of pair ocularity such that performance under MO was generally better than under IO. Experiment 2 showed that this effect may be explained by a change in Glass pattern salience. Specifically, Experiment 2 provided empirical evidence that a Glass pattern can be destroyed by separating paired dots interocularly. It is important to note that this conclusion is consistent with the literature on Glass pattern perception. Glass & Perez (1973) observed that a circular Glass pattern composed of (1) a random dot image and (2) a rotated copy of itself was destroyed when the two images were presented binocularly via anaglyph glasses. The present study nearly replicated this setup, using translational (rather than rotational) Glass patterns; moreover, whereas Glass & Perez based their claims on subjective impression, the present study used objective measures, allowing us to make a stronger claim about the disruption of Glass patterns under binocular viewing conditions.

Although no other papers appear to have examined this effect directly, it agrees with the prevailing theory of Glass pattern perception (Wilson et al., 1997, 2004; Dakin & Bex, 2001; Mandelli & Kiper, 2005). This theory posits two stages of Glass pattern perception: (1) local orientation detection in V1, and (2) global orientation integration in V4. Since V1 may be understood as having a binocular representation rather than a cyclopean one (see Barendregt, Harvey, Rokers, & Dumoulin, 2015, for example), and because the detection of an interocular orientation cue is unlikely to occur in V1, this theory predicts that an interocular Glass pattern will not be detected. This is consistent with our results. To underscore this conclusion, the results of Wilson et al. (1997) suggest that Glass patterns with parallel structure (as in the stimuli of the present study) are only processed locally in V1; they suggest that global pooling in V4 occurs only for other (i.e., concentric, hyperbolic, and

radial) Glass patterns.

Thus, in the context of the literature on Glass pattern perception, the function of Experiment 2 is two-fold: (1) it provides evidence for the effect of Glass pattern salience on the results of Experiment 1, and (2) it replicates an effect that has only been reported once before using subjective measures (Glass & Pérez, 1973).

CRedit authorship contribution statement

Sebastian Waz: Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Visualization. **Zili Liu:** Conceptualization, Methodology, Resources, Writing - review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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