Spatial proximity modulates the strength of motion opponent suppression elicited by locally paired dot displays

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ABSTRACT

Locally paired dot stimuli that contain opposing motion signals at roughly the same spatial locations (counter-phase stimuli) have been reported to produce percepts devoid of global motion. Counter-phase stimuli are also thought to elicit a reduced neural response at motion processing brain area MT/V5, an effect known as motion opponency. The current study examines the effect of vertical counter-phase background motion on behavioral discrimination of horizontal target motion. We found that counter-phase backgrounds generally produced lower behavioral thresholds than locally unbalanced backgrounds, an effect consistent with the idea that counter-phase motion elicits opponency. However, this effect was apparent only if the paired dots were close enough in proximity that they crossed one another during their movement. Furthermore, we found that counter-phase stimuli containing within-pair dot crossing elicits similar behavioral thresholds to non-motion flicker stimuli. These results provide insight into the requirements for activating opponency in the brain and suggest that the brain processes counter-phase and flicker stimuli similarly due to opponency.

1. Introduction

The perception of motion is essential to successfully navigate the world. However, extracting useful motion information from a visual scene is challenging. For example, simple low-level motion detectors cannot distinguish flicker noise from meaningful motion information. Flicker noise occurs with abrupt changes in luminance; any sudden onset or offset of a bright object within a darker visual scene will elicit flicker noise during visual processing. Flicker is associated with omnidirectional motion energy that contains no useful directional information for the observer (Bradley & Goyal, 2008; Qian, Andersen, & Adelson, 1994b). Therefore, it is beneficial for the visual system to possess some mechanism that suppresses the processing of flicker noise during motion perception, allowing for better processing of concurrently-presented directional motion information.

Area MT/V5 of the visual cortex has been postulated to play a role in suppressing flicker processing (Marcar, Zihl, & Cowey, 1997; Snowden, Treue, Erickson, & Andersen, 1991). MT lesions have been shown to impair the discrimination of a motion signal in noise (Newsome & Paré, 1988). Extending this finding, Rudolph and Pasternak (1999) found that monkeys with MT lesions exhibited long-lasting performance deficits in tasks requiring the extraction of motion information from noisy stimuli, even as task performance gradually improved in conditions with less noise. Furthermore, while V1 neurons

fire vigorously to flicker, MT neurons exhibit a relatively muted flicker response (Qian & Andersen, 1994; Snowden et al., 1991).

Classic motion processing models generally contain an opponency stage in which the overall motion output is calculated by subtracting the responses of opposing motion-selective cells (Adelson & Bergen, 1985; Qian, Andersen, & Adelson, 1994b; Simoncelli & Heeger, 1998; van Santen & Sperling, 1984, 1985). Because it suppresses the local omnidirectional motion signals composing flicker noise, motion opponency has been suggested to be play a fundamental role in visual noise reduction (Born & Bradley, 2005; Bradley & Goyal, 2008; Qian et al., 1994b). In a series of influential papers, Qian and colleagues (1994, 1994a, b) presented results suggestive of opponency in the primate brain. They found that visual dot displays containing two opposing motion directions failed to elicit a strong MT response if the opposing motion signals were locally paired and placed spatially near one another, creating a locally balanced stimulus. In contrast, area MT exhibited a stronger response if the opposing signals were unpaired and randomly distributed throughout the display. The balanced stimulus can be said to exhibit counter-phase motion (Lu, Qian, & Liu, 2004; Silva & Liu, 2015), and the acute neural suppression that occurs in response to counter-phase motion is considered a consequence of motion opponency (Heeger, Boynton, Demb, Seidemann, & Newsome, 1999; Lu et al., 2004; Qian & Andersen, 1994).

Locally balanced displays have also been studied behaviorally,

generally finding that observers perceive global motion in the average direction of the locally balanced dot signals (Curran & Braddick, 2000; Edwards & Metcalf, 2010; Matthews, Geesaman, & Qian, 2000; Watanabe & Kikuchi, 2006). Therefore, counter-phase motion can be considered a special case that averages to zero net global motion, consistent with Qian et al.'s (1994a) original behavioral finding that counter-phase displays tended not to produce percepts of global transparent motion.

Perceptually suppressive relationships also exist between multiple simultaneously-presented motion directions in locally unbalanced displays. In the absence of depth or color cues, unidirectional motion perception is reported to be easier than bidirectional transparent motion perception (Braddick, Wishart, & Curran, 2002; Curran, Hibbard, & Johnston, 2007; Mather & Moulden, 1983; Snowden, 1990). In fact, Edwards and Greenwood (2005) found that the coherence threshold required to detect a unidirectional signal was roughly one-third the coherence required to detect a bidirectional signal. These studies provide evidence that the simultaneous perception of two overlapping global motion directions is more difficult than the perception of a single global motion direction. However, the very presence of a bidirectional stimulus does not guarantee hindered processing of an individual motion signal if the second signal is task-irrelevant. Edwards and Nishida (1999) presented a transparent motion stimulus with orthogonal global motions but required participants to pay attention to only a single direction. They found that the amount of task-interference elicited by a coherent motion background was about equal to amount elicited by incoherent motion noise.

Nevertheless, it might still be expected that a horizontal target embedded within a vertical non-opponent background should be less discriminable than a horizontal target embedded within an opponent counter-phase background. The counter-phase background, containing locally-balanced and opposing motion signals, would elicit no perception of global motion due to opponency. Therefore, the target stimulus in this background should effectively be unidirectional, strongly coherent, and readily discriminable. In contrast, a target signal embedded within an orthogonal and locally-unbalanced background may be relatively more difficult to discriminate due to interference from the non-suppressed directional background. Interestingly, Silva and Liu (2015) tested this hypothesis and found the opposite result: participants performed better when a to-be-discriminated target motion was embedded within a background of locally unbalanced directional signals.

If their counter-phase stimulus is assumed to elicit opponency, then Silva and Liu's (2015) result may be surprising. However, their counter-phase stimulus differed from Qian and Andersen's (1994) original stimulus in a number of ways. While both studies used comparable maximum dot separations, Silva and Liu (2015) used two-frame apparent motion and did not allow counter-phase dots to cross within-pairs. These differences may have affected the strength of the opponency elicited by Silva and Liu's (2015) counter-phase displays. For example, two-frame stroboscopic apparent motion is believed to drive MT cells relatively poorly (Mikami, Newsome, & Wurtz, 1986), and behavioral data supports the idea that stroboscopic motion stimuli are better integrated over multiple successive frames (Snowden & Braddick, 1989). If two-frame motion is an unreliable probe of MT activity, the suppression elicited by opponency may be difficult to detect using Silva and Liu's (2015) two-frame stimuli. Furthermore, a localized opponent mechanism should produce the strongest effect when the opposing motions are as close together as possible. The opponency elicited by Silva and Liu's (2015) counter-phase stimulus might have therefore been compromised due to the dots' inability to travel near enough to cross.

In the current study, we carefully examine the consequences of manipulating average within-pair dot separations (Experiment 1) as well as the number of frames used to represent motion (Experiment 2). In Experiment 3, we examine similarities between flicker and counter-phase stimuli and test the effect of background motion coherence on

task performance. All together, these experiments provide new insight into the utility and specificity of the brain's implementation of motion opponency.

2. Experiment 1: Effect of dot crossing

2.1. Experiment 1 method

2.1.1. Task

Participants observed a dot stimulus containing horizontal target motion and vertical background motion. Participants used the arrow keys to indicate whether the target motion was leftward or rightward (Silva & Liu, 2015).

2.1.2. Stimulus dots

The stimulus backgrounds consisted of 1352 white (luminance 19.2 cd/m^2) square dots with a side length of 2 pixels (2.1′) against dark gray (luminance 0.85 cd/m^2). These background dots were locally paired and oriented vertically with variable separation. The dot pairs were distributed throughout the display such that a random but generally uniform coverage of the display was achieved. In order to accomplish this, the paired dots were first arranged as a 26×26 square grid extending 12°. Every other column of the grid was then moved up 13 pixels (13.5′). Each pair was therefore separated from their nearest vertical neighbors by 27 pixels (28.1′), from their nearest horizontal neighbors by 54 pixels (56.2′), and from their nearest oblique neighbors by 31.2′. Finally, each pair was given a random vertical and horizontal offset uniformly sampled between ± 12′. To prevent within-pair dot overlap during the vertical counter-phase movement, every dot was horizontally separated from its paired partner by 4′.

A varying number of target dots were randomly distributed throughout the background grid, and a circular viewing window of diameter 12° circumscribed the grid so that any dot outside the window was not visible to participants. All dots simultaneously traveled in a straight line for 4 frames and moved a total of 8′. Background dots moved vertically, while target dots moved coherently either leftward or rightward. The monitor's refresh rate was 85 Hz, and the dot speed was 3.8°/s.

2.1.3. Experiment 1A conditions

Experiment 1 was carried out in two independent parts using separate participants. In any given Experiment 1A counter-phase trial, the initial vertical within-pair dot separation and the initial movement were set to one of the following: + 24′, + 20′, + 16′, + 12′, + 8′, + 4′, − 0′, − 4′, or − 8′, where the + indicates initial inward movement, and the - indicates initial outward movement. Dots were never vertically separated by more than 24′, the maximal separation Qian et al. (1994a) reported to elicit behavioral effects consistent with opponency.

It is important to note that aside from the background with 8′ initial separation, all counter-phase backgrounds shared the same average dot separation with another counter-phase background moving in the opposite direction. For example, the conditions with initial within-pair separations of 16′ and 0′ both exhibited an average of 8′ vertical separation. For clarity, we will refer to counter-phase conditions by their direction of movement (or the direction with the longest duration, in the case of crossing pairs) and their average dot separation (e.g. outward 8′). For the counter-phase condition with an initial separation of 8′, we will use the term "balanced".

As a comparison for the counter-phase backgrounds, Experiment 1A also tested non-opponent in-phase backgrounds (Lu et al., 2004; Silva & Liu, 2015; Thompson & Liu, 2006; Thompson, Tjan, & Liu, 2013). In-phase stimuli are similar to counter-phase stimuli, except that both dots forming a pair travel in the same direction. Critically, counter-phase and in-phase stimuli contain equal numbers of opposing motion signals. The tested in-phase backgrounds had vertical within-pair separations equal to or near the average separations of the counter-phase

backgrounds. Therefore, in-phase within-pair separations of 16′, 12′, 8′, and 4′ were tested[1]. Schematic illustrations of in-phase and counter-phase stimuli are presented in Fig. 1.

2.1.4. Experiment 1B conditions

Experiment 1B tested counter-phase backgrounds with dot separations large enough that crossing never occurred; all other stimulus parameters were identical between Experiments 1A and 1B. Average Experiment 1B separations were: 10′, 12′, 14′, 16′, 18′, 20′, and 22′. Both inward and outward conditions were tested. During the inward and outward 10′ conditions, the vertical separation was 2′ at the nearest point and 18′ at the farthest point. During the inward and outward 22′ conditions, the vertical separation was 14′ at the nearest point and 30′ at the farthest point. All other dot separations fell between these two extremes.

2.1.5. Stimulus and procedure

Each trial began by revealing a small white fixation cross 300 ms before the dots became visible. The dots began their movement 500 ms after their onset and remained visible for 200 ms after the termination of their movement. Whenever a trial was answered incorrectly, participants heard an auditory beep. All experiments were programmed in Python using the Psychopy library (Peirce, 2007, 2009) and run on Windows 7 using a Dell Optiplex 745 PC and a 17″ Compaq FS7600 CRT monitor. The resolution was 1024 × 768, and the refresh rate was 85 Hz. Participants viewed the display from 100 cm away.

Participants performed a short practice block of in-phase and counter-phase trials before beginning the main experiment to verify that they understood the task. If a participant was unable to achieve 60% accuracy on this block, it was repeated until 60% accuracy was achieved. No participant required more than 2 training blocks, and all participants completed training in < 5 min.

During the main experiment, the number of target dots displayed on each trial was adjusted on a trial-by-trial basis in increments of 7 according to a 2-down, 1-up staircase procedure to obtain the performance threshold (Levitt, 1971). One staircase per condition was used, and all staircases were randomly interleaved. Each condition was presented 100 times, and the threshold was estimated by averaging the last 6 reversals along with the final staircase value. All staircases began at 245 dots. Participants were given a short self-timed break after every 100th trial.

2.1.6. Subjects

Twenty-four participants were recruited for Experiment 1A and twenty-five different participants were recruited for experiment 1B from the UCLA undergraduate subject pool for course credit. All participants had normal or corrected-to-normal vision. Informed consent was obtained, and all participants were treated in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Experiment 1A and 1B results

2.2.1. Experiment 1A results

For statistical convenience, the balanced counter-phase condition was not included in the following analysis. As clearly illustrated in Fig. 2, this does not alter our conclusions in any way. A 3 (phase: in-

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[1] Note that no counter-phase condition has a true average separation of 4′. The counter-phase conditions containing initial within-pair separations of 12′ and 4′ exhibit an average separation of 5.6′. In addition, the true average separation of the balanced counter-phase condition is 4.3′. Resolving the small difference between these average separations proved unreliable on our experimental computers. Therefore, a 4′ in-phase condition was tested as a distance-matched control for all three aforementioned counter-phase backgrounds. For cleaner reporting, this text uses the labels "inward 4′" and "outward 4′" for the counter-phase conditions with 5.6′ average separation.
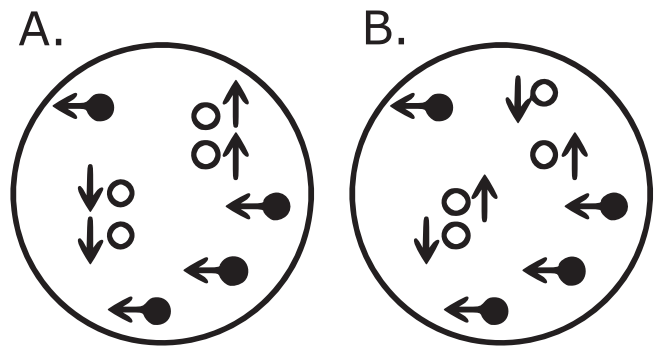

Fig. 1. Diagram of in-phase and counter-phase stimuli. Target dots are colored black and background dots are colored white. The arrows represent the movement of each dot during a trial. A. An in-phase stimulus. B. A counter-phase stimulus.
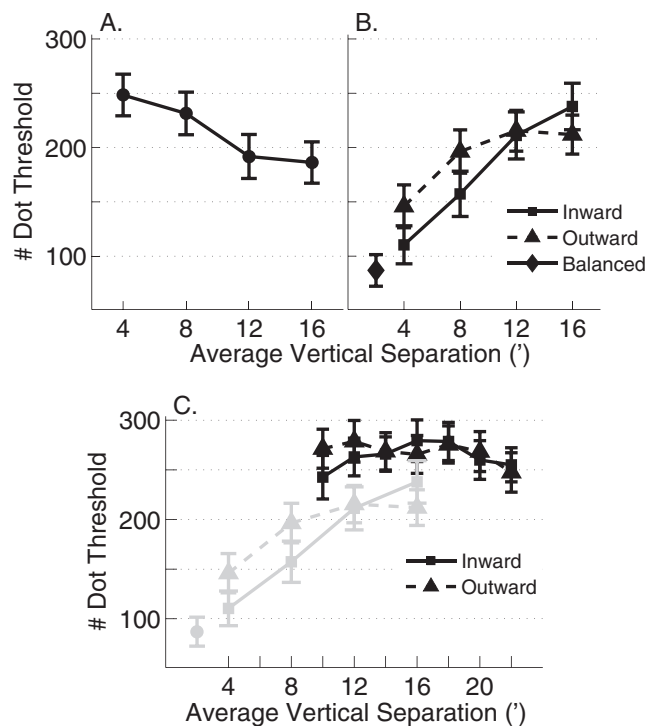

Fig. 2. Experiment 1 thresholds as a function of vertical dot separation. A. Experiment 1A in-phase thresholds. B: Experiment 1A Counter-phase thresholds. The data points with average separations at or below 8′ come from conditions that exhibit within-pair crossing. C. Experiment 1B counter-phase thresholds plotted in black alongside Experiment 1A thresholds plotted in light gray for comparison. Here and in following figures, error-bars are ± 1 standard error of the mean.

phase, counter-phase inward, and counter-phase outward) × 4 (average vertical separation: 16′, 12′, 8′, and 4′) repeated measures ANOVA was run on the data. The main effects of phase and separation were significant, $F(2,46) = 23.0$, $p < .001$, $\eta_P^2 = 0.50$, and $F(3,69) = 20.9$, $p < .001$, $\eta_P^2 = 0.48$, respectively. Pairwise comparisons revealed that in-phase (average: 214.4), counter-phase inward (average: 179.2), and counter-phase outward (average: 192.4) thresholds all significantly differed. The least significant comparison was between the two counter-phase conditions, $F(1,23) = 8.36$, $p = .008$, $\eta_P^2 = 0.27$, uncorrected. A significant interaction was also found, $F(6138) = 45.6$, $p < .001$, $\eta_P^2 = 0.67$. As shown in Fig. 2A and B, each phase condition was affected differently by average separation. This is especially true of in-phase thresholds, which monotonically decrease as separation increases, while both counter-phase conditions monotonically increase with increasing separation. To examine the effect of separation on the difference between inward and outward counter-

phase thresholds, we subtracted the inward thresholds from the outward thresholds for each vertical separation and ran a one-way repeated measures ANOVA on the differences. A significant effect of separation was found, $F(3,69) = 10.2$, $p < .001$, $\eta_P^2 = 0.31$. Planned repeated contrasts found that the difference at 16′ separation (-25.9) was significantly different from the difference at 12′ (4.29), $F(1,23) = 4.40$, $p = .047$, $\eta_P^2 = 0.16$. Furthermore, the difference at 12′ was significantly different from the difference at 8′ (39.0), $F(1,23) = 5.28$, $p = .031$, $\eta_P^2 = 0.19$. However, no significant difference was found between the 8′ and 4′ (35.4) conditions, $p = .74$.

Lastly, we verified whether the differences between inward and outward thresholds were meaningfully different from 0 for each average separation with individual one-sample t-tests, finding that the 12′ difference was not significantly different from 0, $p = .67$. However, the other three differences reached significance, with the least significant being the 16′ difference, $t(23) = -2.99$, $p = .007$, uncorrected.

2.2.2. Experiment 1B results

The Experiment 1B data were analyzed with a 2 (phase: counter-phase inward, and counter-phase outward) × 7 (average dot separation: 22′, 20′, 18′, 16′, 14′, 12′, and 10′) repeated measures ANOVA. No significant main effect of phase was found (inward threshold: 267.5, outward threshold: 267.9), $F(1,24) = 1.01$, $p = .32$. The main effect of average dot separation was small but significant, $F(6, 144) = 3.67$, $p = .002$, $\eta_P^2 = 0.13$. The interaction effect did not reach statistical significance, $F(6144) = 1.91$, $p = .082$, $\eta_P^2 = 0.074$. Fig. 2C plots this data, contrasting it with the Experiment 1A data.

As in Experiment 1A, we subtracted the Experiment 1B inward counter-phase thresholds from the outward counter-phase thresholds and carried out separate one-sample t-tests for each difference. The only comparison to reach significance was the 10′ difference (28.6), $t(24) = 2.28$, $p = .031$ uncorrected. It is interesting to note that while the 16′ difference was significant in Experiment 1A, the same difference was not significant in Experiment 1B, suggesting that the earlier result was spurious. Overall, the few significant effects found in Experiment 1B lack robustness when compared to those from Experiment 1A.

2.3. Experiment 1A and 1B discussion

Experiment 1B thresholds were generally higher than Experiment 1A thresholds, even in shared conditions. We attribute this to random sample error and cohort effects, as the experiments were run with completely separate participants at different points in the academic year. Critically, Experiment 1A found a dramatic relationship between dot proximity and performance that was dependent on phase. In counter-phase conditions, behavioral thresholds increased as dot proximity increased. However, a less striking relationship in the opposite direction was found with in-phase stimuli.

Previous studies have compared counter-phase stimuli to either unpaired or in-phase stimuli (Garcia & Grossman, 2009; Heeger et al., 1999; Lu et al., 2004; Muckli, Singer, Zanella, & Goebel, 2002; Qian et al., 1994a; Thompson et al., 2013), yet little in-depth exploration of in-phase motion has been carried out. The current study suggests that manipulating within-pair separation results in opposite behavioral effects between in-phase and counter-phase stimuli. Because counter-phase stimuli are designed to harness a local opponency mechanism, it is theoretically reasonable that smaller average separations lead to lower behavioral thresholds in trials containing counter-phase backgrounds. However, the opposite effect found in trials containing in-phase backgrounds remains puzzling. Though highly speculative, one possible explanation is that dot proximity might influence in-phase performance due to varying strengths of perceptual grouping. In-phase

paired dots with smaller within-pair separations might be more readily perceived as a unified stimulus element; this stimulus element is larger and more complex than a single dot and might interfere with the task more strongly. Clearly, additional work is required to truly understand the visual processing of in-phase stimuli.

The results of Experiment 1 suggest that task performance is critically dependent on within-pair dot separation. Counter-phase backgrounds produced better performance than in-phase backgrounds when dot proximity was small and dots within-pairs crossed. However, in-phase backgrounds produced better performance than counter-phase backgrounds when dot proximity was too large to allow within-pair crossing, replicating Silva and Liu (2015). Overall, these results are consistent with the idea that counter-phase stimuli do not robustly elicit opponency unless the paired dots are located near enough that they cross during their movement.

Opponency is the proposed mechanism that causes brain area MT to respond weakly to counter-phase motion (Heeger et al., 1999; Qian & Andersen, 1994; Thompson et al., 2013). A potentially related perceptual phenomenon is the tendency to perceive a locally averaged motion direction when viewing paired dot stimuli (Curran & Braddick, 2000; Edwards & Metcalf, 2010; Watanabe & Kikuchi, 2006). In the special case of counter-phase motion, this averaging produces zero net global motion. As a result, the Experiment 1 counter-phase backgrounds were expected to elicit low behavioral thresholds due to opponency. Interestingly, low thresholds were found exclusively when counter-phase dot pairs were positioned near enough to cross one another at some point during their movement. In fact, elevated thresholds were found even when counter-phase dots came within 2′ of crossing. Moreover, the comparison between the inward and outward counter-phase backgrounds revealed a perceptual asymmetry; inward thresholds tended to be lower than outward thresholds. This pattern was entirely confined to the conditions with the three smallest vertical separations across Experiment 1. This may suggest that inward motion elicits stronger opponency in the brain than outward motion, but additional work is required to better understand this asymmetry.

Because Experiments 1A and 1B found fundamentally different results in non-overlapping conditions, we ran a replication study containing counter-phase conditions from both Experiment 1A and Experiment 1B with thirteen new participants. A significant difference between inward and outward conditions was found, $F(1,12) = 9.97$, $p = .008$, $\eta_P^2 = 0.45$. Additionally, a significant main effect of dot proximity was also found, $F(4, 48) = 53.12$, $p < .001$, $\eta_P^2 = 0.82$. The replication data is plotted in Fig. 3. As in Experiments 1A and 1B, only those conditions with dot proximities small enough to allow the paired dots to cross exhibited relatively low counter-phase thresholds. Furthermore, inward thresholds were lower than outward thresholds, an effect again apparent only in conditions with relatively small dot separations. The similarity between the data of the control replication and Experiments 1A and 1B provide additional evidence for the reliability of the Experiment 1 results.
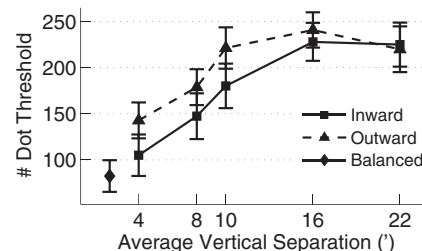

Fig. 3. Replication thresholds as a function of vertical dot separation.

Experiment 1A found that dot proximity is a critical factor in determining whether the in-phase or counter-phase background produces better behavioral performance; performance was higher during counter-phase trials when average dot separation was low, but performance was higher during in-phase trials when dot separation was relatively large. Therefore, Silva and Liu's (2015) result was at least partly due to their counter-phase stimulus using relatively large average dot proximities that did not allow within-pair counter-phase dots to cross. However, another obvious difference between Silva and Liu's (2015) and Qian et al.'s (1994a) stimuli exists; the former used two-frame apparent motion stimuli, while the latter used smooth motion stimuli. Experiment 2 examines whether the use of two-frame stimuli contributes to better in-phase task performance by replicating Silva and Liu (2015) while manipulating the number of frames in the stimulus.

3. Experiment 2: Effect of frame number

3.1. Experiment 2 method

3.1.1. Stimuli and procedure

The stimulus was created similarly to Experiment 1, except for the following differences: To replicate Silva and Liu (2015), counter-phase dots began with a vertical separation either between 4′ and 12′, or between 20′ and 28′. Pairs with larger separations traveled toward one another, while pairs with smaller separations traveled away from one another. In-phase dots were always separated by 16′, the average of the counter-phase dot separation.

The number of frames representing the dot motion varied between 2 and 4. Because the monitor's refresh rate was 85 Hz, each additional frame increased the stimulus presentation length by 1/85 s. As a result, it should be noted that any effect of frame number found in this experiment may in fact be due to an effect of dot speed. Four-frame movies had a dot speed of 3.8°/s, three-frame movies had a dot speed of 5.7°/s, and two-frame movies had a dot speed of 11.3°/s. The experimental procedure was identical to Experiment 1.

3.1.2. Subjects

Twenty-six new undergraduate students from the UCLA psychology subject pool were recruited as in Experiment 1.

3.2. Experiment 2 results

The thresholds were analyzed with a 2 (phase: in-phase and counter-phase) × 3 (frame number: two, three, and four frames) repeated-measures ANOVA. Significant main effects of phase and frame were found, $F(1, 25) = 190.5$, $p < .001$, $\eta_P^2 = 0.88$ and $F(2, 50) = 84.2$, $p < .001$, $\eta_P^2 = 0.77$, respectively. A relatively small but significant interaction was also found, $F(2, 50) = 5.1$, $p = .01$, $\eta_P^2 = 0.17$. Counter-phase dot thresholds (average: 452.4) were always larger than in-phase thresholds (average: 296.7). Therefore, in-phase trials elicited better performance than counter-phase trials, replicating
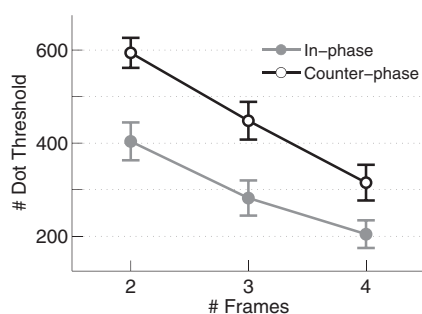
Fig. 4. Experiment 2 thresholds as a function of the number of frames used in the motion stimulus.

Silva and Liu (2015). Planned repeated contrasts found that two-frame thresholds (average: 498.9) were significantly different from 3-frame thresholds (average: 365.1), $F(1,25) = 66.0$, $p < .001$, $\eta_P^2 = 0.73$, and that 3-frame thresholds were significantly different from 4-frame thresholds (average: 259.7), $F(1,25) = 42.2$, $p < .001$, $\eta_P^2 = 0.63$. These data are plotted in Fig. 4.

3.3. Experiment 2 discussion

Experiment 2 examined whether the number of frames used by Silva and Liu (2015) contributed to their counterintuitive finding that counter-phase backgrounds elicited poorer task performance than in-phase backgrounds. The current experiment replicated the previous result in all conditions tested. Counter-phase task difficulty was always greater than in-phase task difficulty, demonstrating that the counterintuitive results found in Silva and Liu (2015), and replicated here, are not due to the use of two-frame stimuli.

It must be noted that a strong main effect of frame number was found; in-phase and counter-phase thresholds both decreased as the number of frames increased. However, Experiment 2 confounded dot speed with frame number. It is therefore impossible to know whether this overall performance change resulted from manipulating dot speed or from manipulating the number of frames used in the stimulus.

Critically, Experiment 2 demonstrated that manipulating frame number does not qualitatively change the relationship between in-phase and counter-phase performance. However, it remains unclear why in-phase performance is robustly higher than counter-phase performance under certain stimulus conditions. In a past study, participants performed a detection task where the target motion was embedded either within orthogonal directional signals or within randomly-moving and incoherent motion noise (Edwards & Nishida, 1999). No performance difference was found between coherent and incoherent conditions. A similar effect may have occurred in Experiment 2. While speculative, Experiment 2 in-phase signals may be more readily perceptually segregated than Experiment 2 counter-phase signals, allowing more independent processing of the target motion during in-phase trials.

Flicker noise contains omnidirectional motion energy at a single point in space. It therefore contributes no meaningful information about real motion in a visual scene. Motion opponency may function to reduce flicker processing in the brain. Because counter-phase motion is locally balanced, it can be considered similar to flicker noise. This similarity is highest at the moment when paired and oppositely-moving dots cross, because this moment contains opposing motion signals in the same location along the axis of motion. If the moment of crossing is critically important for counter-phase stimuli to elicit opponency, this suggests that the human brain's implementation of opponency is highly precise and well-tuned to exclusively reduce the processing of flicker noise. Furthermore, it suggests that crossing counter-phase stimuli and flicker backgrounds may elicit similar behavioral performance. Therefore, Experiment 3 compares flicker noise backgrounds with crossing counter-phase and in-phase stimuli. In addition, Experiment 3 also examines whether a coherent vertical background interferes with the target discrimination task differently than an incoherent background in order to further investigate the low in-phase behavioral thresholds found in Experiment 2.

4. Experiment 3: Flicker stimulus and effect of background coherence

4.1. Experiment 3 method

4.1.1. Stimuli and procedure

Experiment 3 examined coherent and random orientation conditions. During coherent trials, all background pairs were oriented vertically and moved along a common vertical axis. During random trials,

all background pairs were oriented and moved independently, creating a random background with no coherent motion direction.

Experiment 3 also tested a flicker background condition. The first and last frames of the flicker background were identical, but every dot pair was randomly replotted during the central two frames, creating flicker without eliciting any perception of apparent motion. Paired dots were randomly distributed throughout the display in every frame of the flicker background. The flicker within-pair separation was 4′ along the orientation axis (either coherent or random). Experiment 3 also tested the *in-phase 4′* and *balanced counter-phase* backgrounds originally from Experiment 1. All conditions had comparable average within-pair dot separations and all stimuli consisted of 4 frames.

Experiment 1 demonstrated very large differences between in-phase and balanced counter-phase thresholds. Therefore, Experiment 3's in-phase staircases began at the in-phase threshold found in Experiment 1A. Similarly, Experiment 3's counter-phase and flicker staircases began at the balanced counter-phase threshold found in Experiment 1A. All other experimental methods and procedures were identical to Experiment 1.

4.1.2. Subjects

Seventeen new undergraduate students from the UCLA psychology subject pool were recruited as in Experiments 1 and 2.

4.2. Experiment 3 results

A 3 (phase: in-phase, counter-phase, and flicker) × 2 (background motion: coherent and random) repeated-measures ANOVA was used to analyze the Experiment 3 thresholds. Significant main effects of phase, $F(2, 32) = 469.6, p < .001, \eta_P^2 = 0.967$, and background motion type $F(1, 16) = 11.29, p = .004, \eta_P^2 = 0.414$ were found. In addition, phase and background motion interacted significantly, $F(2, 32) = 10.12, p < .001, \eta_P^2 = 0.387$. Planned contrasts found that in-phase thresholds (average: 284.7) were significantly different from both counter-phase thresholds (average: 53.6), $F(1, 16) = 517.1, p < .001, \eta_P^2 = 0.970$, and flicker thresholds (average: 43.6), $F(1, 16) = 662.3, p < .001, \eta_P^2 = 0.976$. However, counter-phase and flicker thresholds did not significantly differ, $F(1, 16) = 2.164, p = .16$. Fig. 5A plots the Experiment 3 thresholds.

In order to investigate the interaction effect, pairwise post hoc comparisons were run for each pair of coherent and random thresholds at every phase condition. We found a significant difference between in-phase random and in-phase coherent thresholds, $p = .003$ uncorrected (random – coherent, mean difference = 49.5). The difference between counter-phase random and counter-phase coherent thresholds was also significant, $p = .018$ uncorrected (mean difference = 11.5). However, note that this difference does not survive Bonferroni correction for 3 comparisons at $\alpha = 0.05$ with critical $p = .0167$. Finally, there was no significant difference between flicker random and flicker coherent thresholds, $p = .44$ uncorrected (mean difference = -3.87).

In the current experiment, the initial staircase positions for each condition were set at the corresponding threshold from Experiment 1.

As a result, the in-phase staircases began at a much higher value than the counter-phase and flicker staircases. Therefore, to verify that the Experiment 3 staircases adequately converged, the average staircase position at each consecutive trial presentation was calculated for every condition. The resulting trial-by-trial staircase positions are presented in Fig. 5B, generally demonstrating good convergence for most conditions. However, the in-phase staircase with random coherence continuously increases with trial number. This suggests that the in-phase random threshold is likely underestimated, further suggesting that the Experiment 3 in-phase threshold data underestimates the effect of motion coherence. However, no such underestimation is present in the counter-phase and flicker threshold data.

4.3. Experiment 3 discussion

Experiment 3 generally found lower thresholds with coherent backgrounds than with random backgrounds. This effect is most apparent in the in-phase condition, likely because only in-phase trials contained unsuppressed background motion. This result is consistent with the notion that coherent in-phase backgrounds can be perceptually segregated, allowing more independent processing and better discrimination of the target motion. Experiment 3 suggests that an additional factor may contribute to the relatively good in-phase performance reported in Silva and Liu (2015); coherent vertical motion may interfere with the discrimination task less strongly than even incoherent motion. Therefore, the results of Experiment 2 and Silva and Liu (2015) may have arisen from a combination of the non-crossing counter-phase background not eliciting strong opponency and the in-phase background not interfering with the discrimination task as strongly as expected.

Nevertheless, the in-phase conditions elicited markedly higher thresholds than the flicker and counter-phase conditions regardless of background coherence. Moreover, comparable thresholds were found in the flicker and counter-phase conditions. This behavioral similarity may suggest a similarity in the visual processing of these stimuli; opponency may have suppressed the directional signals present in the counter-phase background, causing counter-phase and flicker backgrounds to similarly interfere with the discrimination task.

5. General discussion

The current study examined behavioral performance when discriminating a target motion embedded within in-phase, counter-phase, and flicker backgrounds. We found that counter-phase thresholds decreased as within-pair separation decreased. However, this trend only held if the paired dots crossed at some point during their movement. If the dots were separated by more than 2′ throughout their entire lifetime, then behavioral thresholds remained uniformly high. Furthermore, we found that the numerical difference between in-phase and counter-phase thresholds was only subtly manipulated by the use of two-frame stimuli; the effect remained qualitatively similar and robust
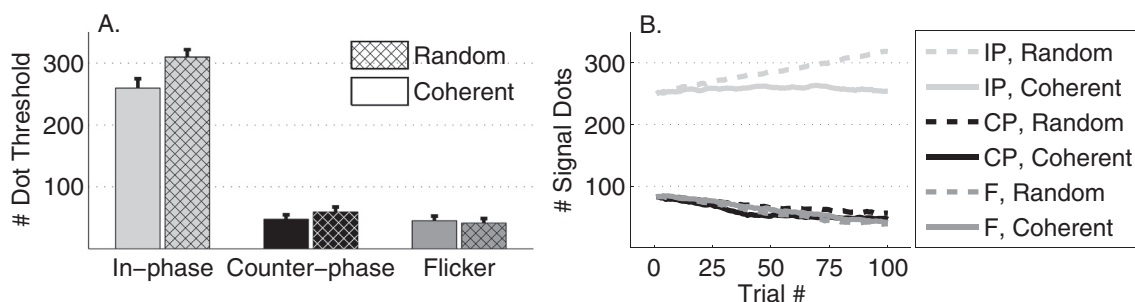

Fig. 5. Experiment 3 threshold and staircase data. A. Average thresholds for in-phase, counter-phase, and flicker stimuli exhibiting coherent or random background orientations. B. Trial-by-trial average staircase behavior in all conditions. The staircase value represents the number of visible target dots at the given trial number.

regardless of frame condition. Finally, we found that the strength of the interference exerted by a crossing counter-phase background was roughly equivalent to the interference exerted by a non-moving flicker background.

In Qian et al. (1994a), counter-phase displays were reported to be devoid of global motion information when the maximum within-pair separation fell within 24′. The current study suggests an additional constraint; the moment when opposing motions cross may be crucially important for activating opponency. Our study found low counter-phase thresholds, consistent with opponency, exclusively in conditions exhibiting within-pair dot crossing. If the dots came even within 2′ of one another without crossing, no evidence for opponency was found.

Interestingly, average dot separation may modulate the strength of opponency differently depending on the spatial dimension of the separation. The current study specifically examined proximity along the axis of motion, finding results suggestive of opponency only when counter-phase dots were located near enough to cross one another. However, previous work examined dot proximity orthogonal to the axis of motion, finding that under certain circumstances, an orthogonal separation of up to 12′ was tolerated before the stimulus appeared transparent (Qian et al., 1994a). The brain's opponency mechanism may therefore require greater local precision along the axis of motion than orthogonal to the axis of motion.

Due to its local balancing, counter-phase motion and flicker noise share similar motion energy profiles, especially at the moment of crossing when both counter-phase dots exactly coincide in time and space. If the strength of opponency elicited by counter-phase motion is dependent on within-pair crossing, manipulating this crossing is an effective way of probing the precision of the brain's implementation of opponency. Overall, the results of the current study are consistent with a highly precise opponent mechanism in the human brain tuned to selectively remove locally-balanced motion energy, such as that found in flicker noise and standard counter-phase stimuli, from further perceptual processing.

6. Conclusions

In the current study, we examined the behavioral effects of in-phase, counter-phase, and flicker backgrounds on target motion discrimination, manipulating the average within-pair separation as well as the number of frames used in the stimuli. Not all counter-phase stimuli we examined produced results suggestive of opponency, and a slight change in average separation produced striking behavioral effects within a restricted range of tested stimuli. Ultimately, this study suggests that the human brain's implementation of opponency is selective for extremely localized opposing motions such as those found in flicker noise.

Acknowledgments

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