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Opponent backgrounds reduce discrimination sensitivity to competing motions: Effects of different vertical motions on horizontal motion perception



Andrew E. Silva*, Zili Liu

Department of Psychology, University of California, Los Angeles, United States

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ABSTRACT

We examined the relationship between two distinct motion phenomena. First, locally balanced stimuli in which opposing motion signals are presented spatially near one another fail to cause a robust firing pattern in brain area MT. The brain's response to this motion is effectively suppressed, a phenomenon known as opponency. Second, past research has found that discrimination sensitivity to a target motion is negatively affected by a superimposed irrelevant motion signal – a process we call “perceptual suppression.” In the current study, we examined how opponency affects the strength of perceptual suppression. We found unexpected results: a target motion embedded within an opponent background was harder to discriminate than a target motion embedded within a non-opponent background. We argue that this pattern of results runs contrary to the clear prediction stemming from the current understanding of the role of opponency in motion processing and tentatively offer an explanation based on recent MT physiology.

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1. Introduction

The brain has a remarkable ability to extract a weak motion signal embedded within a noisy visual scene. Random flicker noise contains motion energy in all directions and therefore strongly stimulates low-level motion detectors (Bradley & Goyal, 2008). This might cause a true motion signal to be lost among the noise created by these spuriously firing detectors. Therefore, some process that suppresses the spurious response is essential. Such a process may occur within brain area MT. For example, Rudolph and Pasternak (1999) reported that MT lesions caused monkeys to exhibit permanent motion discrimination deficits when tested with noisy, minimally-coherent stimuli, though performance on less noisy stimuli was only transiently impaired.

Single unit recordings also implicate area MT in noise reduction. Firing rates are suppressed when MT neurons are simultaneously presented with opposing transparent motions compared to the preferred direction alone (Snowden et al., 1991). However, this suppression is removed when both directions are separated in depth (Bradley, Qian, & Andersen, 1995). In addition, when the display is locally balanced such that two oppositely-moving dots are located in close spatial proximity, MT firing rates drop

considerably and become indistinguishable from the neural response to flicker noise (Qian & Andersen, 1994). This particularly acute neural suppression has been called opponency, as it resembles the theoretical processes through which some motion models take the difference between the responses of two oppositely-tuned motion detectors to arrive at a final motion output (Adelson & Bergen, 1985; Lu, Qian, & Liu, 2004; Qian, Andersen, & Adelson, 1994b; Thompson & Liu, 2006; Thompson, Tjan, & Liu, 2013).

In complex real-world tasks, such as observing the movement of cars during a rainstorm, transparency frequently occurs between motions located at different depth planes. Furthermore, a real-world visual scene is exceedingly unlikely to contain more than one meaningful motion signal at the same local point in space. A good strategy for suppressing noise and sparing meaningful motion information is therefore to selectively suppress transparent signals in the same depth plane as well as signals occurring at the same point within this depth plane. MT firing rates have been found to conform to this pattern (Bradley, Qian, & Andersen, 1995; Qian & Andersen, 1994), leading researchers to conclude that MT's suppressive effects are heavily involved in noise reduction, an idea that remains prevalent in more recent years (Born & Bradley, 2005; Bradley & Goyal, 2008; Bradley, Qian, & Andersen, 1995; Qian, Andersen, & Adelson, 1994b).

The locally balanced dot displays used to study opponency have been described as moving in “counter-phase” and generally consist of many pairs of dots distributed randomly throughout the display

* Corresponding author at: Department of Psychology, University of California, Los Angeles, Los Angeles, CA 90095-1563, United States.

E-mail address: andrewsilva19@gmail.com (A.E. Silva).

(Lu, Qian, & Liu, 2004; Thompson & Liu, 2006; Thompson, Tjan, & Liu, 2013). Dots within pairs are placed in close spatial proximity and travel a short distance in opposite directions before disappearing. As a complement to this stimulus, recent studies have developed an “in-phase” stimulus by reversing the direction of one dot per counter-phase pair (Lu, Qian, & Liu, 2004; Thompson & Liu, 2006; Thompson, Tjan, & Liu, 2013). Both dots within an in-phase pair travel in unison, but any two in-phase pairs may travel in different directions. As a result, the in-phase stimulus maintains a paired-dot spatial structure yet elicits no opponency at area MT (Thompson, Tjan, & Liu, 2013).

Psychophysical studies involving locally balanced stimuli have also produced relevant findings. While Qian and Andersen's (1994) locally unbalanced display elicited a transparent global motion percept, their locally balanced display was reported to elicit no percept of coherent global motion, appearing instead as flicker. Other researchers have examined displays containing different angles of locally balanced motion, finding that they generally create unidirectional percepts in the average signal direction (Curran & Braddick, 2000; Edwards & Metcalf, 2010; Watanabe & Kikuchi, 2006). Counter-phase motion may therefore elicit a special case of local pooling, uniquely resulting in a local average of zero net motion.

It has been widely reported that perceiving a unidirectional stimulus is more difficult than perceiving a transparent stimulus in the absence of color or disparity cues (Braddick, Wishart, & Curran, 2002; Curran, Hibbard, & Johnston, 2007; Mather & Moulden, 1983; Snowden, 1990; Treue, Hol, & Rauber, 2000). In fact, the motion coherence required to detect a transparent signal is roughly triple the coherence required to detect a unidirectional signal (Edwards & Greenwood, 2005). In one study, Snowden (1989) superimposed two independent dot fields that underwent a single motion displacement each trial. The target field shifted horizontally, while the background field shifted vertically, creating a transparent two-frame apparent motion stimulus. Snowden manipulated the displacement magnitude of the background dots, finding that the smallest displacement produced the poorest horizontal discrimination performance. Noting that this displacement also created the most robust percept of vertical motion, Snowden concluded that transparent orthogonal motions mutually suppress one another. A later study reported that the effect of including an irrelevant orthogonal signal on the detection of a target signal was equal to the effect of simply adding incoherent noise dots in equal proportion (Edwards & Nishida, 1999). However, this study tested motion detection, so the level of generalizability to Snowden (1989) task is not clear.

We will now refer to the idea that an irrelevant motion signal causes a decrease in sensitivity to a target signal as “perceptual suppression.” Opponency and perceptual suppression have been independently examined using various methods, but no systematic study detailing their relationship has occurred. Nevertheless, the physiological and psychophysical literatures suggest that counter-phase motion elicits opponency at MT and creates no global motion percept. A stimulus containing a counter-phase background signal and a horizontal target signal should therefore elicit a salient global percept of the target motion, potentially resulting in good performance on a motion discrimination task. In contrast, an in-phase background would elicit no opponency. It should therefore exert stronger perceptual suppression against the horizontal target motion, causing reduced target salience and therefore poorer performance during the discrimination task.

We tested this prediction by conducting a series of experiments examining the effects of different vertical backgrounds on horizontal motion discrimination. Experiments 1 and 2 measured the perceptual suppression elicited by in-phase, counter-phase, and unpaired vertical backgrounds, and Experiment 3 examined

whether or not unidirectional backgrounds exert the same perceptual suppression as non-opponent bidirectional backgrounds.¹ Together, these three experiments found that, contradicting our original prediction, opponency actually strengthened, not weakened, perceptual suppression relative to non-opponent backgrounds. These results may have implications for the underlying processes by which the brain filters signal from noise in motion processing. Lastly, Experiment 4 replicated a past study by Snowden (1989) to verify a potential inconsistency between his data and the current data from Experiments 1, 2, and 3. Some of these results were previously presented at the annual meeting of the Vision Sciences Society (2014).

2. Experiment 1: in-phase versus counter-phase backgrounds

2.1. Experiment 1 motion task

2.1.1. Experiment 1 motion task method

2.1.1.1. *Task.* Participants observed a two-frame apparent motion dot stimulus containing horizontal and vertical displacements and used the arrow keys to indicate whether the horizontal displacement was leftward or rightward.

2.1.1.2. *Stimuli.* The stimulus included a total of 217 white dots (luminance 24.5 cd/m²) with diameters of 1.7 arcmin (0.5 mm) against a solid gray background (luminance 5.5 cd/m²). Of these dots, 128 were designated as “background dots.” These dots were paired vertically and arranged uniformly as an 8 × 8 square grid with a side length of 3.7 arcdeg. This corresponded to a distance of 31.7 arcmin between any pair and its neighbors. Each pair was then given a random vertical and horizontal offset uniformly sampled between 0 and 12 arcmin. The remaining 89 dots were designated as “target dots” and randomly distributed throughout the background. A circular viewing window subtending 3.7 arcdeg circumscribed the square stimulus so that any dot outside the window was not visible to participants. As a result, the average stimulus seen by each subject was actually comprised of 170 dots per trial (50 background pairs and 70 targets) within a circular window.

Each background dot underwent a single displacement of 8 arcmin either upwards or downwards. During the counter-phase trials, dots within pairs traveled in opposite directions. The initial vertical separation between a dot and its counter-phase partner was chosen randomly to be either between 4 and 12 arcmin or between 20 and 28 arcmin. Dots with larger initial separations jumped closer together within pairs, and dots with smaller initial separations jumped further apart. A counter-phase dot was never separated by more than 28 or less than 4 arcmin from its partner. During the in-phase trials, dots within pairs traveled in the same direction, and the separation between a dot and its partner was a constant 16 arcmin, which was the average separation of the counter-phase paired dots. The counter-phase and in-phase backgrounds contained equal numbers of upward and downward motion signals. The target dots underwent a single horizontal displacement of either 5 or 8 arcmin, and any target dots that shifted outside the 3.7 arcdeg boundary “wrapped-around” the display. Fig. 1A and B illustrates these stimuli.

Every trial began with the appearance of a small white fixation cross at the center of the display for 300 ms, after which the first frame of the dot stimulus appeared. After 500 ms, the second frame

¹ We use phrases such as “opponent background” simply to highlight that this stimulus is thought to elicit opponency within area MT, as evidenced by a marked reduction in firing rate (Qian & Andersen, 1994). Likewise, “non-opponent background” refers to a stimulus that does not exert this particularly acute neural suppression.

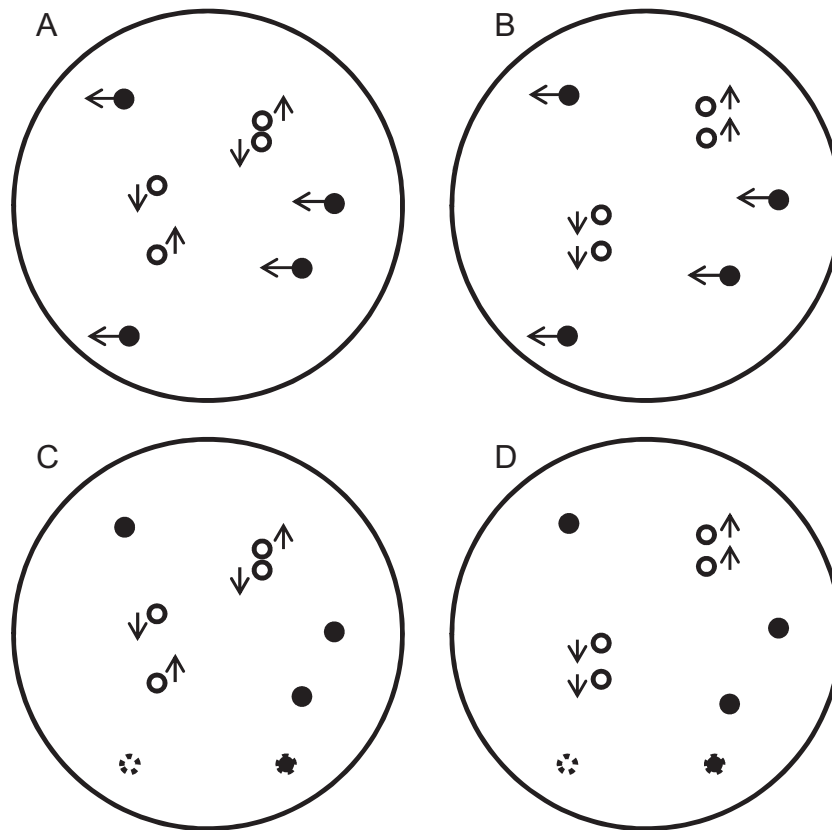


Fig. 1. Schematics of the different conditions in Experiment 1. The target dots are colored black and the background dots are colored white. The arrows represent the trajectory of each dot. (A) The counter-phase motion task. (B) The in-phase motion task. (C) The counter-phase control task. (D) The in-phase control task. In (C) and (D), the dashed outline, unfilled circle represents the initial location of the reflected target dot, while the dashed outline, filled circle represents its location after the onset of the 2nd frame.

of the dot stimulus replaced the first, creating the motion displacement. The second frame remained visible for 200 ms, after which the stimulus disappeared from view. Subjects were allowed a maximum of 5 s from the onset of the second frame to make a keyboard response before the trial was skipped. Skipped trials were removed from analysis. Whenever a trial was skipped or incorrectly answered, participants heard an auditory beep. Participants skipped an average of 2.7 in-phase trials and 3.7 counter-phase trials during their experimental session. However, only eight participants skipped more than two trials throughout their entire session. We reanalyzed the data excluding these participants and found no meaningful differences between those results and the ones reported in the present paper.

All experiments were created using the Python programming language and the Psychopy library (Peirce, 2007, 2009) and run on Windows XP using a Dell desktop PC and a 21" ViewSonic G225f Graphics Series monitor. The resolution was 1600×1200 , and the refresh rate was 85 Hz. Participants viewed the display from 100 cm away.

It is important to note that our stimuli cannot be considered "smooth motion," unlike the stimuli used by Qian, Andersen, and Adelson (1994a). In their paired (counter-phase) condition, they manipulated dot density, speed, and maximum pair separation, finding that no transparency was reported in displays containing 50 dot pairs traveling smoothly at $2^\circ/\text{s}$ with a maximum separation of 24 arcmin. Each dot within a pair began maximally separated from its partner, then traveled toward and through its partner until again reaching the maximum separation. Dot pairs were then randomly replotted. This cycle continued for the duration of the stimulus (1 or 5 s). Our two-frame counter-phase background was similarly designed; on average, 49 dot pairs were visible in the

stimulus and each counter-phase dot was never more than 28 arcmin from its partner. However, we could not allow pairs to cross, as this would have created false correspondence matches. The decision to use two-frame stimuli was made to allow for a more direct comparison to Snowden (1989).

2.1.1.3. Procedure. Participants were required to perform an introductory training block comprised of 26 in-phase and 26 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 3 training blocks, and all participants completed training in less than 5 min.

The experiment contained four within-subject conditions (2 target displacements \times 2 backgrounds). All conditions were randomly interleaved, and each condition was presented 70 times per subject. After every 100th trial, the participants were given a short self-timed break. On average, the experiment was completed in approximately 20 min.

2.1.1.4. Subjects. Twenty-eight undergraduate students were recruited from UCLA's psychology subject pool with self-reported 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).

2.1.2. Experiment 1 motion task results

We calculated d' from the raw data and analyzed the resulting data using a 2×2 repeated measures ANOVA. We found a significant effect of background on discrimination sensitivity, $F(1,$

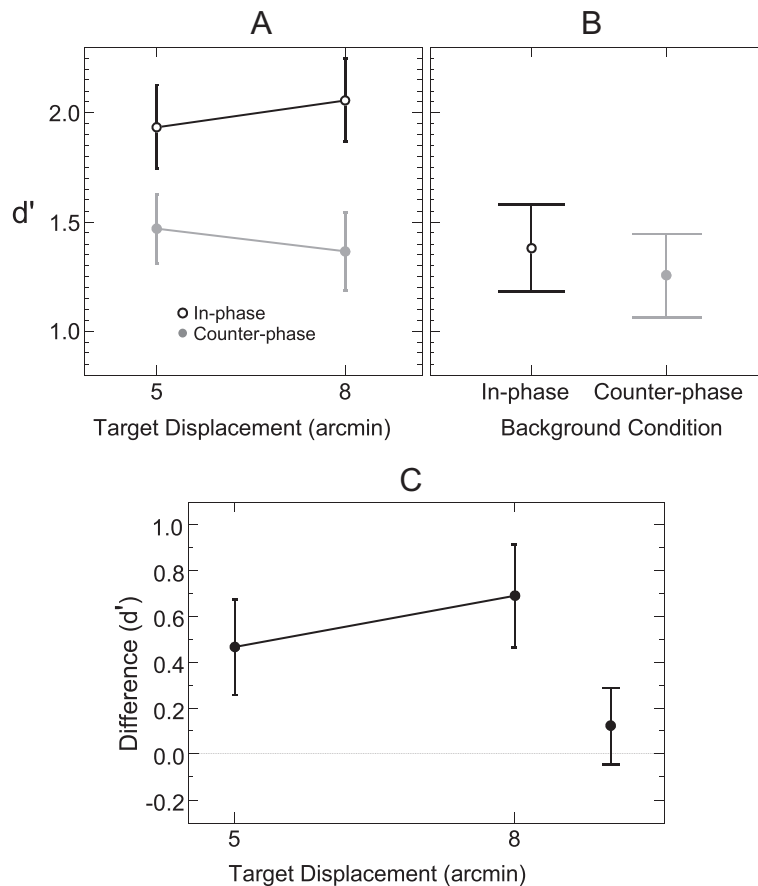


Fig. 2. Experiment 1 results. (A) Performance in the motion task. The X-axis denotes target displacement. (B) Performance in the control task. In (A) and (B), the error bars are ± 1 standard error of the mean. (C) Average within-subject performance differences between the in-phase and counter-phase conditions. The connected points plot motion task data, and the unconnected point plots control task data. In (C), the error bars are 95% within-subject confidence intervals, and the horizontal line represents no difference between conditions.

27) = 60.26, $p < 0.001$, with subjects performing better on in-phase trials ($d' = 2.00$) than on counter-phase trials ($d' = 1.42$). No significant main effect of target displacement was found, $F(1, 27) = 0.02$, and the interaction between target displacement and background was also not significant, $F(1, 27) = 2.15$, $p = 0.15$. Performance in this task is plotted in Fig. 2.

2.2. Experiment 1 control task

Because a significant effect was found, we ran a control density discrimination task to examine whether or not the same effect would be found in a non-motion task.

2.2.1. Experiment 1 control task method

2.2.1.1. Task. Participants observed a two-frame apparent motion dot stimulus containing the same in-phase and counter-phase backgrounds as in the motion task. However, the onset of the second frame also caused a shift of target dot density toward either the left or the right half of the display, and participants used the arrow keys to indicate which half contained more dots after the onset of the second frame.

2.2.1.2. Stimuli and procedure. The control task backgrounds were identical to the motion task backgrounds. However, the target dots underwent a change in spatial distribution rather than a coherent motion displacement. In the first frame of the stimulus, the left and right halves of the display contained equal numbers of target dots. The onset of the second frame caused 13 randomly selected dots from one half to be horizontally reflected to the opposite side. All

other target dots remained stationary. We found that this created a density signal with no subjective percept of horizontal motion, and pilot studies suggested that the difficulty of the control and motion tasks were comparable. The control task is illustrated in Fig. 1C and D.

Similar to the motion task participants, the control participants underwent a training procedure. However, pilots showed that the control task was initially difficult to understand, so the control's training block used a sparse 4×4 grid of background dots so that the density signal was easier to detect during training, facilitating understanding. The standard 8×8 grid was used during the main control experiment, and all other experimental and training procedures were identical between the motion and control tasks.

2.2.1.3. Subjects. Thirty new undergraduate students were recruited for the control task.

2.2.2. Experiment 1 control task results

A paired-samples t -test was used to analyze each subject's control task d' , finding no significant difference between the in-phase ($d' = 1.38$) and counter-phase ($d' = 1.25$) backgrounds, $t(29) = 1.52$, $p = 0.14$. Task performance is plotted in Fig. 2.

2.3. Experiment 1 discussion

During the motion task, the counter-phase background produced poorer discrimination sensitivity to the target motion than did the in-phase background. The counter-phase background contains local motion signals that should "self-inhibit" according to

neurophysiological opponency studies and psychophysical local pooling studies. Nevertheless, this background exerted stronger perceptual suppression against the target motion, contradicting our initial prediction. Interestingly, Snowden (1989) examined how different vertical dot displacements affected horizontal motion discrimination, interpreting his results in a manner similar to our initial prediction. He argued that larger vertical background displacements created a percept comprised primarily of random signals that tended to inhibit one another, causing this background to poorly mask a competing target motion. For convenience, we now refer to this background as Snowden's "faster" background, while his background exhibiting smaller vertical displacements will be called the "slower" background.

Snowden (1989) conceived of a "cooperative-competitive" motion process in which all low-level motion detectors sensitive to similar spatial locations and tuned to similar directions facilitate one another's responses, while detectors tuned to different directions inhibit one another's responses. This may explain the faster background's poor effectiveness as a mask. However, it has also been demonstrated that similar motion speeds mask each other more strongly than dissimilar speeds (Edwards, Badcock, & Smith, 1998; Van Boxtel & Erkelens, 2006). Because different displacements effectively produce different motion speeds, speed tuning effects may have contributed to Snowden's (1989) result.

If the random signals from Snowden's faster background truly inhibited one another, then this self-inhibiting mechanism necessarily differed from the mechanism underlying opponent suppression, as none of Snowden's backgrounds possessed the locally balanced spatial distribution required to elicit opponency. Therefore, the opposite patterns of perceptual suppression elicited by Snowden's faster background and our counter-phase background may have originated from their different underlying self-inhibiting mechanisms. While the mechanism underlying opponent self-inhibition strengthens perceptual suppression, Snowden's non-opponent self-inhibition weakens perceptual suppression.

The non-motion control task found no performance differences. Therefore, the opponency elicited by the counter-phase background likely selectively decreased the participants' motion sensitivity while leaving non-motion sensitivity unaffected. If opponency truly drove this motion-specific effect, then removing this opponency by "unpairing" the counter-phase background should result in performance similar to the in-phase background. We examined this prediction in Experiment 2.

3. Experiment 2: unpaired background

3.1. Experiment 2 method

3.1.1. Stimuli and procedure

In Experiment 2, we compared a new unpaired background to the in-phase and counter-phase backgrounds using the motion task. Only the 8 arcmin target displacement was tested, as it previously produced a numerically larger difference between the in-phase and counter-phase backgrounds. All other experimental procedures were identical to those from Experiment 1.

To create the unpaired background, one dot from each counter-phase pair was moved downward and rightward by 15.9 arcmin (22.5 arcmin diagonally). During the shift, half of all unpaired dots jumped up, and half jumped down.

3.1.2. Subjects

Thirty new participants were recruited as in Experiment 1.

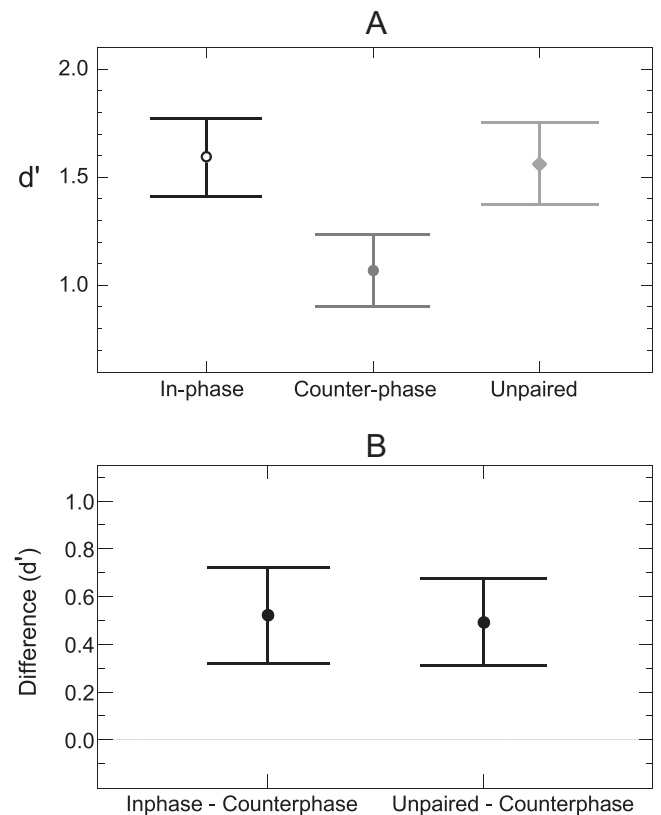


Fig. 3. Experiment 2 results. (A) Average d' in each condition. In (A), the error bars are ± 1 standard error of the mean. (B) Average within-subject performance differences between the in-phase and counter-phase conditions and between the unpaired and counter-phase conditions. In (B), the error bars correspond to 95% within-subject confidence intervals and the horizontal line represents no difference between conditions.

3.2. Experiment 2 results

We calculated d' from the raw data and ran a 1×3 repeated measures ANOVA, finding a significant effect of background, $F(2, 58) = 22.34$, $p < 0.001$. Specific contrasts showed that the counter-phase background ($d' = 1.07$) produced significantly poorer performance than the in-phase ($d' = 1.56$) and unpaired ($d' = 1.59$) backgrounds, $F(1, 29) = 27.90$, $p < 0.001$, and $F(1, 29) = 30.91$, $p < 0.001$, respectively. However, no significant difference was found between the in-phase and unpaired backgrounds, $F(1, 29) = 0.16$. The data are plotted in Fig. 3.

3.3. Experiment 2 discussion

Experiment 2 found that the in-phase and unpaired backgrounds exerted similar amounts of perceptual suppression, while the counter-phase background exerted the most perceptual suppression. These findings are consistent with the idea that the counter-phase effect is driven specifically by its opponent motion signals.

Experiments 1 and 2 together found that vertical motion opponency elicited a motion-specific reduction in horizontal sensitivity. However, only bidirectional backgrounds have been tested thus far, and past physiological (Snowden et al., 1991) and neuroimaging (Garcia & Grossman, 2009) studies have found that non-opponent bidirectional displays inhibit area MT relative to unidirectional displays. Also, various psychophysical tasks have

demonstrated that in general, unidirectional motions are easier to perceive than transparent motions (Braddick, Wishart, & Curran, 2002; Curran, Hibbard, & Johnston, 2007; Edwards & Greenwood, 2005; Mather & Moulden, 1983; Snowden, 1990; Treue, Hol, & Rauber, 2000). Because various costs are associated with bidirectional stimuli relative to unidirectional stimuli, it is plausible that our previously tested non-opponent backgrounds may similarly exert different levels of perceptual suppression relative to a unidirectional background. We examined this issue in Experiment 3 by directly comparing the in-phase background with two different unidirectional backgrounds.

4. Experiment 3: unidirectional versus in-phase backgrounds

4.1. Experiment 3 motion task

4.1.1. Experiment 3 motion task method

4.1.1.1. *Stimuli and procedure.* Experiment 3 compared the in-phase background with a “full” unidirectional and a “half” unidirectional background. The first frame of the full background was identical to the in-phase background. However, the onset of the second frame displaced all background dots in the same direction. In the half background, only one dot from each pair was displaced while the other remained stationary. The half background served as a parametric manipulation to investigate the way in which the total amount of motion signals affects perceptual suppression.

In Experiment 1’s motion task, the larger 8 arcmin target displacement elicited a larger numerical difference between the in-phase and counter-phase backgrounds, suggesting that larger displacements may produce larger effects. Therefore, we tested displacements of 8 and 12 arcmin in the motion task of Experiment 3. All other experimental procedures were identical to those from Experiment 1’s motion task.

4.1.1.2. *Subjects.* Twenty-nine new participants were similarly recruited for this task.

4.1.2. Experiment 3 motion task results

We calculated d' from the raw data and performed a 2×3 repeated measures ANOVA, finding a significant effect of background, $F(2, 56) = 12.63, p < 0.001$. Specific contrasts showed that the half background ($d' = 2.21$) produced significantly better performance than the in-phase ($d' = 1.86$) and full ($d' = 1.89$) backgrounds, $F(1, 28) = 19.44, p < 0.001$ and $F(1, 28) = 14.41, p = 0.001$,

respectively. However, no significant difference was found between the in-phase and full backgrounds, $F(1, 28) = 0.29$. The main effect of target displacement was also significant (8 arcmin $d' = 2.25$, 12 arcmin $d' = 1.72$), $F(1, 28) = 66.47, p < 0.001$. No significant interaction was found, $F(2, 56) = 0.20$. Fig. 4 plots these data.

4.2. Experiment 3 control task

The half background produced better motion sensitivity than the full background, perhaps unsurprisingly given that the full background contained more motion signals. However, whether or not this performance difference was driven by motion-specific perceptual suppression is yet unknown. To examine this, we compared the full and half backgrounds on the control density-discrimination task. Because the full and in-phase backgrounds produced comparable performance in the motion task, Experiment 3’s control task contained no in-phase condition.

4.2.1. Experiment 3 control task method

All stimulus and procedural conventions were identical to the previous control task, except that full and half unidirectional backgrounds were used. Thirty-five new undergraduates participated in this task.

4.2.2. Experiment 3 control task results

We calculated d' and analyzed the data using a paired-samples t -test, finding no significant difference between the full ($d' = 1.30$) and half ($d' = 1.38$) backgrounds, $t(34) = 0.56$. Performance in this task is plotted in Fig. 4.

4.3. Experiment 3 discussion

The motion task found a significant difference between the full and half unidirectional backgrounds, but the control task failed to find such a difference. Therefore, the greater number of moving background dots likely caused the full background to exert stronger motion-specific perceptual suppression than the half background.

Experiments 1, 2, and 3 found no performance differences between the in-phase, unpaired, and full unidirectional backgrounds, but the self-inhibiting counter-phase background produced a robust decrease in performance. In contrast, Snowden (1989) found that his faster background, also believed to be self-inhibiting, produced the best performance. Therefore, different

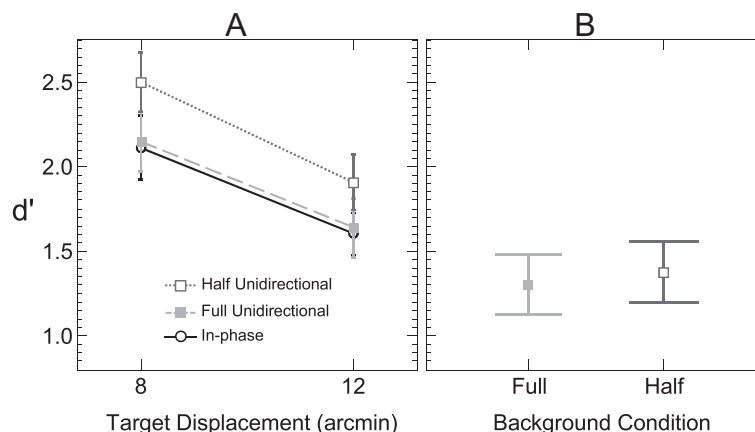


Fig. 4. Experiment 3 results. Average estimates of d' in Experiment 3. (A) Performance in the motion task. The X-axis denotes target displacement. (B) Performance in the control task. The error bars are ± 1 standard error of the mean.

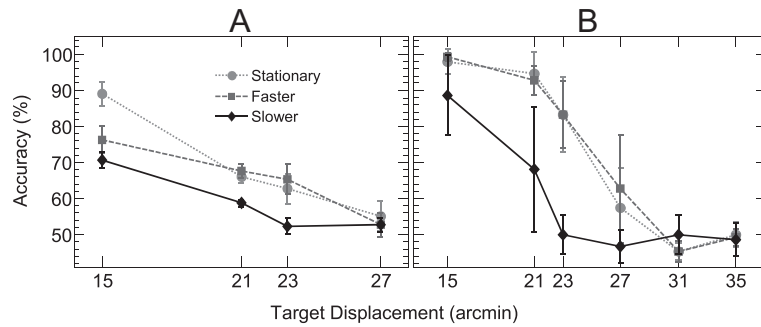


Fig. 5. Experiment 4 results. (A) Performance (percent correct) in the replication. (B) Data from Snowden (1989), averaged across all three reported subjects for comparison. The X-axis denotes target displacement (arcmin). The error bars are ± 1 standard error of the mean.

mechanisms may underlie the “self-inhibition” of opponent and non-opponent backgrounds. In order to empirically verify his data, we recreated Snowden’s (1989) study in Experiment 4.

5. Experiment 4: replication of Snowden (1989)

5.1. Experiment 4 method

5.1.1. Stimuli and procedure

Every trial contained 400 background dots and 400 target dots of diameter 0.5 mm (luminance 35.9 cd/m^2), randomly distributed within a circular aperture subtending 3.7 arcdeg. The dots fell against a dark gray background (luminance 1.5 cd/m^2). Participants viewed the display from a distance of 300 cm. All dots underwent a single vertical (background) or horizontal (target) displacement 100 ms after the onset of the stimulus. In any given trial, the horizontal displacement could be 15, 21, 23, or 27 arcmin. Snowden also tested larger displacements, but they produced chance performance and were thus not used in our replication. Participants indicated the direction of the horizontal shift using the arrow keys, and no feedback was given.

Three different background conditions were tested. In the “stationary” condition, only the target dots were displaced while the background dots remained stationary. In the “slower” condition, all background dots were displaced up or down by 10 arcmin. Finally, in the “faster” condition, all background dots shifted up or down with the same magnitude as the horizontal displacement for that particular trial. Snowden claimed that the slower background created a robust unidirectional motion percept, while the faster background created an “almost nondirectional” percept (pg. 1098). Snowden tested a fourth background condition in which no background dots were present, but this condition was not included in our replication because it was irrelevant to our question of interest.

All 12 conditions (4 target displacements \times 3 backgrounds) were randomly interleaved, and each condition was presented 50 times. Before performing the main task, all participants underwent the same training procedure as in our previous experiments. Therefore, our replication differed methodologically from the original study in two ways. First, we included the training block. Second, we excluded certain conditions as previously described. In addition, the luminance intensities used in this replication were also likely different from the original intensities, as they were not reported in the original report.

5.1.2. Subjects

We recruited 6 observers to perform this study. All observers were psychophysically experienced and naïve to the purpose of the study.

5.2. Experiment 4 results

We now report performance in percent correct rather than d' for a direct comparison with Snowden’s original data. The overall replication performance (64.1%) was poorer than in the relevant conditions of the original study (77.1%). Even so, the replication and the original study found similar patterns of results. A 3×4 repeated measures ANOVA on the replication data revealed significant effects of background condition and target displacement, $F(2, 10) = 9.49$, $p = 0.01$ and $F(3, 15) = 67.64$, $p < 0.001$, respectively. Specific contrasts showed that the slower background (58.6%) produced significantly poorer performance than both the stationary (68.2%) and faster backgrounds (65.5%), $F(1, 5) = 14.3$, $p = 0.01$ and $F(1, 5) = 6.86$, $p < 0.05$, respectively. However, the stationary and faster backgrounds did not differ significantly, $F(1, 5) = 3.42$, $p = 0.12$. The interaction between background condition and target displacement was also significant, $F(6, 30) = 2.74$, $p = 0.03$. Fig. 5A plots the replication data, and Fig. 5B presents the original data for comparison.

5.3. Experiment 4 discussion

The replication produced poorer overall performance than the original study. This is likely due to different luminance levels of the stimulus between the two experiments, as the original paper did not report these values. Additionally, we note that our methodological changes may have affected our results. Nevertheless, the replication and the original experiment found similar data patterns despite the replication’s poorer overall performance.

The faster condition produced similar performance to the stationary condition, while the slower condition produced the poorest performance. This finding is consistent with the idea that the weaker dot correspondence of the faster background created random self-inhibiting signals, causing this background to poorly mask the target motion. Yet, Experiments 1, 2, and 3 found that self-inhibition due to opponency led to the opposite pattern of results. All together, these findings suggest that different mechanisms may underlie the modulation of perceptual suppression when opponent and non-opponent self-inhibiting signals are presented.

6. General discussion

We compared the strength of perceptual suppression exerted by a counter-phase background with that exerted by in-phase, unpaired, and unidirectional backgrounds. No difference was found between the non-opponent backgrounds, but the counter-phase background produced markedly poorer performance on a horizontal motion discrimination task.

In Experiment 4, we successfully replicated Snowden's (1989) original data. Snowden interpreted his results partially by hypothesizing that his faster background contained self-inhibiting signals and therefore failed to strongly inhibit the competing target motion. However, our self-inhibiting counter-phase background produced the opposite pattern of results. Therefore, non-opponent and opponent self-inhibiting backgrounds may modulate perceptual suppression through different underlying mechanisms. It is important to note that no experiments discussed above actually prove that the faster background is truly self-inhibiting. Alternative interpretations of the Experiment 4 data are certainly possible. We also note that some stimulus differences exist between the replication study and Experiments 1, 2, and 3. Relative to our first three experiments, Experiment 4 used a shorter display time, the dots were more numerous but subtended fewer degrees of visual angle, the magnitude of the target displacements were larger, and a different stimulus contrast was used.

The primary effect reported in this paper is the motion-specific decline in performance during trials with a vertical counter-phase background relative to other non-opponent backgrounds. However, when using two-frame motion stimuli, it is also important to consider the effect of different rates of false-correspondence matches between conditions. Our counter-phase condition was designed so that within-pair dot displacements were perceptually unambiguous; paired dots never crossed over each other. However, due to the specific dot distances chosen, the in-phase background may have exhibited higher rates of false correspondence matches.

Dots within in-phase pairs were separated by 16 arcmin and shifted up or down by 8 arcmin. As a result, the initial location of one dot from each pair was at the exact midpoint of the final locations of both dots within that pair, creating some ambiguity about the displacement direction of that particular dot. While this ambiguity is perceptually resolved with the simultaneous displacement of the second dot, it may have nevertheless contributed to the reported effect. To rule this out, we reduced the background displacement by one pixel and repeated the Experiment 1 motion task with 18 new participants. We found data patterns similar to the main experiment (in-phase $d' = 0.94$, counter-phase $d' = 0.74$, $F(1, 17) = 7.02$, $p = 0.017$), though performance was markedly worse, likely because these shorter displacements created stronger motion signals with greater masking abilities (Edwards, Badcock, & Nishida, 1996).

To be sure that the revised in-phase and counter-phase stimuli exhibited equal rates of false correspondence matches, we ran a strict nearest-neighbor analysis. This analysis looked at the initial location of each individual dot and then found the nearest dot location in the second frame. If the nearest location belonged to a single dot, and if this single dot was the correct corresponding dot, then it was labeled a "correct match." Otherwise, it was labeled a "false match." We found nearly identical false correspondence rates between in-phase (9.1%) and counter-phase (9.2%) backgrounds and therefore concluded that factors unrelated to different false correspondence rates were involved in the observed effect.

It might also be argued that some general mechanism unspecified to motion processing, such as attentional capture, caused the observed effect. A vertically moving background is irrelevant when discriminating horizontal motion, so participants may have tried to ignore the background during the motion task. If counter-phase motion signals are simply more difficult to ignore, the observed effect may not actually reflect any underlying motion processing. While the null results of the control task challenge this idea, it might be further argued that participants deliberately attended to both backgrounds during the control task, as all dots might have been interpreted as relevant during the control's dot-density

judgments. The results of the control task may have thus obscured the difference in perceptual salience between in-phase and counter-phase backgrounds.

The above hypothesis explains the Experiment 1 data, though it is unclear why the counter-phase background should be more salient than the in-phase background, as all backgrounds were equated for characteristics such as contrast and motion speed. Furthermore, the viewing aperture, small dot size, large background jitter, and fast presentation time of both stimulus frames made it virtually impossible to reliably identify whether any individual dot belonged to the background or to the target. As a result, the observers were required to attend to the global motion of the entire stimulus in order to be successful in either task. For these reasons, we believe that our effects indeed reflect underlying motion processing of opponency and perceptual suppression rather than a general attentional process.

It has been suggested that MT opponency, which is thought to occur as a result of competitive inputs from V1 synapsing onto the same MT subunit, decreases the neural response to flicker noise during motion processing (Born & Bradley, 2005; Bradley & Goyal, 2008; Qian & Andersen, 1994; Qian, Andersen, & Adelson, 1994a, 1994b; Snowden et al., 1991). Flicker noise exhibits locally omnidirectional motion energy and therefore activates every low-level motion detector sensitive to the relevant spatial location. With opponency acting upon this noise, it fails to cause a strong MT response. Opponency may therefore act as a filter, selectively removing the flicker response from the neuronal signal. Presumably, this filtered neuronal signal ultimately contributes to a more salient motion percept, increasing the observer's sensitivity to any motion that co-occurs with irrelevant noise.

Psychophysical studies have examined in more detail the perceptual effects of locally balanced motion, concluding that global motion perception in paired dot displays is computed from a local pooling of each pair rather than from the individual dots themselves (Curran & Braddick, 2000; Edwards & Metcalfe, 2010; Watanabe & Kikuchi, 2006). Because this local pooling effectively results in motion cancellation during opponent counter-phase motion, such local averaging is consistent with the belief that opponency functions to reduce noise. Therefore, it was natural to predict *a priori* that a vertical counter-phase background should produce better performance than a vertical in-phase background during a horizontal motion discrimination task. Yet, our results sharply contradicted this prediction. One important caveat to our study is that in order to examine the effect of opponency on perceptual suppression in displays similar to those used by Snowden (1989), we elected to use two-frame apparent motion. Whether such results can generalize outside of this context is an interesting question for future exploration.

It is clear that MT neurons that fire maximally to vertical motion generally fire little to vertical counter-phase motion (Qian & Andersen, 1994). Furthermore, the fMRI BOLD response at area MT is reduced when viewing opponent counter-phase motion relative to non-opponent motion (Heeger et al., 1999; Muckli et al., 2002; Thompson, Tjan, & Liu, 2013). Any reasonable explanation for why our vertical counter-phase background led to a decrease in horizontal discrimination performance must therefore consider that this background is also associated with a systematic inhibition of vertical motion detectors. Though it remains highly speculative, we propose a hypothesis that attempts to reconcile our findings with the established literature on opponency.

One possible explanation of our data is that an inhibition of horizontal motion processing simply co-occurs with vertical opponency. While classic directional tuning studies suggest that an MT neuron is unlikely to respond vigorously to a motion orthogonal to its preferred direction (Albright, 1984; Britten & Newsome, 1998; Kohn & Movshon, 2004; Lee & Lee, 2012; Snowden, Treue,

& Andersen, 1992), a recent study argues that a significant portion of MT neurons may contain multiple preferred directions, typically between 30° and 90° apart (Richert, Albright, & Krekelberg, 2013). Therefore, some amount of overlap may exist between the neurons that process vertical and horizontal motions.

Richert, Albright, and Krekelberg (2013) argued that unlike the standard unidirectional tuning profile commonly associated with MT cells, the complex directional tuning found in half of the cells they studied might serve to signal complex directional patterns. In other words, the same neuron may contribute to the processing of multiple directions of motion, implicating a system in which partially overlapping populations of neurons process distinct motion directions. However, if multiple directions rely on overlapping neuronal architectures for processing, then suppressing the shared portion of those architectures with opponency may also negatively affect the processing of all other directions associated with that shared neuronal population. Vertical opponency may therefore disrupt the processing of a range of motions, potentially explaining the decreased horizontal discrimination observed in the present psychophysical study. However, such an explanation is highly speculative, and the full extent of the perceptual implications of Richert, Albright, and Krekelberg's (2013) reported neurons is not yet understood, nor is it currently clear how such complex neurons fit with past literature detailing physiological and psychophysical effects consistent with the standard model of MT processing.

7. Conclusions

The present study found that presenting a background motion known to psychophysically suppress vertically-sensitive MT neurons negatively influenced horizontal discrimination. This result might be consistent with the idea that the neural architecture supporting horizontal discrimination overlaps with the neural architecture suppressed by vertical opponency, though the mechanism truly underlying the observed effect remains open to debate and experimentation. Nevertheless, within the context of past psychophysical and physiological literature, our findings illustrate a robust and counter-intuitive effect of vertical counter-phase backgrounds on horizontal motion discrimination when viewing apparent motion.

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