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 omni-directional 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 con-currently-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 oppo-nency 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 an-other, creating a locally balanced stimulus. In contrast, area MT ex-hibited 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 mo-tion 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