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

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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.

#### 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

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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





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(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.<sup>1</sup> 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  $cd/m^2$ ) with diameters of 1.7 arcmin (0.5 mm) against a solid gray background (luminance  $5.5 \text{ cd/m}^2$ ). Of these dots, 128 were designated as "background dots." These dots were paired vertically and arranged uniformly as an  $8 \times 8$  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

<sup>&</sup>lt;sup>1</sup> 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.

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