POTENTIAL STIMULUS CONTRIBUTIONS TO COUNTERCHANGE DETERMINED MOTION PERCEPTION

by

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This dissertation was prepared under the direction of the candidate's dissertation advisor, Dr. Howard S. Hock, Department of Psychology, and has been approved by the members of her supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

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Prior research has explored the counterchange model of motion detection in terms of counterchanging information that originates in the stimulus foreground (or objects). These experiments explore counterchange apparent motion with regard to a new apparent motion stimulus where the necessary counterchanging information required for apparent motion is provided by altering the luminance of the background. It was found that apparent motion produced by background-counterchange requires longer frame durations and lower levels of average stimulus contrast compared to foreground-counterchange. Furthermore, inter-object distance does not influence apparent motion produced by background-counterchange to the degree it influences apparent motion produced by foreground-counterchange.

DEDICATION

I dedicate this manuscript to my encouraging and loving husband, Ted Park and our son, Matt Park, who is the joy of our lives. It was on Ted’s strong shoulders that I was able to accomplish this work. (Ted would like it mentioned that, when I attempted to recruit him as a subject, he failed to perceive apparent motion.) Matt and Ted have provided unwavering support and acceptance over the many years of this graduate research. They are the rocks and loves of my life.

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POTENTIAL STIMULUS CONTRIBUTIONS TO

COUNTERCHANGE DETERMINED MOTION PERCEPTION

FIGURES

I. INTRODUCTION

Apparent motion is described as "apparent" because no physical movement is involved yet an impression of continuous movement is perceived. A classic example of single-object apparent motion (standard apparent motion) occurs when one object appears against a contrasting background, disappears with a frame-change while an identical object horizontally parallel to the first appears in an adjacent location (see Figure 1). With alternation of this frame-to-frame pattern and given specific time, spatial, and luminosity constraints, the result is the perception of one object moving continuously from the location in the first frame to the location in the second frame.

In the generalized version of standard apparent motion (Johansson, 1950), two objects, whose luminance is different from the background luminance, are presented together in one frame (as shown in Figure 2). When the luminance values of the two objects trade places from one frame to the next, the result is the perception of object motion. This stimulus differs from the standard apparent motion stimulus where only one object is visible in a single frame, but the percept of object motion is similar. Note that in both the standard and generalized versions of apparent motion, the objects' surface luminance is the key variable that changes from frame-to-frame. The background luminance remains static.

This is not to say the background luminance is irrelevant to the perception of apparent motion. Hock, Kogan, and Espinoza (1997) established that the perception of motion in the generalized apparent motion stimulus depends upon a specific ratio of luminance contrasts in the stimulus objects (L_1 and L_2), background (L_b), and the average of the entire stimulus (L_m). The ratio $(L_1-L_2)/(L_m-L_b)$ was introduced by Hock as the "background-relative luminance contrast" (BRLC). The BRLC proved to be the single variable that best predicted motion perception, regardless of the magnitude in change of object luminance. With BRLC an independent variable, observers' measurements of perception of object motion could be represented by a single psychometric function rather than separate psychometric functions for different luminance stimulus values. In other words, the BRLC newly defined motion perception generated by the generalized apparent motion stimulus as the result of contrasts between the background luminance, average luminance, and the luminance differences between the two objects. The time-varying object luminance in a stimulus was no longer the single variable contributing to the perception of motion. This was, perhaps, the first step towards the evolution of the counterchange model of motion detection.

Relevant Early Apparent Motion Research

Apparent motion was first explored experimentally by Exner in 1875. Exner demonstrated that two appropriately temporally and spatially separated electric sparks could be perceived as an object in motion. With this stimulus, Exner demonstrated three distinct perceptual events and the temporal separation that defined them. Later to be refined by Wertheimer in 1912, smooth movement of sparks, or objects, was termed “beta” motion. “Partial movement” described the , sensation of the object moving up to a certain point along the trajectory between the flashes, disappears, and then reappearing in movement again later along the trajectory. “Phi” motion, referred to the percept of movement, but without any specific form (figureless movement). This terminology is still used today (Sekuler, 1996).

Following Wertheimer, Korte and Neuhaus further varied stimulus parameters for apparent motion, ultimately leading to what are referred to as “Korte’s laws” (Korte, 1915; Neuhaus, 1930). Korte’s laws are more generic “rules of thumb” because the relationship of the perception of apparent motion with stimulus parameters is, in reality, much more complex (e.g., Kolers, 1972; Wagemans et al., 2012). Briefly, Korte’s laws express relationships between intensity, frame duration, spatial separation, and inter-change interval (a temporal interruption between altering frame durations) for the perception of apparent motion. 1) larger separations between objects require higher intensities, 2) slower frame durations require higher intensities, 3) larger separations between the objects require slower frame durations, and 4) as frame duration increases, the motion percept’s tolerance for the time length of an inter-change interval decreases. For the purpose of these experiments, the term “intensities” refers to the objects’ luminance contrast with the background.

Once physiological studies confirmed the existence of distinct cells in the visual cortex designed to detect specific orientation (Hubel & Wiesel, 1962), the research focus shifted from explaining the complex phenomenology of apparent motion to the more basic question of how neural systems detect motion. This led to proposals of neural computational models to explain motion detection. Neural computational models continue to spur both psychophysical and physiological research regarding the perception of motion.

Neural Mechanisms for Motion Detection

Reichardt detectors. The Reichardt detector (1961) was originally proposed within the context of insect vision and became a springboard for many more elaborate motion energy models to come. The fundamental property of the detector is a temporal delay in one of a pair of neural units. The delay allows simultaneous stimulation of a third neural unit causing it to fire at the presentation of temporally varying luminance changes. Figure 3 illustrates a simplified version of a rightward Reichardt detector’s three neural units. The circles in the figure (S_L and S_R) represent two spatially separated neural units that tap the visual field in two points and, in response to light, send a signal to a third neural unit (M). This signal represents the temporal luminance pattern of the motion stimulus, a comb function for object (stroboscopic) motion or a sine wave for a drifting sinusoidal grating. Note that one of the S_L/S_R signals takes longer to arrive at M due to a temporal separation of the input represented by Δt. The temporal filter does not alter the basic shape of the comb or sinusoidal function, but does alter the phase. The M neural unit correlates output from S_L and S_R. Therefore, an input from both S_L and S_R arriving simultaneously at M will result in a maximum response from the detector. If the two inputs do not simultaneously arrive but do overlap some, there will be less integration and M will respond to a lesser extent. M will not respond, or will weakly respond, if the two inputs arrive at very dissimilar times.Reichardt postulated that motion detectors are a blend of two units similar to the one above but tuned to motion in opposite directions, as depicted in Figure 4. (Again, the illustration is simplified.) The response of the left neural unit (M_L) is subtracted from that of the right (M_R) to yield the motion detector's response. A positive result indicates rightward motion while a negative result indicates leftward motion.

The final computational stage of calculating the difference also allows for the perception of nonmotion. If a nonmoving stimulus is presented, the first unit in the rightward detector sends a signal that reaches M after a delay due to the temporal filter. The second unit in the rightward detector is also stimulated and sends a signal to M which, when correlated, causes M to fire. Because the leftward detector is similarly activated, the difference between the M_L and M_R outputs will be zero, signaling no motion.

The Reichardt model assumes there are many such detectors with a variety of temporal delays and spatial distances between neural units. This allows motion perception over a wide range of spatial and temporal ranges. In some cases however, a Reichardt detector may signal motion in the wrong direction due to aliasing that can occur with luminance patterns that create temporal frequency functions with a half period smaller than the spacing between S_L and S_R.

Elaborated Reichardt detectors. This issue, and the fact that experimental studies began to suggest motion detectors are selective for spatial frequency in addition to temporal frequency (Adelson & Bergen, 1985; Watson & Ahumada, 1983) led to the modification of Reichardt's motion detector into what are known as "elaborated Reichardt detectors" (Lu & Sperling, 1995; van Santen & Sperling, 1985). The elaborated Reichardt detector (ERD) functions as a correlation model in a fashion similar to the original. Van Santen and Sperling replaced the first stage inputs aligned to points in the visual field (S_L and S_R) with spatial frequency selective filters (eliminating the aliasing problem) and added several pairs of temporal filters. Using a variety of temporal and receptive fields, the ERD was capable of indicating the correct direction of motion for apparent motion stimuli of any spatial or temporal frequency.

Motion energy detectors. Other researchers proposed ERDs using Fourier-analytic methods for extracting information. Fourier-analytic ERDs assume the visual system is composed of spatiotemporal filters designed to detect oriented spatiotemporal information, known as motion energy. By deriving the spatial and temporal frequencies of a motion stimulus using a space-time Fourier transform, the apparent motion stimulus (an object moving horizontally from left to right) can be characterized with a motion energy diagram as shown in Figure 5. Temporal frequency is plotted in terms of its dependence on spatial frequency. A diagonal orientation indicates motion while a vertical orientation indicates the absence of motion. Steeper slopes will result from faster speeds, positive slopes will result from motion from right to left, and negative slopes will result from motion from left to right. Directional information provided to the motion energy detector is known as “directional energy” (DE). It is the spatiotemporal orientation in the motion energy diagram that is detected by the motion energy ERDs proposed by Adelson and Bergen (1985) and Watson and Ahumada (1983).

Second-order detectors. Motion energy models were designed to explain spatiotemporal variations in luminance. However, there are apparent motion phenomena that are not luminance-defined. Consequently, Lu and Sperling (1995b) proposed three separate types of motion detecting mechanisms in the visual system. First-order mechanisms respond to luminance changes and motion is signaled as the result of motion energy analysis. Second-order mechanisms compute the same motion energy analysis as first-order mechanisms but detect spatiotemporal variations in second-order attributes such as texture and contrast (as opposed to luminance). Though second-order (or non-Fourier) motion stimuli are invisible to first-order detectors because they lack oriented motion energy in their Fourier transform, the second-order mechanism extracts motion information by what Lu and Sperling term a “texture grabber.” Texture grabbers include a receptive field, a temporal bandpass filter, and full-wave rectification prior to extraction by the standard motion energy computation. First- and second-order mechanisms are believed to be monocular, bottom-up processes based upon a simple motion-detecting circuit.

Third-order detectors. Existing higher in the visual system after signals from both eyes combine, third-order mechanisms are proposed to detect motion invisible to first and second-order mechanisms (Blaser, Sperling, & Lu, 1999; Lu & Sperling, 1995; Lu & Sperling, 1995). Lu and Sperling (2001) have identified four types of motion stimuli they believe to be third-order, but as research progresses first-, second-, and third-order stimuli continue to be debated and, in some cases, disproved (Hock, Gilroy, & Harnett, 2002). The evolving research regarding counterchange suggests it may be a viable candidate for a third-order motion detecting mechanism with properties that may influence or at least compliment lower order first- and second-order motion. Third-order motion will be discussed in more detail within the context of counterchange.

Counterchange. Consider once again the motion stimuli depicted in Figures 1 and 2 where a decrease in luminance contrast of an object's surface relative to its background is paired with an increase in luminance contrast of an adjacent object's surface relative to its background. The stimulus will first impact the activation of antagonistically organized receptive fields. A decrease in object luminance relative to the background will cause a receptive field with an excitatory center to decrease its activation while an increase in object luminance contrast relative to the background will cause a similarly organized receptive field to increase its activation. The increase and decrease of receptive field activation will feedforward to the increase and the decrease subunits of the counterchange detector depicted in Figure 6 (Hock et al., 2002). The degree to which the decrease and increase biphasic subunits are activated depends upon how the feedforward information temporally aligns with the biphasic response state of the subunit. With proper overlap, the transient responses of the increase and decrease biphasic subunits' correlated response will reflect the degree they overlap and integration occurs. Correlated output will signal motion with a response that is also transient and proportional to the maximum of the motion detector's transient response. Importantly, the increase subunit has a lower, no-stimulus resting level, creating an asymmetry impacting the correlated response of the detector. It is this asymmetry that prevents the need for a time delay as proposed by the Reichardt detector and prevents motion aliasing. The viability of the counterchange detector as a third-order mechanism stems from research investigating its role as a first- or second-order mechanism. Hock, Gilroy, & Harnett (2002) utilized the generalized apparent motion stimulus and the BRLC measure previously described in the review of Hock, Kogan, and Espinoza (1997) to design a stimulus where first-order motion energy was present but counterchange information was absent. The co-changing condition stimulus, shown in Figure 7a, provides first-order directional motion energy as evidenced by a Fourier space-time transform. Additionally, the left object and the right object of the stimulus exchanged luminance values over a wide range of BRLC values that previously induced the perception of motion. In this stimulus, however, both objects increased their luminance contrast with the background from frame-to-frame. Motion was not perceived irrespective of the BRLC values and the presence of motion energy. In a counter-changing condition of the same experiment, (see Figure 7b) one object's luminance contrast with the background increased and the other object's luminance contrast with the background decreased (counterchange information was present). Motion was always perceived. Direction for apparent motion was specified by the direction of change in the luminance contrast between the object and the background. For this two-frame stimulus, motion begins with the object whose luminance contrast with the background decreases and ends at the object whose luminance contrast with respect to the background increases. (Figure 6 captures the directionality of the motion percept with the differing shape of the biphasic response in the decrease subunit compared to the increase subunit). The findings demonstrated the presence of first-order motion energy is not adequate for the perception of motion in the generalized apparent motion stimulus. The influence of counterchange may also be necessary.

The second-order mechanism for perception of motion includes nonlinear rectification of stimulus information prior to a neural analysis of Fourier motion energy by a first-order type mechanism (Chubb & Sperling, 1988; Lu & Sperling, 1995). This rectification causes luminance values encoded by the visual system to become positive relative to the background luminance. Such a mechanism could influence the perception of motion in experimental conditions where object luminance values were greater than the background for one object and lower than the background for another object. Hock et al. (2002) simulated the rectification process on the previous experimental stimuli. If the perception of motion depends on a second-order mechanism that derives first-order motion energy, rectified stimuli should produce motion in both the co- and counter-changing conditions. Instead, motion was perceived only in the counter-changing condition and not for the co-changing condition. Furthermore, direction of motion was specified in accordance with counterchange information. As with first-order mechanisms, the influence of counterchange appears to be necessary to mechanisms classified as second-order.

Because attentional tracking was proposed by Lu and Sperling (1995b) to be one basis for third-order motion perception, Hock et al. (2002) explored its role with a counterchange stimulus. In the absence of counterchange, motion was frequently perceived when observers attended to the object and shifted attention from one location to the other. Motion was not frequently perceived when attention was fixed midway between the two objects. When object direction was specified by counterchange, there was little influence of attention. Results indicated that attention is not necessary to perceive motion when it is specified by counterchange.

Counterchange as an informational basis for the perception of apparent motion has been further supported by a working computational model (Hock, Schöner, & Gilroy, 2009) and experiments applying the counterchange theory to other illusions such as the line motion illusion. The line motion illusion (LMI) involves adjacent surfaces where one surface changes in luminance contrast. Depicted in Figure 8, the resulting illusion is one of a new surface sliding in front of the originally presented surface. Explanations for the LMI are based upon high-level mechanisms that could provide feedback to lower-level motion detectors such as in illusions of impletion/morphing (Downing & Treisman, 1997; Holcombe, 2003) and others requiring attentional processes (Hikosaka, Miyauchi, & Shimojo, 1993a, 1993b; Shimojo, Miyauchi, & Hikosaka, 1997; Von Grünau, Dubé, & Kwas, 1996). In a series of experiments, Hock and Nichols (2010) demonstrated that there is also a feedforward-to-counterchange motion detector explanation to the LMI percept. They concluded that simultaneous changes in edge contrast and oppositely signed changes in surface/background contrast could create, by itself, the LMI. Though not necessary to the percept (as the LMI was, in certain cases, perceived in the absence of counterchange) it was concluded that the same counterchange that signals motion in the generalized apparent motion stimulus can signal motion for the higher-order LMI stimulus. Furthermore, because the source of counterchange was from both edge and surface-to-background contrasts, it is now thought that different types of receptive fields (center-surround as well as edge detector neurons) provide the input to the biphasic subunits of the counterchange motion detector.

Building upon the line motion illusion, Hock and Nichols (2013) paired counterchange and motion energy simultaneously in a stimulus with signals for motion in the opposite directions. The stimuli consisted of six adjacent or nearly adjacent rectangles. The rectangles were never spatially displaced from frame to frame. Instead, the luminance of each rectangle was lightened one-by-one, sequentially from right-to-left or left-to-right, over six frames. The percept changed directions with frame duration; slow frame durations produced motion in the direction specified by counterchange while fast frame durations produced motion in the direction specified by motion energy. Dominance of motion energy at faster frame durations is explained by the counterchange detector's biphasic subunits; the most recent input is amplified while the preceding input is inhibited. For fast frame durations, the integration of excitation with inhibition in the counterchange detector subunits will mute the overall activation of the detector. Likewise, slower frame durations will provide time for the biphasic subunits to recover from preceding inputs and be properly positioned for integration, resulting in a stronger correlated response to a counterchange stimulus (Hock et al., 2009).

As experimental work has progressed, the concept of counterchange information has given second-thought to a long-standing habit of classifying motion stimuli information into independent categories of first- second- and third- order mechanisms. Cleary, it is not that simple. Patterns of counterchange detected by the counterchange mechanism may work in tandem with other motion detecting mechanisms. For example, counterchange stimuli are capable of producing motion even when one object of a stimulus is luminance-defined (first-order) while it's partner object is defined by patterns (second-order); as long as counterchange is present, motion is perceived (Hock & Gilroy, 2005).

Receptive Fields. Receptive fields are patches of receptors, each having either an excitatory or inhibitory response to a particular stimulus at a particular spatial location in the visual environment. Collectively, these receptors send messages to a neuron and, when the messages collectively reach the neuron's threshold, the neuron fires. Receptive fields, such as those discovered by Hubel and Wiesel (1962) via single-cell recordings in the cat striate cortex (area V1 of the visual cortex), respond to bars of a specific orientation. Hubel and Wiesel labeled these as “simple” cells because their receptive fields were easily mapped into excitatory and inhibitory subregions by shining spots of light across all areas of the receptive field and recording the neuron’s response. Ultimately, the spatial mapping of the neural response showed the preferred stimulus of the neuron. Though each spot of light elicited only a weak response, once the preferred stimulus was discovered (a line of a certain orientation) and presented to the neuron, it was maximally excited. Other neurons’ receptive fields, called “complex” cells, are not so easily mapped. Still, a variety of stimuli have been matched to receptive fields throughout the visual system, including luminance and luminance changes (both stationary and temporal), contrast-defined edges, motion, color, etc.

Center-surround receptive fields have a characteristic organization of excitatory and inhibitory receptors and are illustrated in Figure 9. They are circularly symmetric with either an ON-center circled by an OFF -surround or an OFF-center circled by an ON-surround. For luminance-detecting ON-center receptive fields, light falling in the excitatory center region will increase a neuron’s firing rate whereas light falling in the inhibitory surround region decreases its firing rate. The opposite is true for OFF-center receptive fields. Receptive fields with center-surround organization are found throughout the visual system. Beginning in the retina, the center-surround receptive field organization recurs upwards through the visual system, at all major processing stages, and are prominent in the middle temporal (MT) visual area of the brain; an area critical to perception of motion (Allman, Miezin, & McGuinness, 1985a, 1985b; Berezovskii & Born, 2000; Raiguel, Van Hulle, Xiao, Marcar, & Orban, 1995; Tadin & Lappin, 2005).

Receptive fields early in the visual system are most limited in terms of the visual space within which they can detect luminance change. However, when their output is integrated and processed by receptive fields higher in the visual system, the visual space that is represented grows and the information becomes more complex. Physiological research of the monkey visual cortex suggests that integration of retinal receptive field information into a higher-level pattern structure takes place as early as V1. Area V1 receptive fields, containing a complete representation of the visual field seen by the eyes, receive input from the lateral geniculate nucleus of the thalamus (LGN) and subsequently provide output to higher cortical visual areas

(Gilbert & Wiesel, 1992; Maunsell & Newsome, 1987; D. C. Van Essen, Felleman, DeYoe, Olavarria, & Knierim, 1990; David C Van Essen & Gallant, 1994). More recently, fMRI research has established similar findings in humans (Smith, Singh, Williams, & Greenlee, 2001).

In natural vision, luminance contrast variations provide cues that motion is present. Often those variations are slow in the natural environment (as opposed to fast-object motion in an experimental setting). It is important to consider how temporal frequency and luminance contrast information is interpreted and relayed by receptive fields at successive stages of the visual hierarchy in order to understand motion perception (Adelson, 2000; Knill & Kersten, 1991; Purves, Shimpi, & Lotto, 1999; Williams & Atkinson, 2002). There is substantial evidence of luminance contrast dependence impacting receptive field dynamics. Primate visual cortex cells have been found to respond along a facilitation-to-suppressive continuum relative to stimulus contrast (Peng & Van Essen, 2005). Furthermore, receptive field output with regard to motion contrast levels of moving gratings have been found to impact the firing rate of monkey V1 neurons in a consistent but nonlinear manner that is qualitatively different from the effect of the same contrast changes to stationary gratings (Geisler, Albrecht, & Crane, 2007).

To infer if levels of the receptive field involvement in a stimulus differ across hierarchical levels, psychophysicists often manipulate local filters with small stimuli and higher-level filters with larger stimuli. At the higher-levels, where processing is more complex, results from psychophysical experiments can often be counterintuitive. Driving in fog can lower many visual skills yet motion stimuli with small displacements can be more accurate under low contrast with the improvement mirrored in the higher-level middle temporal (MT) area of the visual system (Seitz, Pilly, & Pack, 2008).

It is a strong working theory however, that visual response to changes in contrast from receptive fields' feedforward input to biphasic neurons, such as those represented by the subunits in the counterchange detector, result in a relaxing of the biphasic response curve in low contrast conditions which in turn could lead to greater temporal integration of the subunits in the counterchange detector. The opposite impact on biphasic neurons occurs in high contrast conditions (Stromeyer III & Martini, 2003; Stromeyer III, 2003). Also important to the integration of the biphasic subunits of the counterchange detector is the speed at which the feedforward input from receptive fields reaches them. There is evidence of temporal asymmetry between ON- and OFF-center luminance receptive fields with ON-center excitation traveling faster through its respective pathway than OFF-center surround excitation (Chichilnisky & Kalmar, 2002; Del Viva, Gori, & Burr, 2006; Lankheet, Lennie, & Krauskopf, 1998).

Now that counterchange has been isolated as a critical stimulus characteristic to first- second- and third-order motion stimuli, experimental work continues to define its role in other apparent motion stimuli and to investigate the feedforward input that activates the counterchange detector. This is the purpose of the four experiments described in the following overview. They begin with a newly discovered apparent motion stimulus, where counterchange originates from the *background* of a stimulus rather than the *objects*. This stimulus serves as a foundation for the first two experiments that follow. The subsequent experiments were developed in order to explore the results of Experiment 1 for clues to ON/OFF receptive field feedforward effects on the biphasic subunits of the counterchange detector.

Experimental Overviews

In a counterchange apparent motion stimulus, the frame changes create the oppositely signed luminance contrast changes in the objects relative to the background. Luminance contrast information is detected by receptive fields and excitatory responses are fed-forward to the biphasic subunits of the counterchange detector. One subunit at one object location responds transiently to decreases in stimulus contrast while the subunit at the other object location responds transiently (and with a different temporal profile with a lower resting level) to increases in stimulus contrast. When the transient responses to decreases and increases in stimulus object-to-background contrast overlap in time, the excitatory phases of the two biphasic responses integrate and signal motion. If relatively longer frame durations are required to produce the perception of motion, it would suggest that the biphasic subunits need the longer time span to achieve their full response and integrate to produce the motion signal. This could mean that the input fed-forward from the receptive fields is slower, causing the biphasic detectors to relax and allow more time for integration. Tolerance for longer frame durations and tolerance for longer inter-stimulus intervals are indicative of slower time scales for the detection of counterchange.

Experiment 1: Time scale differences in foreground- vs. background-counterchange at low, medium, and high average stimulus contrasts. Previous counterchange research has utilized stimuli where counterchange is produced by the manipulation of the objects' luminance. In other words, the counterchanging luminance source is from the foreground, the objects that appear to move. Experiment 1 introduces an apparent motion stimulus where the *object* luminance remains static while the *background* alternates in luminance contrast. In other words, Experiment 1 was designed to explore the counterchange detector's response to apparent motion stimuli that occurs in two ways. (1) The luminance of the objects changes while the luminance of their background remains constant. Changes in receptive field excitation are due to changes in the luminance falling in the center of center-surround receptive fields. (2) The luminance of the objects remains constant (one is lighter than the other), while the luminance contrast of the background, which is intermediate to the luminance values of the two objects, changes. Changes in receptive field excitation are now due to changes in the luminance covering the surround portion of the center-surround receptive fields. The two versions of this apparent motion stimulus (foreground- and background-counterchange) are depicted in Figure 10. Figure 10b depicts the background-counterchange condition (BG); the background luminance is temporally varied and object luminance is static. The background, whose luminance value is between that of the two objects, shifts away from the luminance value of one object but towards the luminance value of the other object, creating the counterchange. Figure 10a depicts the foreground-counterchange (FG) condition; where alternating luminance of the objects is the source of counterchange. For both stimuli 10a and 10b, motion between the objects is perceived as long as a decrease in object-to-background contrast is paired with an increase in object-to-background contrast. Motion perception for FG and BG conditions were tested at three levels of average stimulus contrast, low, medium (med), and high, and across a wide range of frame durations (FD) (16.7 ms to 500.1 ms).

Experiment 2: Effects of inter-object distance on motion in foreground- compared to background-counterchange. Typically, and consistent with Korte's third law, wider separations in the objects of an apparent motion stimulus, require longer FD values for motion to be perceived. Experiment 2 explores the effect of inter-object distance (the spatial separation of the objects) in the FG and BG conditions on the perception of motion. An inter-object distance (IOD) of 120 min (the same IOD used in Experiment 1) and a wider IOD of 360 min were tested in both FG and BG conditions with the average low contrast from Experiment 1. The FD ranged from 75 ms to 675 ms within each FG/BG condition by IOD combination. Except for the wider IOD of 360 min and FD range, the stimuli were identical to the low contrast stimuli in Experiment 1.

Experiment 3: Reversed polarity of objects in foreground-counterchange at low, medium, and high average stimulus contrasts.. Experiment 3 attempts to distinguish temporal differences in the ON/OFF excitatory center and OFF/ON excitatory surround receptive field input to the counterchange detector by creating two conditions where the luminance polarity of the objects relative to the background are reversed. The FG condition from Experiment 1 was presented as (a) either a light object on a dark background (light on dark) or (b) a dark object on a light background (dark on light). The stimuli are depicted in Figure 11. The same stimulus average contrast levels of low, med, and high used in Experiment 1 were repeated in Experiment 3, regardless of whether the condition was dark-on-light or light-on-dark. Because the FG condition did not require the long frame durations of the BG condition, the temporal range of frame durations was narrowed to allow for testing on a finer time scale (from 100.2 to 367.4 ms).

Experiment 4: Reversed polarity of objects in average low contrast foreground-counterchange with inter-change intervals Hock and Gilroy (2009) used a two-flash paradigm to show that the counterchange detector would signal motion by pairing the decrease in object-to-background contrast resulting from the offset of one object flash with a temporally delayed increase in object-to-background contrast from a neighboring object's flash onset. The temporal delay is known as the inter-change interval (ICI). Consistent with Korte's fourth law, they found that briefer flashes required longer ICIs in order for motion to be optimally perceived. If there are temporal differences in the ON/OFF excitatory center and OFF/ON excitatory surround receptive field input to the counterchange detector, an ICI inserted between the contrast changes of the objects might further delay a slower excitatory surround input to the biphasic subunits. Thus, the perception of apparent motion in the dark-on-light condition might differ from that in the light-on-dark condition. To that end, Experiment 4 modifies the low average stimulus contrast reverse polarity stimuli from Experiment 3 (Figure 11) into a two-flash presentation with an ICI ranging from 0 to 200 ms inserted between flashes.

Hypotheses and Predictions

Activation from the biphasic subunits of the counterchange detector (for object counterchange), is proposed to stem from feedforward excitatory input from antagonistically organized ON-center or OFF-center receptive fields (excitation is produced by the center or the surround, respectively). Other types of antagonistically organized receptive fields, such as edge detectors, are also proposed to support counterchange, particularly for the line motion illusion. However, the focus of this research is the center-surround receptive field.

The rate-of-change of the receptive field excitatory output is proposed to differ when luminance changes occur in the center region compared to the surround region of center-surround receptive fields. Surround region excitatory output is proposed to have a slower rate of change. This difference, depending on its magnitude, should impact the biphasic subunits of the counter-change detector. A faster rate-of-change in a receptive field results in a steep slope to full excitation and quicker detection by the biphasic subunits of the counterchange detector. A slower rate-of-change indicates a more gradual slope to full excitation and a potentially slower-to-threshold activation of the biphasic subunits. As a result, the perception of apparent motion due to changing the background luminance (exciting the receptive field surround) may require longer frame durations than the perception of apparent motion due to foreground-counterchange (exciting the receptive field center).

Previous object-defined counterchange research has found an increase in counterchange detector response with increases in stimulus contrast. There is also evidence that the temporal response profile of biphasic cells changes with stimulus contrast, with higher contrast compressing and lower contrast relaxing the profile in time. Changes in object-to-background luminance contrasts in an object-defined counterchange apparent motion stimulus results in differences in the time scale of motion signal responses (faster time scales for higher levels of contrast and slower time-scales for lower levels of contrast). Therefore, the hypotheses for Experiment 1 are two-fold: (1) The likelihood of perceiving apparent motion in both the FG and BG conditions will be comparatively greater for shorter frame durations at higher levels of average luminance contrast, for which time scales are expected to be faster. This would suggest that average stimulus contrast impacts the time scale of the biphasic subunits that are the basis for the perception of counterchange motion. (2) Longer frame durations will be required when stimulus contrast changes are produced by changes in the luminance of the background compared to contrast changes produced by changes in the luminance of the objects. This would indicate that changes in receptive field feedforward excitation are slower when changes in the luminance fall in the surround portion of center-surround receptive fields (BG condition) compared to the center (FG condition).

Does previous counterchange research impact these hypotheses? Previous counterchange research utilizing luminance-defined objects has not investigated repetitively cycled sets of frame durations for foreground-counterchange using relatively large objects. Compared to the experiments presented here, previous research for object-induced counterchange has utilized stimuli with object sizes much smaller (144^2 min smaller in some cases) and only two frame durations. Average stimulus contrasts in previous counterchange research are roughly similar to those used here, however. Hock et al., (2002) found optimal motion for the 267 ms two-frame counterchange stimulus at high contrast and the proportion of motion perceived increased with BRLC values. This is consistent with the hypothesis for Experiment 1 as it relates to the effect of contrast on the foreground- and background-counterchange conditions, but its predictive value here is limited. The larger objects used in these experiments increase the salience of the objects and impacts the perception of apparent motion (Glasser & Tadin, 2011; Paffen, van der Smagt, te Pas, & Verstraten, 2005) Because this dissertation is the inaugural investigation of background-counterchange, previous counterchange research is not applicable to background-counterchange predictions, except to predict that in the presence of counterchange, motion will be perceived.

Experiment 2 compares the effect of inter-object distance in the average low contrast stimulus across both foreground- and background-change conditions. If Korte’s third law holds, greater separation between the objects will require slower frame durations in both conditions. Preference for slower frame durations at low contrast, whether due to the relaxing of the biphasic subunit response or slower input from receptive fields, will increase the temporal opportunity for integration of the biphasic subunits in both conditions. However, as hypothesized in Experiment 1, an even slower time scale in the counterchange detector response is anticipated for the background-counterchange condition, where excitatory feedforward input from the counterchange detector stems from the slower surround. Slower responses predict a longer lasting temporal opportunity for integration of the biphasic subunits. Therefore, the impact of inter-object distance may be less noticeable in the background-counterchange condition where the time scale is slower. That is, the background-counterchange condition may be “slow enough” due to its own mechanics for the motion percept to sustain across a wider inter-object distance. In summary, the hypothesis for Experiment 2 is that the impact of inter-object distance on perception of motion will be greater in the foreground-counterchange condition than in the background-counterchange condition.

Experiments 3 and 4 are related to ON-center and OFF-center receptive fields’ feedforward input to the biphasic subunits of the counterchange detector. The foreground-counterchange stimulus from Experiment 1 was altered into two conditions: (1) light objects on a dark background and (2) dark objects on a light background. Experiment 3 compares the two conditions across frame duration values at the same high, medium, and low average stimulus contrast levels used in Experiment 1. Experiment 4 compares the two conditions with an inter-change interval inserted between the flashes at average low contrast. If differential center-surround receptive field input impacts the response of the biphasic subunits of the counterchange detector, the light-on-dark condition should create faster responses and greater integration of the biphasic subunits. Therefore, it is hypothesized that more motion will be perceived for faster frame durations in Experiment 3 and (consistent with Korte’s fourth law) for longer inter-change intervals in Experiment 4 for the light-on-dark condition compared to the dark-on-light condition.

This dissertation is the starting point for exploring the counterchange motion detector’s response to object movement when counterchange originates from the background (a new counterchange stimulus) compared to counterchange originating from the foreground (the objects). Differential results from foreground- vs. background-counterchange will then be considered in light of experiments manipulating receptive field input at different levels of contrast, polarity of the objects, inter-change intervals, and inter-object distance.

II. METHOD

Experiment 1: Time Scale Differences in Foreground- vs. Background-counterchange at Low, Medium, and High Average Stimulus Contrasts

Participants. The three participants were the author and two undergraduate students from Florida Atlantic University. The undergraduates were naïve with respect to the purpose of the experiment.

Materials. Stimuli were created using Symantec C++ for Macintosh (Version 7) and presented with a Power Macintosh 7300/180 computer. Each frame of the stimuli consisted of two square objects with variable luminance centered within a larger rectangle of variable luminance. The frame was centered in the screen of a NEC MultiSync FP955 monitor (screen luminance <.001 cd/m2). When viewed from a distance of 35.5 cm (maintained by a head restraint), the simultaneously visible objects subtended a visual angle of 48 x 48 min and were 120 min apart (center-to-center). The background rectangular frame surrounding the objects subtended a visual angle of 15 deg wide x 5 deg high.

Pairs of frames were cycled four times within each trial for one of nine randomly ordered frame durations: 16.7, 33.4, 50.1, 66.8, 83.5, 100.2, 300.6, 400.8, or 501.0 ms. In the foreground-counterchange (FG) condition, the luminance of the objects varied from frame-to-frame while the background luminance was held constant across frames. In the background-counterchange (BG) condition, the luminance of the background varied from frame-to-frame while the object luminance was held constant across frames.

Michelson (1962) contrast ratios were calculated for each object in each frame of the stimuli by subtracting the luminance value of the object from the background luminance value and dividing by the sum of the same two luminance values. The Michelson contrast ratios for the left and right objects, which alternated from frame-to-frame, were averaged to provide a stimulus average frame-to-frame ratio ($\bar{M}$). The $\bar{M}$ values for the three average stimulus contrasts tested in each of the FG and BG conditions were: .1 (low average contrast), .3 (medium average contrast), or .5 (high average contrast). The change in object-to-background M ratios from one frame to the next (ΔM) was matched across average contrast levels and kept to a minimum (<.06) in order to minimize ceiling effects in the perception of motion. Larger changes in the Michelson contrast between frames have been proven to increase the perception of motion (e.g., Gilroy & Hock, 2004; Kulikowski & Tolhurst, 1973; Pantle & Sekuler, 1969).

In the FG condition, the left object decreased in luminance from 44.3 cd/m^2 in frame 1 to 38.9 cd/m^2 in frame 2, increased back to 44.3 cd/m^2 in frame 3, and so on. The luminance of the right object alternated in the opposite pattern, beginning with an increase in luminance from 38.9 cd/m^2 in frame 1 to 44.3 cd/m^2 in frame 2, followed by a decrease in luminance back to 38.9 cd/m^2 in frame the, and so on. For the FG condition, the luminance of the background rectangle was a constant 34.2 cd/m^2 for average low-contrast blocks of trials ($\overline{M}$ = .1, ΔM = .04), 22.4 cd/m^2 for medium (med) average contrast (M) blocks of trials ($\overline{M}$ =.2, ΔM = .05) and 13.8 cd/m^2 within high average contrast blocks of trials ($\overline{M}$ =.3, ΔM = .04). From frame 1 to frame 2, the left object-to-background contrast decreased while the right object-to-background contrast increased. The counterchanging contrast pattern was reversed in frame 3 and reversed again in frame 4, providing the necessary counterchange information for the perception of back-and-forth apparent motion.

In the BG condition, the left object's luminance was always below the background luminance while the right object's luminance was always above the background luminance. The alternating frame-to-frame background luminance produced the same pattern of counterchanging contrast for the foreground objects as in the FG condition. Background luminance decreased from 25.7 cd/m^2 in frame 1 to 23.7 cd/m^2 in frame 2, followed by an increase in luminance back to 25.7 cd/m^2 in frame 3, and so on. The left and right object luminance values of the foreground were held constant at 20.1 (left) and 30.1 (right) cd/m^2 for the low stimulus ($\overline{M}$ =.1, ΔM =.04), 13.2 (left) and 47.2 (right) cd/m^2 for the M stimulus ($\overline{M}$ =.3, ΔM = .05), and 8.5 (left) and 7.4 (right) cd/m^2 for the high stimulus ($\overline{M}$ = .5, ΔM= .04). As in the FG condition, from frame 1 to frame 2, the left object-to-background contrast decreased while the right object-to-background contrast increased.

The counterchange contrast pattern reversed on each successive frame, providing the necessary counterchange information for the perception of back-and-forth apparent motion.

Procedure. Separate blocks of 72 trials were presented for each of the three average contrast levels (low, med, and high) within each of the FG and BG conditions. The 72 trials were composed of eight repetitions of nine unique frame durations (16.7, 33.4, 50.1, 66.8, 83.5, 100.2, 300.6, 400.8, or 501.0 ms). The frame durations were randomized within sub-blocks made up of nine trials each. Six blocks (two at each level of average contrast) in either the FG or BG condition made up a testing session. The blocks were presented in a predetermined, counterbalanced order so that no two average contrast levels were presented back-to-back. Sessions alternated between FG and BG until completion of twelve testing sessions.

Participants were instructed to maintain fixation midway between the two squares throughout the trial and to avoid shifting their attention between the squares. Using the computer keyboard, the participants provided a positive response when they saw object motion between the two squares at any point in the trial and a negative response when object motion was not clearly perceived. Participants pressed the space bar if they were unsure of their response.

Experiment 2: Effects of Inter-Object Distance on Motion in Foreground- Compared To Background-counterchange

Participants. The three participants were the author and two undergraduate students from Florida Atlantic University. The undergraduates were naïve with respect to the purpose of the experiment. One of the undergraduate students was a participant in Experiment 1.

Materials. The stimulus-generating materials (programming language, monitor, viewing distance, etc.) were identical to Experiment 1. Spatial and luminance characteristics of the stimuli were identical to average low contrast stimuli in both the FG and BG conditions in Experiment 1, including M ratios for the objects, ΔMvalues, and $\bar{M}$ values. The exception was the varying inter-object-distance (IOD); the objects were either 120 or 360 min apart (center-to-center) when viewed from a distance of 35.5 cm. The 120 min IOD was identical to the IOD in Experiment 1.

Procedure. Separate blocks of 72 trials were presented for each of the IOD conditions (120 or 360 min separation) within each of the FG-counterchange and BG-counterchange conditions. The 72 trials were determined by 8 repetitions of nine frame durations (75, 150, 225, 300, 375, 450, 525, 600, or 675 ms). The frame duration order was randomized within sub-blocks of 9 trials. Six blocks in either the FG or BG condition made up a testing session. Each block presented either the 120 min or 360 min IOD. IOD values alternated from block to block within each condition. The first testing session presented the FG condition; the second testing session presented the BG condition with IOD block-order identical to the previous testing session in the FG condition. Condition-defined (FG or BG) sessions continued to alternate until the completiton of eight testing sessions. The IOD block-order was reversed every two testing sessions.

Experiment 3: Reversed Polarity of Objects in Foreground-counterchange at Low, Medium, and High Average Stimulus Contrasts

Participants. Participants were the same participants who participated in Experiment 1 with the addition of a professor at Florida Atlantic University, who was not naïve as to the purpose of the experiment.

Materials. The stimulus-generating materials (programming language, monitor, viewing distance, etc.) were identical to Experiment 1. The stimuli from the FG condition in Experiment 1 became the stimuli for the light object on a dark background (light-on-dark) condition in Experiment 3. Stimuli for the dark object on a light background (dark-on-light) condition were created by reversing the polarity of the luminance values of the stimulus while keeping other characteristics of the stimulus the same, including M ratios for the objects, ΔMvalues, and $\bar{M}$ values for the three contrast levels. In the dark-on-light condition, the left object decreased in luminance from 34.0 cd/m^2 in frame 1 to 30.0 cd/m^2 in frame 2, increased to 34.0 cd/m^2 in frame 3, and so on. The right object alternated in an opposite pattern, beginning with an increase in luminance from 30.0 cd/m^2 in frame 1 to 34.0 cd/m^2 in frame 2, followed by a decrease to 30.0 cd/m2 in frame 3, and so on. The background rectangle’s luminance was held constant at 38.9 cd/m^2 in the low stimulus, 59.6 cd/m^2 in the M stimulus, and 95.8 cd/m^2 in the high stimulus. This produced a pattern of object-to-background counterchanging contrast identical to the light-on-dark condition, but for the opposite luminance polarity.

Procedure. Separate blocks of 72 trials were presented for each of the three average contrast levels (low, med, and high) within each of the two conditions (light-on-dark and dark-on-light). The 72 trials were determined by eight repetitions of nine frame durations (100.2, 133.6, 167.0, 200.4, 233.8, 267.2, 300.6, 334.0, or 367.4 ms). The frame duration order was randomized within sub-blocks of 9 trials. Three blocks (one at each average level of contrast) in the light-on-dark condition and three blocks (one at each average level of contrast) in the dark-on-light condition made up a testing session. Participants engaged in one testing session each day beginning with the dark-on-light condition, where the three average contrast blocks were presented in a predetermined order, followed by the light-on-dark condition, where the three average contrast blocks were repeated in the same order. The presentation order of the average contrast blocks was counterbalanced across testing sessions with no contrast levels presented back-to- back. The condition order of dark-on-light- and light-on-dark alternated for each testing session until the completion of twelve testing sessions. Participants' procedure for indicating the perception of motion (or not) was identical to that in previous experiments.

Experiment 4: Reversed Polarity of Objects in Average Low Contrast Foreground-counterchange With Inter-change Intervals

Participants. The participants were the same three participants in Experiment 1.

Materials. The stimulus-generating materials (programming language, monitor, viewing distance, etc.) were identical to previous experiments. With the exception of the IOD, widened slightly to 150 min, the spatial composition and luminance values of the light-on-dark stimulus and the dark-on-light stimulus were identical to the average low contrast stimuli in Experiment 3, including M ratios for the objects, $\bar{M}$ values for the three contrast levels and ΔM values between frames. A flash consisted of a change in an object's luminance contrast with respect to the background lasting for 50 ms, at which point the object's luminance returned to its beginning state. Specifically, after the left object was presented for an initial "get ready" duration of 300 ms, the following cycle was repeated four times: (1) the left object was flashed for 50 ms, (2) the inter-change interval (ICI) was inserted, and (3) the right object was flashed for 50 ms.

Procedure. Separate blocks of 72 trials were presented at average low contrast within each of the two conditions (light-on-dark and dark-on-light). The 72 trials were determined by 8 repetitions of nine ICIs (0, 20, 40, 60, 80, 100, 120, 140, 160, 180, and 200 ms). The order of ICIs was randomized within sub-blocks of nine trials. Six blocks in either the light-on-dark or dark-on-light condition made up a testing session. Conditions alternated from one testing session until the completion of six testing sessions. Instructions to participants for this experiment were identical to the preceding experiments.

Data Analyses

Historically, analyses from psychophysical experiments in vision research have been presented mostly in graphic format, often with the scientists' choice of transformation or model best suited to "tell the story" behind the experimental data. Journal reviewers and universities, however, have increasingly requested statistical tests to substantiate effects found in experiments, often resulting in a force-fitting of psychophysical data to traditional statistical approaches with strict assumptions such as analysis of variance (ANOVA) (Knoblauch & Maloney, 2012; Moscatelli, Mezzetti, & Lacquaniti, 2012).

Many psychophysical experiments utilize the repeated measures cross-over design, where every subject is exposed to all levels of all factors (treatments) over many exposures. In other words, every cell representing a unique factor level or combination of factor levels contains an equal number of repeated discrete responses from each subject. All subjects are exposed equally to the combinations of factors and their levels via a carefully designed order planned to either manipulate or eliminate carryover effects. Data from these "balanced" designs are often proportions, representing subjects' discrete responses to a stimulus. However, the underlying distribution, against which means and variances are tested, is binomial in nature. Sometimes, a binomial distribution can be similar to a normal distribution, but only when the probability (P) of an event on every event is equal to chance (P=.5) and the sample size is very large. If the underlying binomial distribution's form is not normal or unknown, then, a key benefit of a balanced design is at risk. That is, each subject serves as his or her respective control, with random error in responses "canceling out" to zero over many repetitions. Meticulous counterbalancing in experimental designs and strict controls in the testing environment are hallmarks of psychophysics, creating data sets that are often, but not always, robust to violations of the assumptions of Repeated Measures ANOVA (RM-ANOVA) (Quinn & Keough, 2002; Williams & Atkinson, 2002).

The RM-ANOVA is a form of Multivariate Analysis of Variance (MANOVA) where individual subject responses are organized into a $n\ x\ p$ matrix (X) with n representing the number of subjects and p the number of responses for each individual. The number of parameters to be estimated is denoted by q and the $q\ x\ p$ matrix is represented by α. The RM-ANOVA model can be expressed as the matrix equation $Y = X\alpha + e$. The mean responses for a given subject are found on the $i{:}th$ row of $X\alpha$ and the subject's deviation from the means is found on the $i{:}th$ row of e. The matrix e includes all sources of random deviation from the means of $X\alpha$, both of which are expected to have a multivariate normal distribution.

Now, due to the increase in personal computing power, psychophysicists are being called to utilize alternative analyses with underlying assumptions more appropriate to their data such as Generalized Linear Mixed Models (GLMM) (Moscatelli et al., 2012). (Depending on discipline, this approach may be referred to as hierarchical linear, mixed-effect, or variance component modeling.) In general, a repeated measures GLMM has the matrix equation form $Y_i\ =\ X_i\beta\ +\ \mathrm{Z}_i u_i\ +\ e_i$ where y_i is a vector of a subject's repeated responses for $i = 1, \ldots n$ subjects. The fixed effects design matrix for each subject is represented by X_i and β is the vector of regression coefficients. The extra term Z_i represents the design matrix for the random effects and u_i is a vector of random effects. Within-subject errors are represented by e_i. Both u_i (random effects) and e_i (within-subject residuals/errors) are assumed to be independent (Saarinen, 2004).

The GLMM was the analysis of choice for these experimental data sets for several reasons. First, data were collected in the form of the number of *yes* responses compared to the total number of *no* responses weighted by the total number of trials presented. The dichotomous dependent variable has two mutually exclusive categories coded 0/1 to indicate whether or not motion was perceived by the subject. The goal of analyses were to estimate the likelihood of the "yes, motion was perceived" category under a variety of visual environments. Estimated likelihoods may be expressed via probability, odds, or log-odds. If motion is observed 25 out of 100 times, the probability is 25/100; for every 100 opportunities, motion is observed 25 times (or one of four times (1/4). This same probability, expressed in odds, is 25/75, for every 25 times motion is observed, it is not observed 75 times (or (1/3). An odds of one signifies equal probability that an event will occur or not occur. Odds larger than one signify an event will more likely occur than not. Odds less than one signify the opposite; an event will more likely not occur than occur. While the range of all possible probabilities is 0 to 1, the range of all possible odds is $0\ to\ \infty$. Odds are a nonlinear transformation of probability space, bounded by 0 and 1, to a space beginning at 0 to positive infinity. The natural logarithm of odds, termed “logit” or “log-odds”, ranges from negative infinity to positive infinity and is centered at 0 which corresponds to a .5 probability. Logit models map probabilities into points in the linear log-odds space making the form of the model linear (Beauchamp, 2009; Jaeger, 2008).

Calculating coefficients or analyzing variance with probability data (bounded between zero and one) is problematic. The relationship between the independent variables and the dependent variable probabilities is nonlinear. A linear relationship is required by both general linear models (GLM) and GLMMs. However, the relationship between the independent variable and probability data will be linear if the probability data are converted via a logit or log-odd function, and GLMMs are capable of this. (Naturally, the assumption is that the dependent-independent variable relationship in question is linear within the range of parameters being analyzed.).

A second problematic assumption of RM-ANOVA is that a set of data’s variances and covariances within all factors and factor-level combinations must conform to the characteristic of sphericity. That is, variances and covariances in the data set must be homogeneous. The assumption of sphericity is often violated (Maxwell & Delaney, 2004) as it was for the experimental data presented here. Mauchly’s (1940) test indicated violation of sphericity in all five experimental data sets.

Though not relevant here, it should be noted that ANOVA is not able to analyze datasets with missing values while GLMM is robust to missing data (if data are missing in a random fashion). Furthermore, within-subject independent variables must be categorical for RM-ANOVA. In many psychophysical studies, the important predictor variable is time or another independent variable that is better represented as a continuous, non-categorical measurement. GLMM can incorporate continuous independent variables (Bolker et al., 2009; Heck, Thomas, & Tabata, 2013; West, Welch, & Galecki, 2014).

Violations of RM-ANOVA assumptions carry risks of erroneous conclusions, particularly an inflation of Type 1 error (Jaeger, 2008). Validity of results of cross-over repeated measures designs are improved with the use of GLMMs; this is one reason results may lead to different conclusions than RM-ANOVA. In addition, new insights may emerge through the use of GLMMs because (a) model-fitting with GLMM is tailored to the experimental question and (b) effect variances and covariances are thoroughly examined for patterns. If necessary, GLMMs can allow for different trajectories (or their interactions) for each individual subject. Termed “random effects”, GLMM allows individual subject trajectories to differ in slope, intercept, or both. Furthermore, random effects can be matched to a variety of covariance structures in order to determine the best model fit. Individual subject residuals (errors) are then calculated according to each subject’s variance from their own trajectory rather than from the mean trajectory. These are important improvements over RM-ANOVA, which more coarsely compiles subject variance.

In summary, GLMMs have the important advantage of allowing the researcher to match the variance in subject data to specialized variance-covariance structures in order to account for different patterns of within-subject and cross-factor correlations in the data (e.g. learning over time and adaptation) (Littell, 2006; Seltman, 2014). In other words, rather than assuming that variances and covariances are homogeneous within a dataset, GLMMs allow for inspection or “unpacking” of the variance and exploration of differences that may be the result of experimental manipulations (Maxwell & Delaney, 2004). The more accurate modeling of the variance and covariance at each level of the sampling hierarchy leads to reduced standard errors of the variance components, which in turn may increase sensitivity of testing of fixed effects and contrasts (Quené, Bergh, & den Bergh, 2008).

Generalized Linear Mixed Models, like RM-ANOVA, controls for correlations among repeated observations for each individual but does so in a different manner. It allows for the addition of one or more random effects for the subjects. These extra parameters take the form of additional residual terms, each term having its own estimated variance. In other words, the model may control for the effect of the subject. In the simplest GLMM, the random intercept model, a subject may be allowed to be higher or lower at a specified point on the mean trajectory, such as the starting value of a sequence of events, but slopes of the trajectories are consistent. By controlling for the intercept, it is taken out of the original error term.

The greatest advantage of the GLMM is their flexibility. They can address clustered subjects, repeated measures and cross-over designs where there are repeated measures not only on the subject but across each stimulus. Time can be treated as categorical or continuous and unbalanced data does not drop subjects from the model (Grace-Martin, 2014).

III. RESULTS

Experiment 1: Time Scale Differences in Foreground- vs. Background-counterchange at Low, Medium, and High Average Stimulus Contrasts

Previous experimental work has explored counterchange produced by the manipulation of the surface of the objects that appear to move in an apparent motion stimulus. This experiment introduces a stimulus where the objects' properties remain static while the background alternates in luminance contrast. In other words, it is now possible to explore the counterchange detector's response to apparent motion stimuli that occurs in two ways. (1) The luminance of the objects changes while the luminance of their darker background remains constant. Center-surround receptive field excitation is due to changes in the luminance falling in the center of ON-center receptive fields. Counterchange information is provided in the foreground-counterchange condition (FG) due to changes in the objects' surface luminance, one decreasing and the other increasing simultaneously, relative to the background luminance. (2) The luminance of the objects remains static (one is lighter than the other), while the luminance contrast of the background, intermediate to the luminance values of the two objects, changes. Receptive field excitation is now due to changes in luminance changes falling on the center-surround spatial fields' OFF-center excitatory surround (see Figure 10). Counterchange information is provided in the background-counterchange condition (BG) due to the intermediate changes in background luminance causing a simultaneous decrease in luminance contrast between one object and its background with an increase in luminance contrast between the other object and its background. As long as a decrease in object-to-background luminance contrast is paired with an increase in object-to-background contrast, counterchange is present, and motion is perceived.

Motion perception for FG and BG stimuli were tested at low, medium (med), and high average stimulus contrast at frame duration (FD) values ranging from 16.7 ms to 500.1 ms. (To create a wide range of frame duration (FD) values, and to investigate smaller FD values on a finer scale, the FD intervals were not evenly spaced.) In summary, FG- and BG-counterchange were investigated in terms of how the two sources of counterchange responded to changes across FD values in low, med, and high average stimulus contrasts.

The untransformed means of motion/nonmotion responses in addition to the average standard error of each subject for each FG/BG x low/med/high average contrast x FD value combination are presented in Figure 12. The amount of motion perceived over the range of frame durations tested was greater for the FG condition at all three average levels of contrast, but most notable at low and med average stimulus contrasts. Ceiling and floor effects were observed in data sets for all subjects for some FG/BG x low/med/high x FD combinations. Individual subject data trajectories representing their respective proportions of motion perceived over each FG/BG x low/med/high x FD combination varied in terms of their overall proportion of motion perceived and slope across FD values. Therefore, averaged data should be interpreted with caution. Subjects were consistent, however, in the “trend” of their perception of motion. All subjects perceived the most motion in the FG condition and, for both FG and BG conditions, at low average stimulus contrast and longer FD values. This is reflected in the averaged subject data in Figure 12.

A full complement of repeated measures generalized linear mixed models (GLMM) on the logit transformed means of the forced-choice categorical dependent variable were tested using condition (FG or BG), average stimulus contrast (low, med, and high) and FD value. Consistent fixed factor effect p values of p = 0 for successful models as well as consistent p values of p = 1 for failed models, in addition to highly inflated F values, were observed in all models tested. Further investigation revealed these results were due to separations in the data that were too large for valid results. Separation of data was due primarily to the uneven spacing of FD values tested, some being much wider apart than others, as well as floor and ceiling effects. This resulted in a logistic regression issue often denoted as the “Hauck-Donner phenomenon” (Hauck, Jr. & Donner, 1977). The Hauck-Donner phenomenon, though rarely addressed in the statistical literature, causes the likelihood approximation logistic regression to fail in these circumstances (Bůžková*, Lumley, & Rice, 2011). Alterations to the model were made, the most prominent being treating the categorical FD variable as continuous. This allowed for a successful GLMM with the logit link for the means as is appropriate for binomial dependent variables. Like all subsequent GLMMs reported, modeling was conducted with a top-down approach. In other words, all factors and their interactions were fully loaded into the model and then insignificant effects were removed as predictors (or not) until the best model fit was obtained.

The Akaike Information Criterion (AICc) (DeLeeuw, 1992), corrected for small sample sizes, was 5,507.86 in the optimal GLMM that included a random effect for subject intercept. The overall effect of repeated sessions was allowed to vary randomly but was not subject-specific. The FG condition produced significantly greater proportions of perceived motion than did the BG condition [F(1,960) = 129.07, p < .05]. Main effects for contrast (low contrast resulted in the most motion) and FD were also significant [F(2, 960) = 12.41, p < .01] and [F(1, 962) = 165.84, p < .01)], respectively. Two-way interactions were significant for FG/BG condition by FD [F(1, 962) = 23.99, p < .01] and low/med/high contrast by FD [F(2, 962) = 21.14, p < .01)]. The FG/BG condition by low/med/high contrast two-way interaction was not significant. Most importantly, the three-way FG/BG condition by low/med/high contrast by FD interaction, was significant [F(1,962) = p < .01] indicating that the main effects of the factors FG/BG condition, low/med/high contrast, and FD, as well as the two-way interactions, were carried by the differences in perceived motion at specific FD values within specific low/med/high contrast comparisons. Because frame duration was treated as a continuous variable, t-tests were not appropriate. Figure 13 illustrates the results of the GLMM with logit-link results, with estimates translated back from the log to the original scale. Note that standard errors reflect the continuous variable FD and would have been greater for categorically-binned intervals. Both averaged proportion graphs and GLMM graphs of estimated means are presented in Experiment 1, as they differ in their overall appearance due to the treatment of FD as a continuous variable. For all other experiments, only graphs of GLMM estimated marginal means are presented.

Clearly both average stimulus contrast and FD value impacted both the FG- and BG-counterchange motion in a similar fashion. For all low/med/high average stimuli contrasts, as FD increased, so did perception of motion. However, for the FG stimulus, more motion was perceived. Due to ceiling effects in the FG condition at all low/med/high contrasts and ceiling effects in the BG condition at low contrast, the slopes over the range of FD values could not be accurately compared. Such a comparison is necessary to conclude any differences in time scale of the counterchange detector between the two motion percepts. However, it is visible that the amount of motion perceived over increasing FD values shows BG-counterchange has a slower take-off than does FG-counterchange and stimuli with average low contrast are preferred by the counterchange detector in both FG/BG conditions .However, contrary to FG-counterchange, low contrast appears to be more *necessary* to produce a stable, ceiling-level of the BG-counterchange motion percept.

The results demonstrated that apparent motion is perceived as the result of the new BG-counterchange apparent motion stimulus in low contrast conditions. Neither hypothesis for Experiment 1 was proven true. Rather, the likelihood of perceiving apparent motion in both the FG and BG conditions was *not* greater for shorter frame durations at higher levels of average luminance contrast, for which time scales are expected to be faster. The opposite result was found. Both FG and BG conditions elicited greater motion at faster FD values at low contrast. While longer frame durations were required for apparent motion to be perceived in the BG compared to the FG condition, differences were primarily quantitative. An increase in motion perception was noted for both FG and BG conditions as FD values increased. Possibly, because of ceiling effects, no time-scale differences in the two conditions were found.

Results could be indicative of a counterchanging contrast system for motion detection where, in an overall low contrast environment, there is a relaxing of the biphasic response profile providing more opportunity for integration of the biphasic subunits resulting in the perception of motion. This is consistent with Stromeyer (2003) who has tested biphasic cell responses to an apparent motion stimulus of pairs of gratings (one low contrast grating and one high contrast grating in the pair). He found a facilitation of motion direction detection when the low contrast grating was presented *before* the high-contrast grating. Strong masking of direction detection was observed in the opposite condition when the high-contrast grating was presented before the low-contrast grating. When the two gratings were presented with a temporal overlap, the masking effect diminished. Results were explained by a shorter, compressed temporal response function by biphasic cells for high-contrast stimuli and a more relaxed, longer temporal response function for biphasic cells at low-contrast stimuli. If one of the biphasic subunits of the counterchange detector has a temporally compressed response at high contrast, it may well be back to its negative resting state by the time a lower contrast object appears, preventing temporal integration and the signaling of counterchange motion. At low contrast, there is more opportunity for longer biphasic temporal response profiles to integrate. This would explain the preference for the average low-contrast stimulus conditions from the results of Experiment 1. Possibly, FG-counterchange (which reaches ceiling at 100 ms with the low contrast stimulus) induces the more relaxed, longer biphasic subunit temporal response function more efficiently than does BG-counterchange (which reaches ceiling at 401 ms with the low contrast stimulus).

Is FG-counterchange's greater efficiency in relaxing of the temporal response function of the biphasic subunit due to center-surround receptive field input? Possibly, if the receptive field input induced by FG-counterchange reaches the biphasic subunits of the counterchange detector faster than receptive field input induced by BG-counterchange. The FG-counterchange stimulus excites ON-center receptive fields. The BG-counterchange stimulus excites the oppositely organized surround of OFF-center receptive fields. Differential input from oppositely organized center-surround receptive fields might suggest excitatory center responses are temporally stronger and/or faster than excitatory surrounds. (Recall that only the excitatory responses of center-surround receptive fields are passed forward to the biphasic subunits of the counterchange detector). Furthermore, the OFF-center receptive field feedforward input from the excitatory surround may be not shaped as sharply by inhibition (Cavanaugh, Joiner, & Wurtz, 2012). This could potentially impact the shape of the temporal response of the biphasic subunit's response in the BG condition, with integration of the relaxed responses reaching threshold when contrast is low and FD values are long.

Experiment 2: Effects of Inter-object Distance on Motion in Foreground- Compared to Background-counterchange.

The concept of a more latent but relaxed, longer lasting temporal response of the biphasic subunit to OFF-center receptive field input compared to ON-center receptive field input, presented the question of whether the integration in the subunits biphasic response would be greater for BG-counterchange compared to FG-counterchange. Recall that Korte's third law states that wider separations in the objects will require longer FD values. Wider inter-object distances (IOD) means wider separation of the biphasic subunits, as they are aligned (like receptive fields) to points in the visual field. Presumably, the longer FD values required for wider IOD values allow more time for the temporal responses of further-apart biphasic subunits to integrate.

Experiment 2 explored the effect of FD and IOD in both the FG- and BG-counterchange stimuli on the perception of motion at average low contrast. The IOD conditions were created by manipulating the spatial distance of the objects in the stimuli from Experiment 1 so that both FG and BG condition were tested against two IODs (120 min and 360 min) at average low contrast only, where all subjects could perceive the BG-counterchange motion. Because Experiment 1 revealed that the BG condition required long frame durations for subjects to perceive sufficient motion, a wider range of FD values was tested in Experiment 2, spaced 75 ms apart and ranging from 75 ms to 675 ms.

For the best fitting model (AICc = 6,160.13), subject trajectories were allowed to vary in the slope and intercept over FD. Also, the repeated sessions were allowed to have a non-subject-specific random effect. No overall main effect of BG/FG condition was present. FD and IOD showed significant main effects [$F(2, 1{,}260) = 146.89$, $p <.01$] and [$F(1, 1{,}260) = 190.43$, $p < .01$)], respectively. The only significant two-way interaction was for IOD and FD [$F(2, 1260) = 10.06$, $p < .01$. Most importantly, a three-way interaction was observed for FD, IOD, and FG/BG condition [$F(2,1260) = 39.14$, $p < .01$]. Post-hoc paired-sample t-tests revealed that the three-way interaction was due to differences in IODs in the FG condition at certain FD values. Specifically, 150 [$t(2) = 3.937$, $p < .01$], 225 [$t(2) = 3.25$, $p < .01$], and 300 ms [$t(2) = 2.887$, $p = .01$]. Graphs of results are displayed in Figure 14.

Of most interest is the lack of IOD effect on the BG counterchange condition. These results are potentially explained by greater temporal integration of the biphasic subunits due to greater relaxation of the biphasic subunits' temporal response function to OFF-center surround input. OFF-center surround input, proposed to be more latent and sustained, is suspected to provide the input to the biphasic subunits in the BG condition. For the FG-counterchange the wider 360 min separation between the objects required longer FDs to reach ceiling (450 ms) than did the 120 min separation, suggesting less integration of biphasic subunits for the wider IOD. The hypothesis for Experiment 2 was supported by the results. The impact of inter-object distance was less noticeable, in fact, negligible, in the background-counterchange condition where the time scale is presumed to be slower. That is, the background-counterchange condition may be “slow enough” due to its own mechanics for the motion percept to sustain across a wider inter-object distance.

Experiment 3: Reversed Polarity of Objects in Foreground-counterchange at Low, Medium, and High Average Stimulus Contrasts

Experiment 3 attempted to manipulate the temporal characteristics of receptive field input to the counterchange detector by reversing the luminance polarity of the foreground-change condition in Experiment 1 at the same levels of average contrast (low, med, and high) used in Experiment 1. The FG condition from Experiment 1 was presented as (a) either a light object on a dark background or (b) a dark object on a light background. The stimulus is depicted in Figure 11. Because the FG condition did not require the long frame durations of the BG condition, the temporal range of frame durations was narrowed to allow for testing on a finer time scale (from 100.2 to 367.4 ms).

. As in Experiment 1, Experiment 3 required that FD be treated as a linear variable in order to create a successful model. In this case, the reason was not separation of data, but excessive degrees of freedom for the low sample size. For the best fitting model (AICc = 6,603.08), subject slope and intercept included random effects of FD for subject with an autoregressive covariance matrix matching the residuals. Average contrast level and FD showed significant main effects [F(2, 1,284) = 16.72, p <.01] and [F(1, 1,284) = 47.10, p < .01)], respectively. The main effect for condition (light-on-dark vs. dark-on-light) was not significant. One two-way interaction was observed for average contrast by FD [F(2,1284) = 8.896, p < .01]. A three-way interaction was found for condition by low/med/high average stimulus contrast by FD [F2,1284) = 5.92, p < .01].

Because FD values were treated as a continuous variable, post-hoc comparisons were not appropriate. However, as illustrated in Figure 15, this experiment predominantly illustrated the effects of average level of contrast for counterchange motion perceived across FD values with the low-average stimulus condition producing optimal motion effects for all FD values.

The hypothesis for Experiment 3 was not supported by the results. There were no overall differential effects of light-on-dark vs. dark-on-light conditions, regardless of the average stimulus contrast.

Experiment 4: Reversed Polarity of Objects in Average Low Contrast Foreground-counterchange With Inter-change Intervals.

Because no differential effects of frame duration on proportion of perceived motion were evident as the result of reversing the polarity of the stimulus in Experiment 3, the FD values tested were presumed to allow a wide range of opportunity for temporal integration of biphasic subunit response. Narrowing the opportunity for temporal integration of increase and decrease subunits provided a finer sieve to investigate receptive field input that might differ due to stimulus polarity. Thus, Experiment 4 modified the reverse polarity stimuli from Experiment 3 into a two-flash presentation with an ICI ranging from 0 to 200 ms inserted between flashes with interval spacing of 20 ms between each ICI. Hock and Gilroy (2009) used a two-flash paradigm to show that the counterchange detector would signal motion by pairing the decrease in object-to-background contrast resulting from the offset of one object flash with the increase in object-to-background contrast from a neighboring object's flash onset. Though no differential effects of frame duration on proportion of perceived motion were evident as the result of reversing the polarity of the stimulus in Experiment 3, the insertion of an inter-change interval (ICI) might separate the timing of receptive field input to a degree that differences in integration of biphasic subunits as a result of reversed polarity might be observed. The stimuli were presented at average low contrast, where floor effects due to the ICI, were less likely to be observed.

For the best fitting model (AICc = 4,244.49) ICI and condition (light-on-dark vs. dark on light) showed significant main effects [F(2, 1,176) = 23.71, $p < .01$] and [F(1, 1,176) = 4.89, $p < .05$)], respectively. The two-way interaction of condition with ICI was not significant. Graphs of model results are displayed in Figure 16.

Of primary interest is the greater difference in quantity of motion perceived for the light-on-dark condition compared to the dark-on-light condition. The differences in quantity between conditions could be attributed to intensity of the ON-center excitation compared to the OFF-center excitation. There were no obvious differential effects on the time scale of the biphasic subunits response to receptive field input. Both conditions indicated that optimum integration of the biphasic subunits' response occurs with an ICI interval of approximately 60 ms.

The temporal response function of ON-center and OFF-center excitation may differ. A latency between the onset of inhibition and excitation has been found in the cat LGN with inhibition occurring prior to excitation regardless of whether ON- or OFF-center cells are excited by the stimulus. This latency between the inhibition of ON-center neurons and the excitation of OFF-center neurons has been found to be smaller than the latency between excitation of OFF-center neurons and inhibition of ON-center neurons (Freund, Wita, & Brüstle, 1972). The earlier onset of inhibitory responses from receptive fields to a dark-on-light stimulus may be important to the overall level and timing of the counterchange detector response.

IV. DISCUSSION

Previous research has associated differences in average luminance contrast with differences in the time scale of responses to changes in contrast (faster time scales for higher level of contrast and slower time scales for lower levels of contrast). The first hypothesis for Experiment 1, that the odds of perceiving apparent motion would be greater for shorter frame durations and for higher levels of average luminance contrast, for which time scales were expected to be faster, proved incorrect. For the second hypothesis, longer frame durations seemed to impact foreground-counterchange (FG) and background-counterchange (BG) in a similar fashion. Longer frame durations were preferred by both FG-and BG-counterchange conditions. No discernable differences in time scale between the two conditions were observed. As such, no conclusions regarding differential ON-center excitatory feedforward input and OFF-center surround excitatory feedforward input to the biphasic detectors could be drawn.

Changes in contrast from receptive field feedforward relationships to biphasic neurons, such as those represented by the subunits in the counterchange detector, have been proposed to result in a relaxing of the biphasic temporal response profile in low contrast conditions. This could create greater opportunity for temporal integration of the subunits and firing of the counterchange detector in the low average contrast stimulus. The opposite impact on biphasic neurons is proposed to occur in high contrast conditions, with a compression of the biphasic temporal response profile. This could create less opportunity for temporal integration of the subunits and firing of the counterchange detector in the high average contrast stimulus.

This explanation also holds for the results of Experiment 2, where only the FG-counterchange condition was impacted by manipulation of the inter-object distance (IOD). For FG-counterchange, the wider 360 min separation between the objects required longer FDs to reach ceiling (450 ms) than did the 120 min separation, suggesting less integration of biphasic subunits for the wider IOD. Greater temporal integration of the biphasic subunits in the BG-counterchange condition, due to greater relaxation of the biphasic subunits' temporal response function to OFF-center surround input may explain the lack of effect of IOD on BG-counterchange. That is, the background-counterchange condition may be "slow enough" due to its own mechanics for the motion percept to sustain across a wider inter-object distance.

Experiments 3 and 4 utilized only FG-counterchange to investigate differential effects of ON-center excitatory input and OFF-center surround excitatory input to the biphasic subunits of the counterchange detector. The polarity of the objects was reversed in the two conditions. Light-on-dark presented light objects on a dark background while dark-on-light presented dark objects on a light background. Experiment 3 found no differences in the two conditions, just overall effects of average stimulus contrast consistent with Experiment 1. The FG-counterchange elicits more motion at low contrast.

Experiment 4 attempted to "tease out" differential effects for light-on-dark vs. dark-on-light conditions by inserting an inter-change interval (ICI) in the average low contrast FG-counterchange stimulus from Experiment 3. A greater difference in quantity of motion was perceived for the light-on-dark condition compared to the dark-on-light condition. The differences in quantity between conditions might be attributed to intensity of the ON-center excitation compared to the OFF-center excitation. There were no obvious differential effects on the time scale of the biphasic subunits response to receptive field input. Both conditions indicate that optimum integration of the biphasic subunits' response occurs with an ICI interval of approximately 60 ms.

The temporal response function of ON-center and OFF-center excitation is not presumed to be the same. Latency between the onset of inhibition and excitation has been found in the cat LGN with inhibition occurring prior to excitation regardless of whether ON- or OFF-center cells are excited by the stimulus. This latency between the inhibition of ON-center neurons and the excitation of OFF-center neurons has been found to be smaller than the latency between excitation of OFF-center neurons and inhibition of ON-center neurons (Freund et al., 1972). The earlier onset of inhibitory responses from receptive fields to a dark-on-light stimulus may be important to the overall reduced level of the counterchange detector response in the dark-on-light condition.

An alternative explanation to differential effects of FG-counterchange and BG-counterchange may lie in the receptive fields in area MT. In area MT, neurons have been found with center-surround antagonism (sometimes called “local motion” neurons) as well as “wide-field” neurons that prefer large moving fields and show no surround suppression (Allman et al., 1985a; Born, Groh, Zhao, & Lukasewycz, 2000; Raiguel et al., 1995). It is proposed that, in area MT, wide-field neurons signal background motion and center-surround neurons signal object motion (Born et al., 2000).

It is logical to assume, in order to perceive object motion, the objects must first be distinguished from the background. The center-surround properties of neurons in MT may be important for communicating relative motion between object and background. Tadin and Lappin (2005) measured the effects on monkeys’ eye movements to moving objects by microstimulation of two sites in area MT. Stimulation at the MT site where receptive fields are organized with antagonistic surrounds shifted monkey eye movement pursuit in the preferred direction of the neurons. Stimulation at wide-field neuron sites shifted pursuit in the opposite direction. Tadin and Lapin proposed that the signaling of object motion in the opposite direction activated wide-field neurons. They hypothesized that neurons’ receptive field center–surround mechanisms contribute to the behavioral segregation of objects from the background.

Perhaps background-counterchange requires construction of depth for perception of object motion. Kolers (1972) extensively manipulated the paths of motion in apparent motion displays. In experiments with a fixed barrier interposed between two shapes, Kolers found that under the proper conditions the path of motion appeared to move forward or backward around the barrier using depth as an alternative to passing the motion of the object through the barrier. Kolers found that the construction of depth took the visual system more time to execute than did the transformation of a figure. Future research could test subjects perception of depth in the FG- and BG-counterchange conditions. If depth is constructed in order for the objects to move in the BG-counterchange condition, it is likely that phi motion, rather than beta motion, is perceived.

Asking subjects to discern the two types of motion across FG- and BG-counterchange conditions is potentially fruitful.

Another area requiring future investigation is the preference for low average stimulus contrast in the stimuli used here, particularly for short frame durations as compared to the preference for high contrast stimuli in previous counterchange experiments. These stimuli used repeated cyclic frame durations and much larger objects than in previous counterchange research. The role of object size and length of exposure to counterchange must be explored, as well as directionality of perceived motion and the contribution of motion energy to background-counterchange

Linking psychophysical experimental results with microscopic neural responses to explain counterchange apparent motion requires inference across two distinctly different sciences and are difficult, at best, to prove. However, as neural physiological research regarding receptive field characteristics and accumulating evidence from psychophysical research with counterchanging stimuli evolves, so will the inferences that can be deduced.

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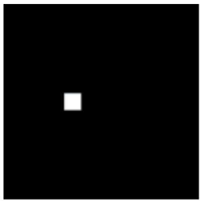
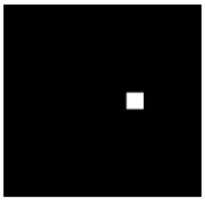


Frame 1



Frame 2

Figure 1. Example of a classical single-object apparent motion stimulus. Also referred to as a “standard” apparent motion stimulus, alternation of this frame-to-frame pattern results in the perception of one object moving continuously from the location in the first frame to the location in the second frame.

Frame 1

Frame 2

Figure 2. Generalized version of a single-object apparent motion stimulus. When the luminance values of the two objects trade places from one frame to the next, the result is the perception of object motion. This stimulus differs from the standard apparent motion stimulus in Figure 1 (where only one object is visible in a single frame), but the percept of object motion is similar.

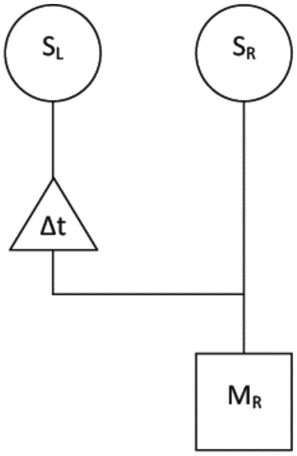


Figure 3. A simplified diagram of a rightward Reichardt motion detector. The circles (S_L and S_R) represent two spatially separated neural units that tap the visual field in two points and, in response to light, send a signal to a third neural unit (M_R).

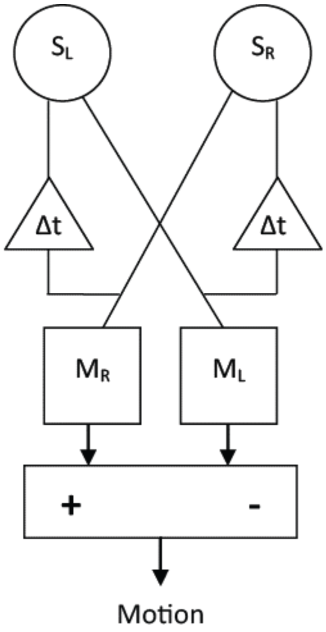


Figure 4. Coupled Reichardt detector detects both rightward and leftward motion. The response of the left neural unit (ML) is subtracted from that of the right (MR) to yield the motion detector's response. A positive result indicates rightward motion while a negative result indicates leftward motion.

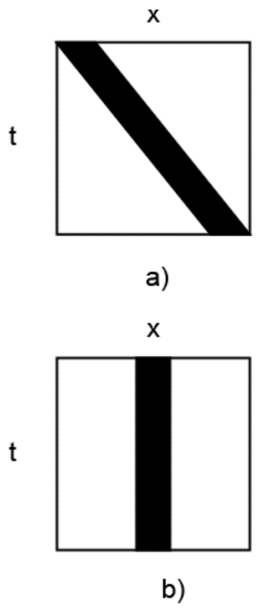


Figure 5. A space/time plot of (a) an object moving rightward and (b) a stationary object. Also referred to as a “motion energy” diagram. Steeper slopes will result from faster speeds; positive slopes will result from motion from right to left, and negative slopes will result from motion from left to right. The directional information provided to a motion energy detector is referred to as “directional energy” (DE).

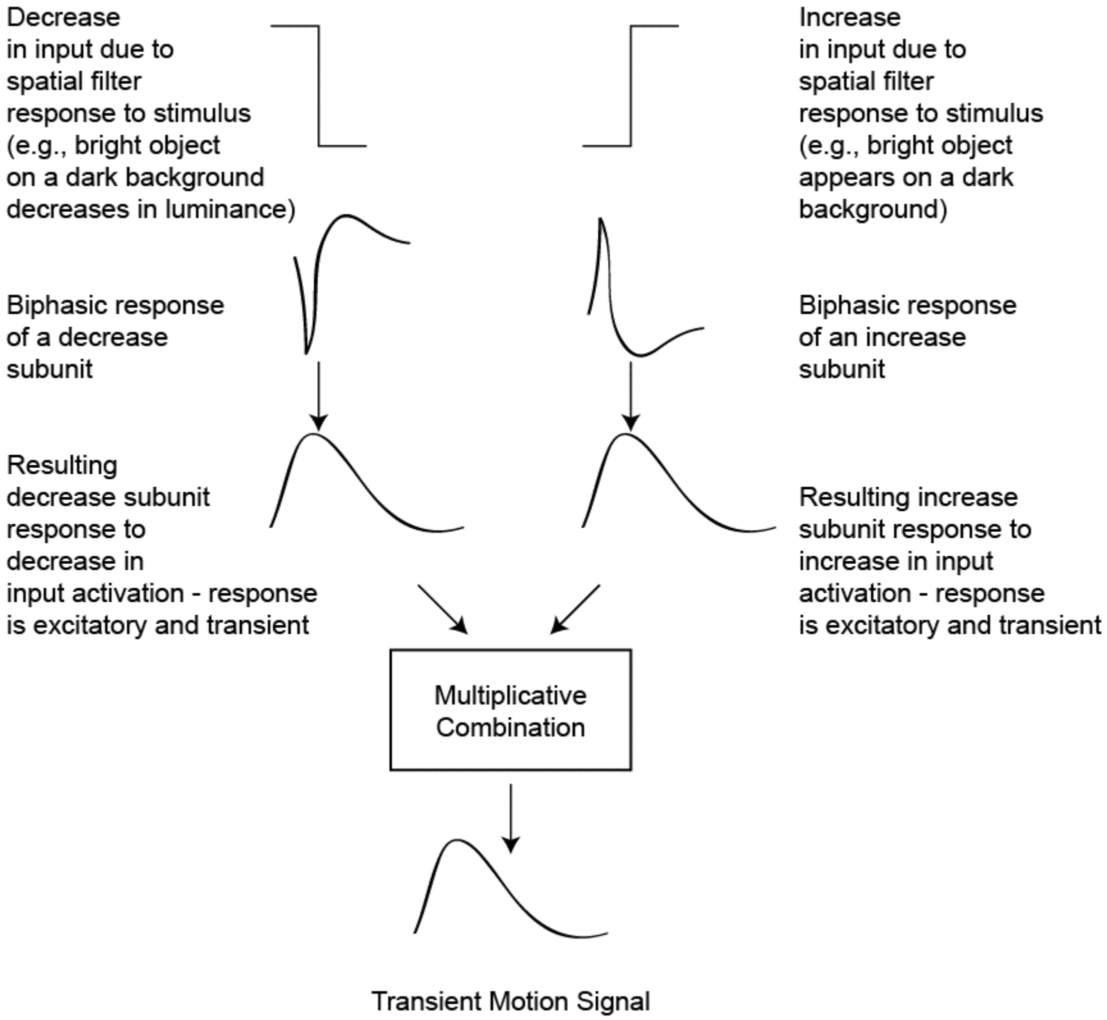


Figure 6. Counterchanging contrast model for motion detection. The increase and decrease of receptive field activation will feedforward to the increase and the decrease subunits. The directionality of the motion percept is captured by the differing functions of the biphasic response in the decrease subunit compared to the increase subunit. With proper integration, the correlated response of the decrease and increase subunits will signal motion.

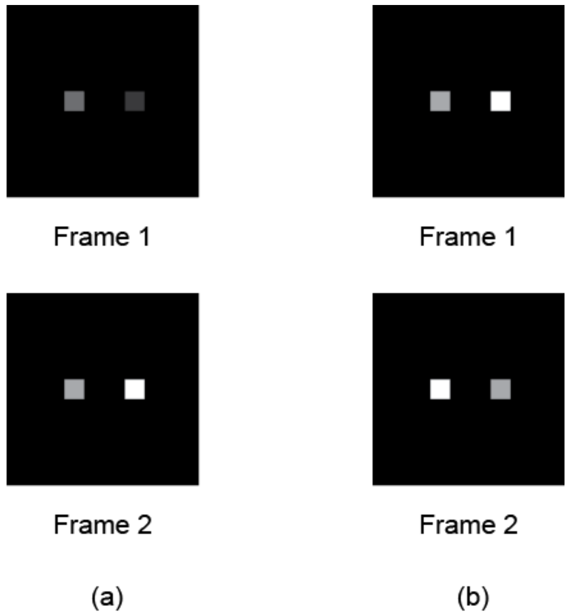
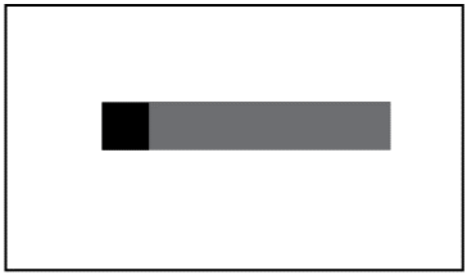
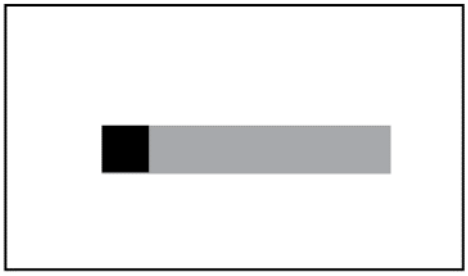


Figure 7. Illustrations of the (a) co-changing and (b) counter-changing conditions. Both stimuli contain directional energy (DE) as evidenced by a Fourier space-time transform. However, counterchange is only present in (b) and motion is only perceived for (b). The direction of motion for (b) is leftward, as motion begins with the object whose contrast with respect to the background decreases and ends at the object whose contrast with respect to the background increases.



Frame 1



Frame 2

Figure 8. The generalized line motion illusion produced via counterchanging contrast. The contrast of the edge increases while the contrast of the bar surface with the background decreases. The resulting illusion is one of a new surface sliding in front of the originally presented surface.

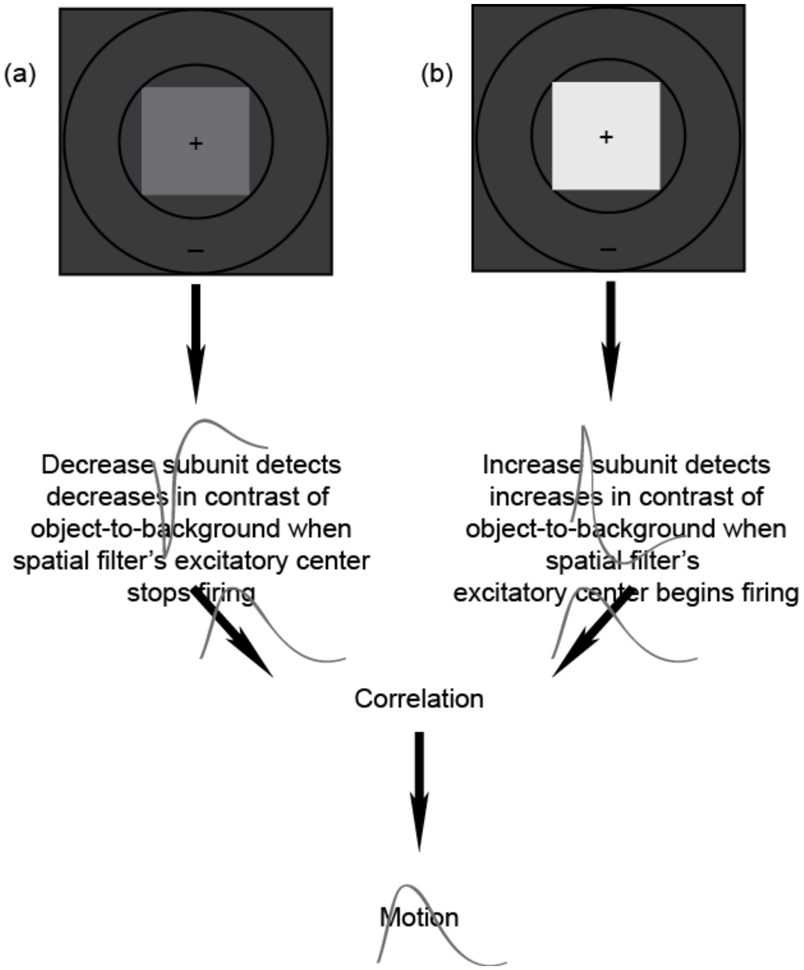
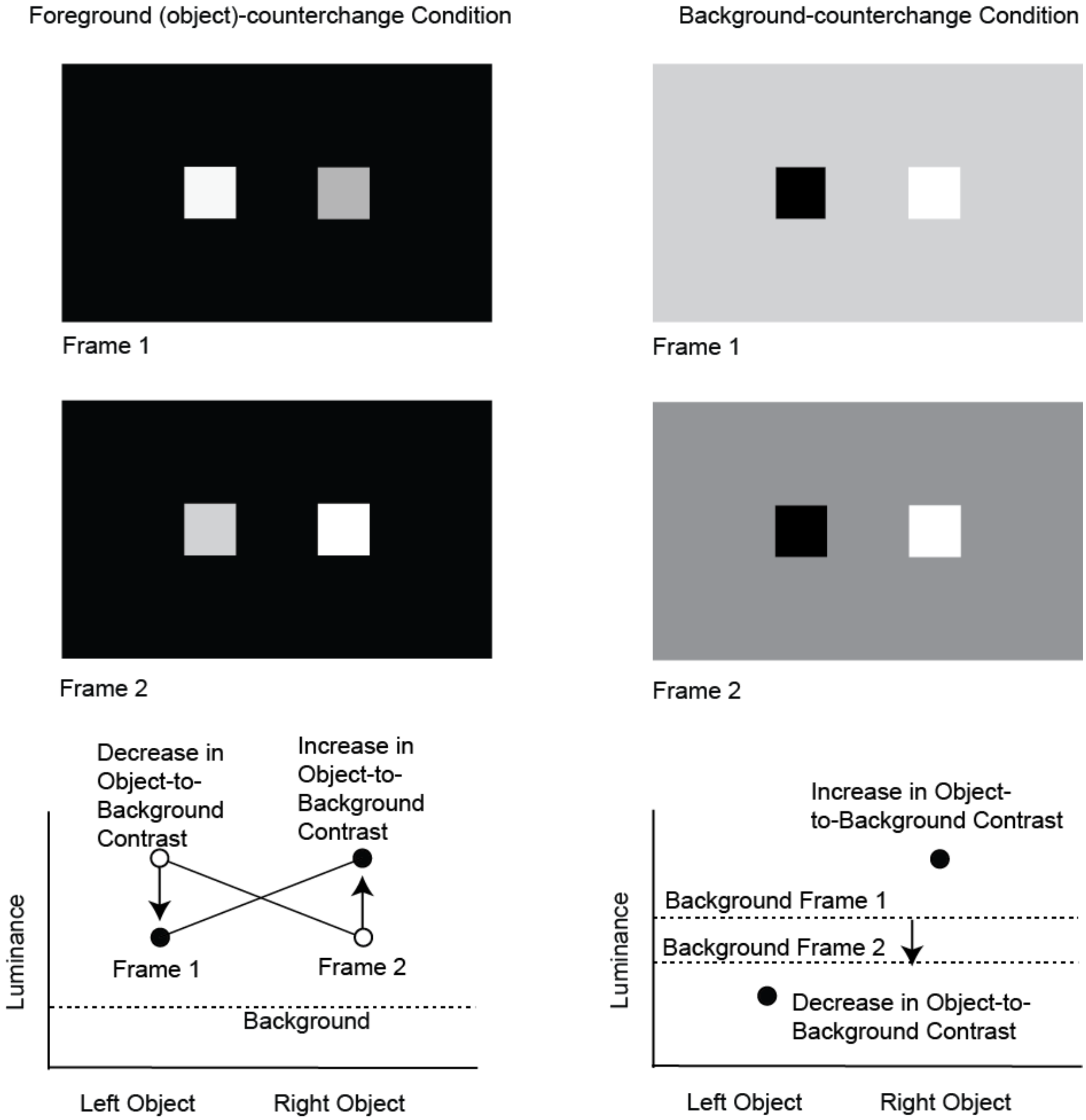
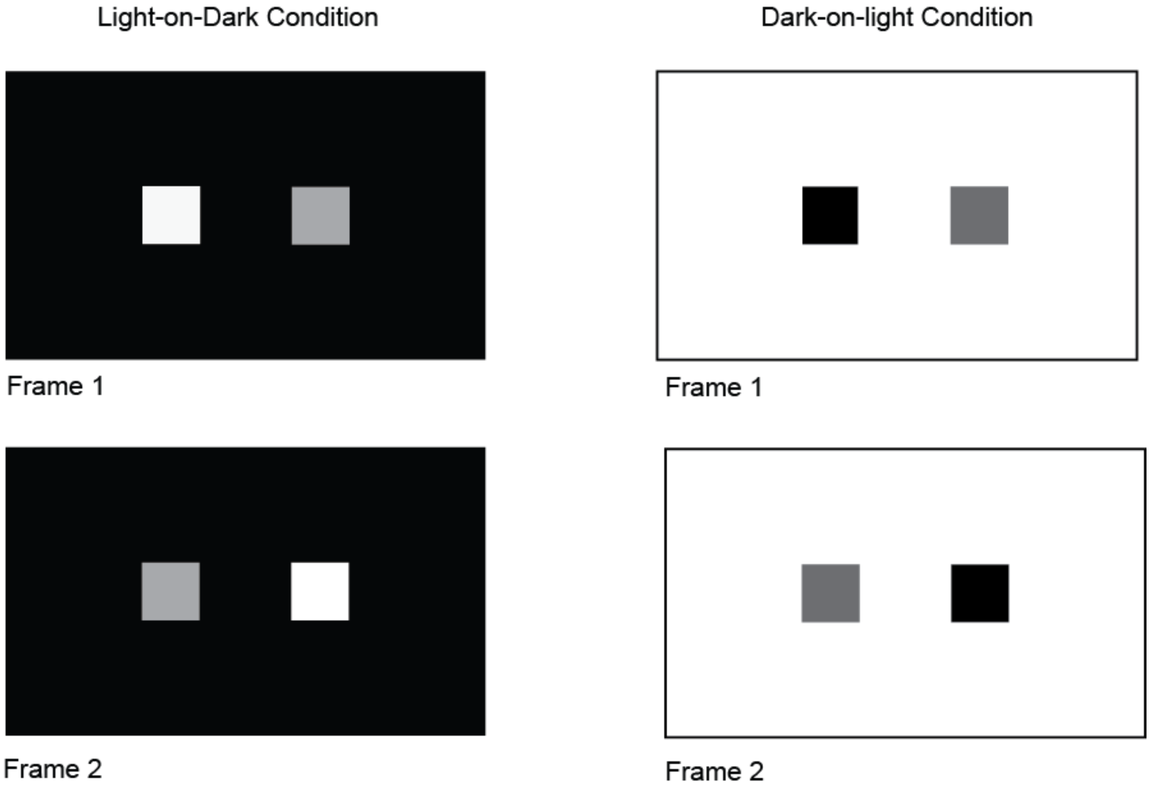


Figure 9. The proposed input to the biphasic decrease and increase subunits of the counterchange detector are center-surround receptive fields (for the generalized apparent motion stimuli used in experiments). In this case, the object changes in luminance while the background remains static in luminance. Therefore, only the ON-center excitatory center signals increases and decreases in object luminance contrast relative to the background.



(10a) (10b)

Figure 10. In the foreground-counterchange condition, the object luminance varies from frame-to-frame while the background luminance is held constant across frames. In the background-counterchange condition, the background luminance varies from frame-to-frame while the object luminance is held constant across frames.



11(a)

11(b)

Figure 11. Light-on-dark vs. dark-on-light stimuli for reversed polarity in Experiments 3 and 4. Excitatory input from the center of ON-center receptive fields should feedforward to the biphasic subunits in Figure 11(a). Excitatory input from the surround of OFF-center receptive fields should feedforward to the biphasic subunits in Figure 11(b).

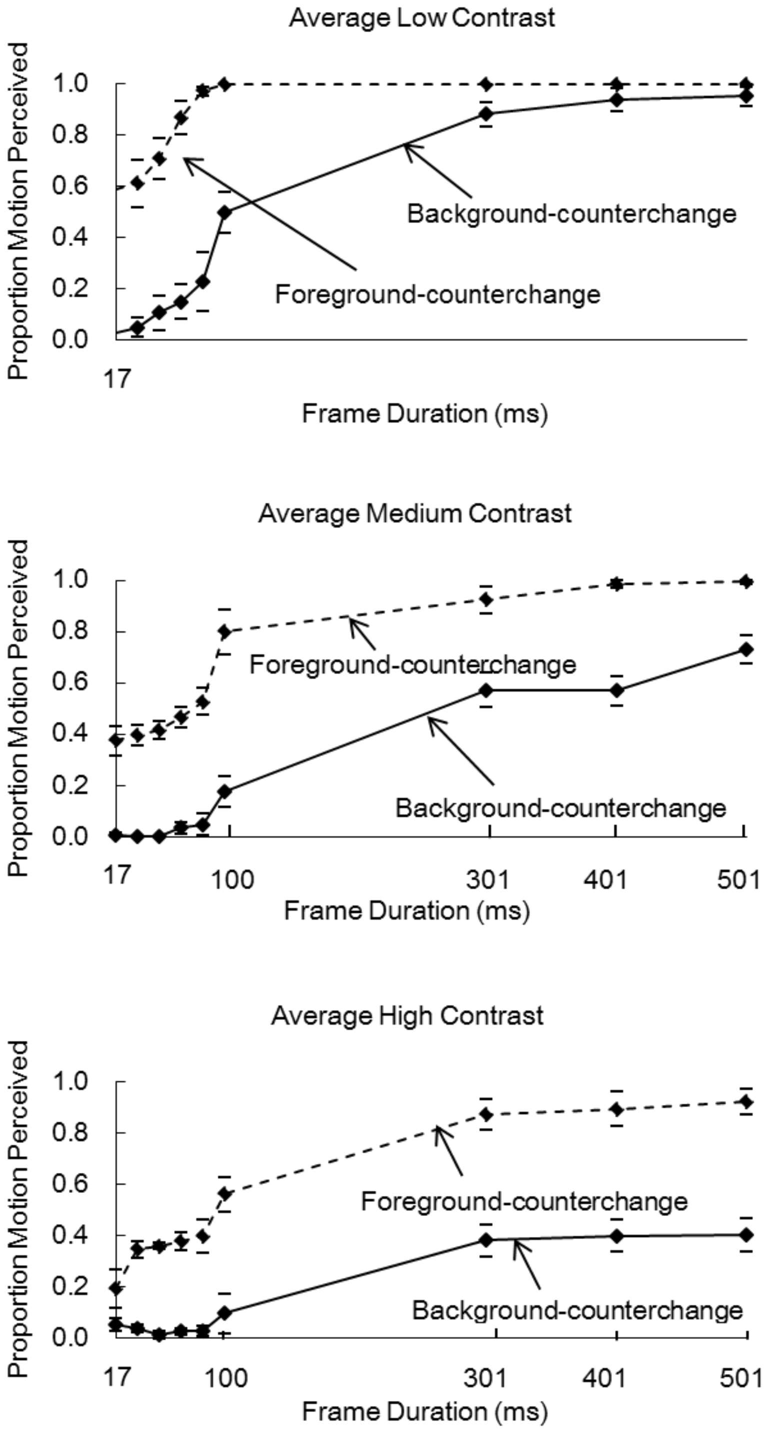


Figure 12. Experiment 1: Proportion of apparent motion perceived for foreground-counterchange and background-counterchange stimuli at average low, medium, and high contrasts. Bars show the averaged standard error of the mean for participants.

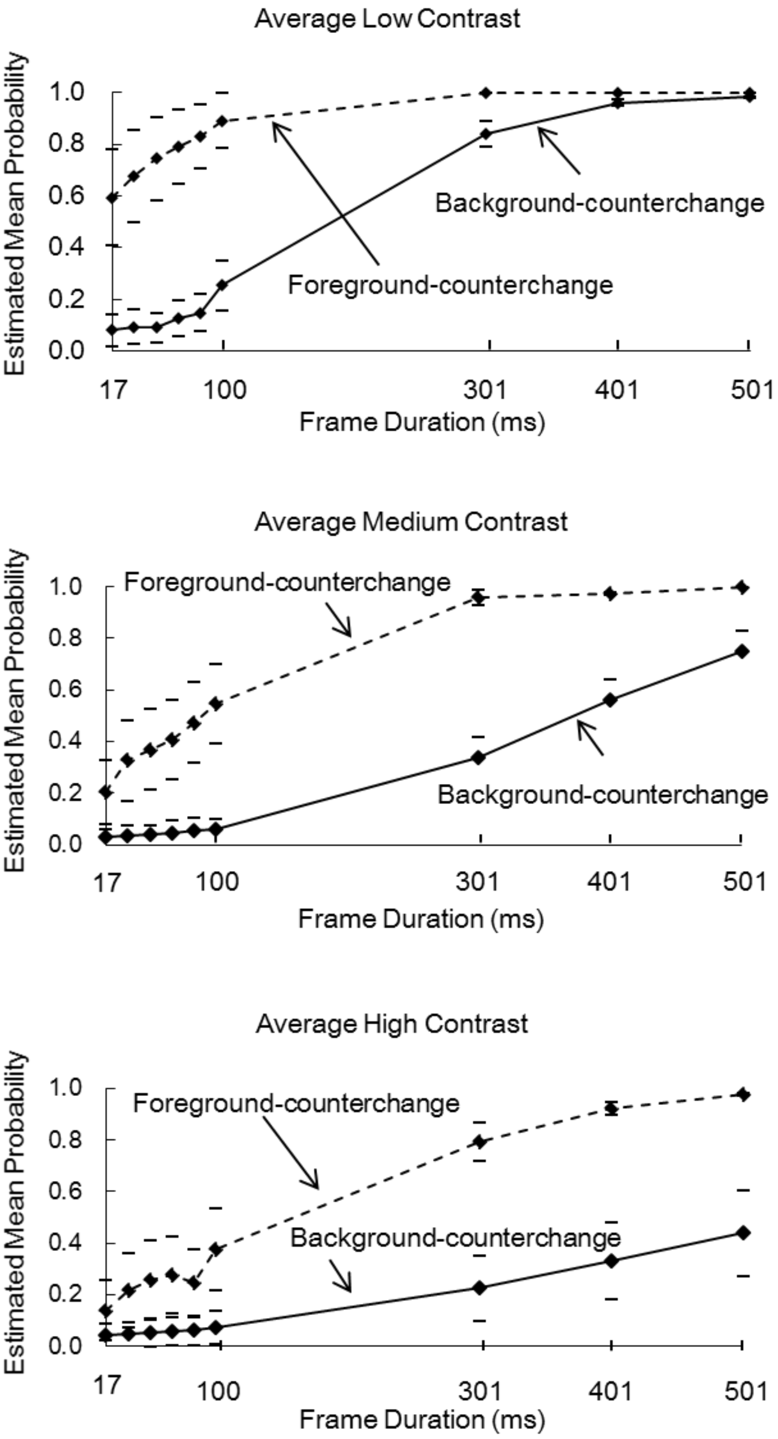


Figure 13. Experiment 1: Estimated mean probabilities for Experiment 1 as predicted by a generalized linear mixed model with a logit link function and frame duration treated as a continuous variable. Bars show the predicted standard error of the mean.

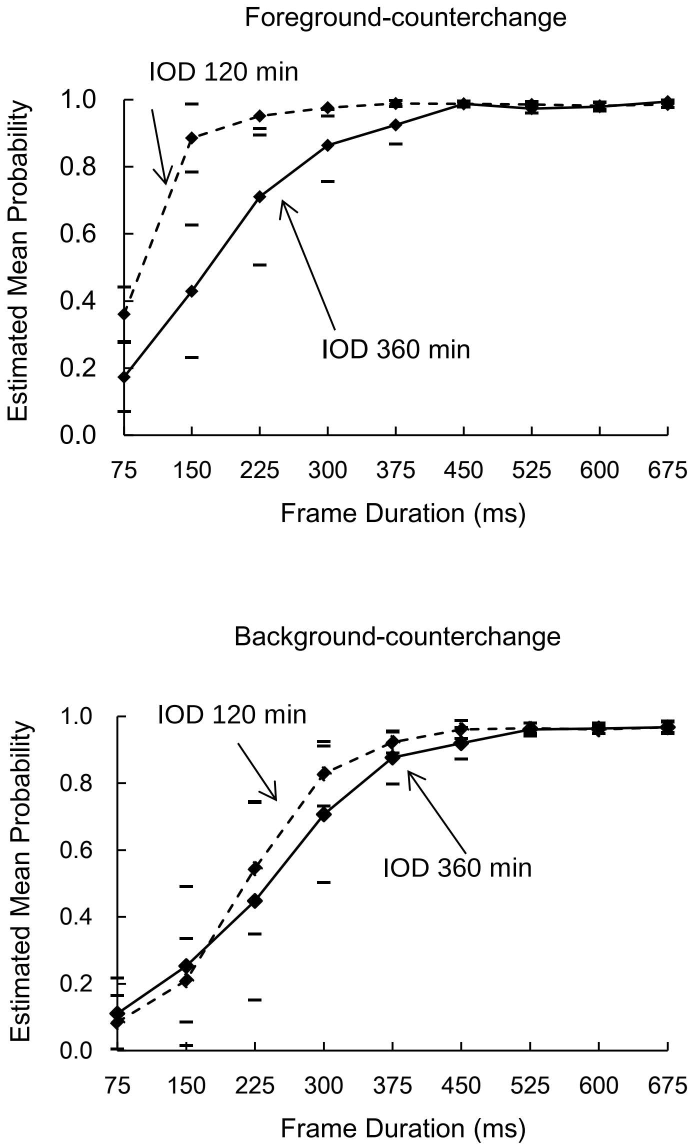


Figure 14. Experiment 2: Effect of inter-object distance on average proportions of apparent motion perceived for foreground-counterchange and background-counterchange conditions across frame duration values. Both conditions were presented at average low contrast. Bars reflect the standard error of the mean.

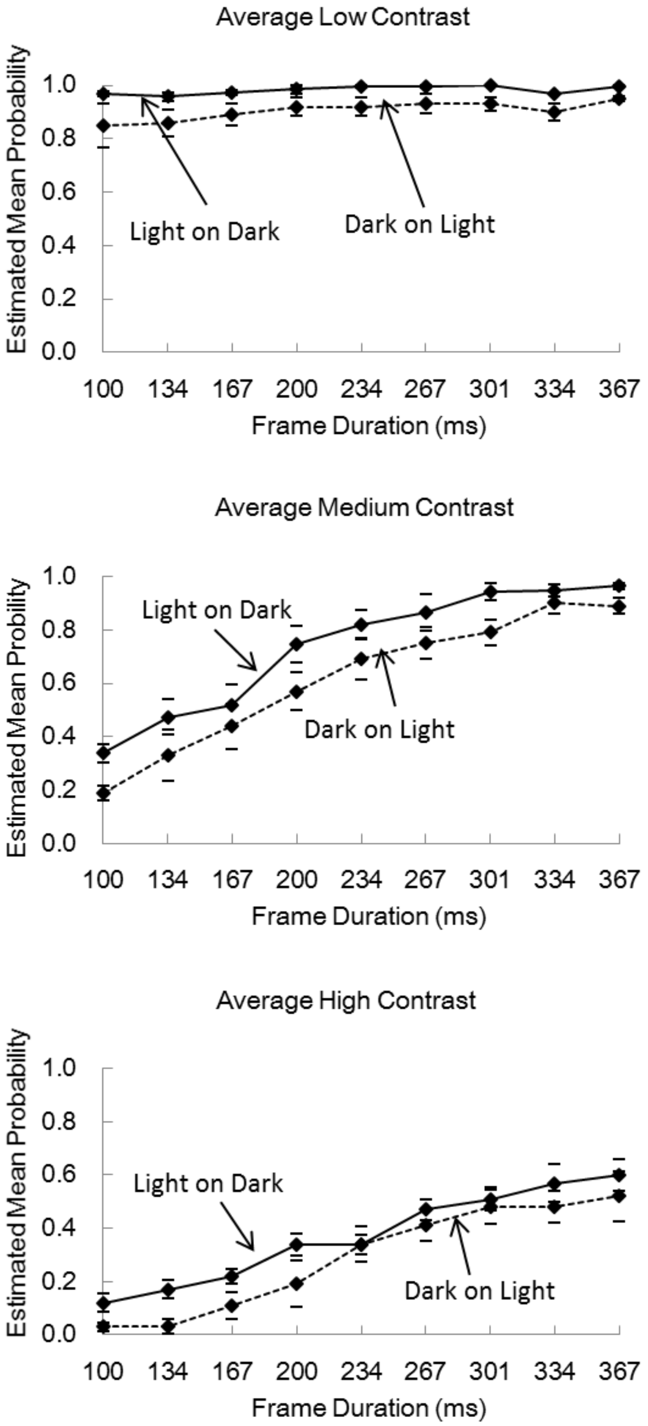


Figure 15. Experiment 3: Effect of frame duration on average proportions of apparent motion perceived for reversed polarity conditions (light object on dark background and vice-versa) of the foreground-counterchange stimulus from Experiment 1. Stimuli were presented at average low, medium, and high contrasts. Bars reflect the standard error of the mean.

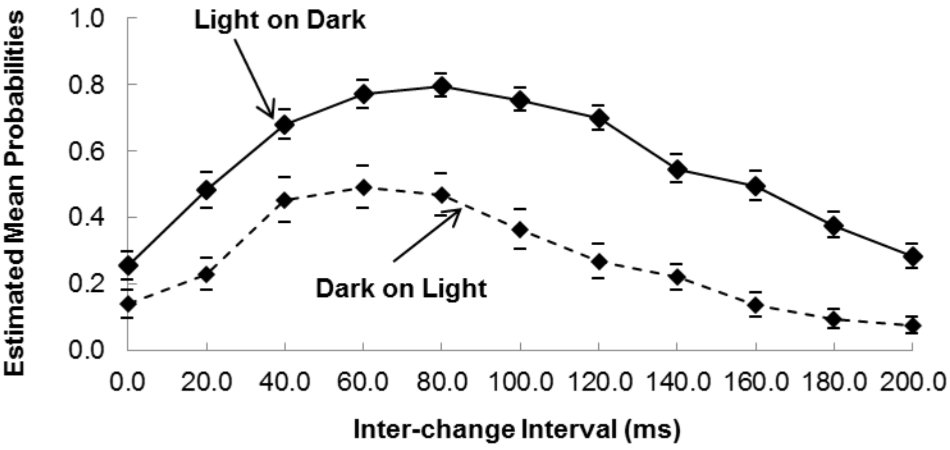


Figure 16. Experiment 4: Effect of inter-change interval on estimated mean probabilities of apparent motion perceived for foreground-counterchange stimuli with luminance polarity reversed via light-on-dark and dark-on-light conditions. Stimuli were presented at average low contrast. Bars reflect the standard error of the mean.

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