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ORIGINAL ARTICLE

Dirk Kerzel

Asynchronous perception of motion and luminance change

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Abstract Observers were asked to indicate when a target moving on a circular trajectory changed its luminance. The judged position of the luminance change was displaced from the true position in the direction of motion, indicating differences between the times-to-consciousness of motion and luminance change. Motion was processed faster than luminance change. The latency difference was more pronounced for a small (116–134 ms) than for a large luminance decrement (37 ms). The results show that first-order motion is perceived before an accurate representation of luminance is available. These findings are consistent with current accounts of the flash-lag effect. Two control experiments ruled out that the results were due to a general forward tendency. Localization of the target when an auditory signal was presented did not produce forward displacement, and the judged onset of motion was not shifted in the direction of motion.

Keywords Position Judgments · Consciousness · Luminance · Motion · Modular Perception · Flash-lag effect

Introduction

Motion perception may be classified into the perception of first- and second-order motion (reviews in Cavanagh & Mather, 1989; Lu & Sperling, 1995). First-order motion arises when differences in mean luminance (or color) between two adjacent areas of an image are displaced. For instance, when a spot of light is moved across a dark screen, the luminance difference between the spot and the background is continuously displaced and first-order motion results. For the present purpose it is important to note that two elementary stimulus conditions are necessary to produce first-order motion: a luminance difference and a change of position of the luminance difference. Further, two areas may have the same mean luminance and color, but differ in their texture, first-order motion or binocular disparity. These properties are referred to as second-order stimulus attributes because they emerge from the relation of two or more points in the image. If second-order stimulus attributes are displaced, second-order motion results. For instance, the line orientation in a texture consisting of horizontal line segments may change from horizontal to vertical at successive positions. In this case, the feature "vertical" is seen to move in the texture.

A large body of literature exists that describes the stimulus conditions supporting the perception of first- or second-order motion (reviews in Braddick, 1980; Cavanagh & Mather, 1989; Lu & Sperling, 1995). For instance, first-order motion is still perceived even if relatively long blank intervals separate successive presentations of the luminance difference: A spot of light may be briefly flashed at one position and reappear at a different position after a blank inter-stimulus-interval (ISI). If the ISI does not exceed about 200 ms, a motion percept known as apparent motion results (e.g., Neuhaus, 1930; Ramachandran & Anstis, 1986). However, when the duration of the blank ISI is increased beyond 200 ms, a mere succession of two stimulus presentations and no motion is perceived.

In contrast to previous research that characterized the stimulus conditions that lead to perception of motion, the present paper asked how accurately the stimulus is represented when first-order motion is perceived. Remember that first-order luminance-defined motion may result when the position of a luminance difference changes. Thus, one may be led to think that the perception of first-order motion and the perception of the luminance difference and its displacement are synchronous events.

D. Kerzel
FB 06, Psychologie und Sportwissenschaft,
Abteilung Allgemeine Psychologie,
Otto-Behaghel-Str. 10F, 35394 Gießen, Germany
E-mail: dirk.kerzel@psychol.uni-giessen.de
Tel.: +49-641-9926107
Fax: +49-641-9926119

The flash-lag effect

Recent experiments cast doubt on this seemingly plausible hypothesis. In research on the flash-lag effect, the perceived position of a brief luminance difference (a stationary flash) was compared with the perceived position of a continuously displaced luminance difference (a moving object). It was observed that the flash was perceived to lag behind the moving object although the two objects were physically aligned (Nijhawan, 1994). If, for instance, the object moved to the right, and the flash appeared at the same horizontal position below the moving object, the perceived position of the flash was below and left relative to the moving object. This effect clearly shows that the perception of luminance difference in a moving object is different from the perception of luminance difference in a stationary object. A number of hypothesis have been put forth to explain the effect. The flash lag was attributed to the extrapolation of motion, latency differences in the perception of luminance differences, temporal pooling, and postdiction (overview in Krekelberg & Lappe, 2001). Although the issue is far from settled, the differential latency hypothesis (Patel, Ogmen, Bedell, & Sampath, 2000; Whitney & Murakami, 1998; Whitney, Murakami, & Cavanagh, 2000) is of interest to the present investigation. It states that the time-to-consciousness of a luminance difference in a moving object is shorter than the time-to-consciousness of a luminance difference in a brief stationary flash. This indicates that the perception of motion is more than the sum of luminance difference displacements: The perception of motion may change processing times. Compared to a luminance difference in a stationary object, the luminance difference in a moving object is processed faster such that a stationary object is perceived to lag a moving object.

Studies on the flash-lag effect compared the perception of luminance differences in a moving object to the perception of a luminance difference in a single, isolated flash. Here, we ask how luminance differences in a moving object itself are processed. Given that first-order motion results from the displacement of luminance differences, one may assume that motion perception and the perception of luminance differences are synchronous events. In other words, one may assume that an accurate representation of luminance differences is the basis of first-order motion perception. The present study focuses on the temporal aspects of this representation: When is an accurate representation of luminance differences formed relative to the perception of motion?

To measure when observers accurately perceive the luminance difference that is displaced during first-order motion, the luminance difference was changed unpredictably, and observers were asked to indicate the position of the luminance change. For instance, observers may see a bright white object moving on a gray background and at a random point along the trajectory, the object changes its luminance from bright white to light gray. If motion perception was based on the accurate representation of luminance differences that are displaced across space, observers should be highly accurate in this task. If, however, the perception of motion and the perception of luminance difference were dissociable, inaccuracies may result.

Asynchronous perception of motion, color, and form

It was already demonstrated that times-to-consciousness of form, color, and motion differ. When a change of form or color had to be judged relative to a change of motion direction, it turned out that the change of direction had to occur some time before the form or color change to be perceived as synchronous. This indicates that the times-to-consciousness of form and color were shorter than of motion: Form was perceived before motion by about 50 ms, and color was perceived before orientation by about 60 ms (Moutoussis & Zeki, 1997). In the present study, it was investigated whether times-to-consciousness of motion and luminance difference differ. Such a finding would be surprising for two reasons: First, luminance difference is the elementary feature that constitutes first-order motion perception. Second, both the detection of luminance change (contrast over time) and the perception of motion are assumed to be functions of the magnocellular stream and the associated parietal areas in the visual cortex (MT) because of the fast response characteristics of the magnocellular stream and its high contrast sensitivity (Merigan & Maunsell, 1993). Therefore, one may expect the perceptual and neural representation of these two features to be closely coupled.

Experiment 1

The method used here is related to classical studies on the "perception time" (i.e., the time-to-consciousness) conducted by Hazelhoff and Wiersma (1924). In these studies, the observer pursued a moving target with the eyes. At some point during the pursuit, a flash was presented and the observer was asked to localize the target position at the time of the flash. In this situation, the observer misperceived the flash as having occurred at a position further in the direction of the eye movement. Hazelhoff claimed that the localization error was a measure of the time it takes to register the flash, the time-to-consciousness (but see Mateeff & Hohnsbein, 1989; Mateeff, Yakimoff, & Dimitrov, 1981): While the flash was processed at a subconscious level, the eye continued to follow the moving target. When the flash reached consciousness, the observer would register the current eye position and report this position at the end of the trial (judged eye position). Thus, the distance between true and judged eye position at flash presentation, d, divided by the velocity of the eye movement, v, gives the time-to-consciousness of the flash, $t = \frac{d}{v}$. The problem with this method is that it assumes that the observer may accurately perceive and remember the position of the eye during smooth pursuit. There is reason to doubt this assumption (Brenner, Smeets, & van den Berg, 2001; Kerzel, 2000).

Here, observers were presented with a small object rotating around a central stationary point. The eyes were motionless and directed at the center of rotation. At an unpredictable position, the luminance of the rotating object was changed. That is, the luminance difference between target and background which was continuously displaced on a circular trajectory was changed. Observers were asked to indicate the position of the change. Differences between the true position of the change and the judged position of the change would indicate that the perception of first-order motion and the perception of luminance difference are dissociable events. There are two possible outcomes: (1) Target motion reaches consciousness earlier than the luminance change. In this case, the target would move away from the true onset of the luminance change before the change reached awareness. Consequently, the target position associated with the change would be displaced from the true change position in the direction of motion. (2) The luminance change reaches consciousness earlier than target motion. In this case, the target would be perceived at a position preceding the true onset of the change when the luminance change reaches awareness. The position associated with the change would be displaced from the true change position opposite the direction of motion.

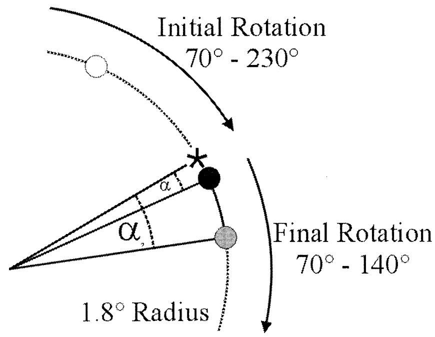

Fig. 1 Stimuli and results of Experiment 1. The target (70 cd/m2) moved randomly for 70° – 230° before it changed its luminance to gray (24.1 cd/m^2) or black (0 cd /m^2). The target rotated at 23.4 r.p.m (2.56 s per rotation). The luminance change is indicated by an asterisk. After the change, the target continued to move randomly for 70°–140°. Observers perceived the luminance change after the actual change. The judged position of the luminance change was displaced by $\alpha_1 = 5.2°$ for the large luminance decrement (black target), and $\alpha_2 = 16.3°$ for the small luminance change (gray target). Angular displacement was converted into time intervals.

Methods

Participants Eight students at the Ludwig-Maximilians-University Munich participated for pay. All reported normal or corrected-to-normal vision and were naive as to the purpose of the experiment.
Apparatus and stimuli The stimuli were created using a Matrox Millenium graphics card on a 21" (diagonal) screen with a refresh rate of 96 Hz. The display had a resolution of 1280 (H) x 1024 (V) pixels. The background was dark gray (8.4 cd/m2), the target was a 0.16° white (70.4 cd/m2) filled circle moving on a virtual circle with a radius of 1.8° (see Figure 1). Similar to the dial of a clock, 24 equally spaced lines pointed radially outward from the center of the circle. The lines were 0.18° long and started at 2.39° from the circle center. In the center of the virtual circle (the center of the screen), a 0.09° fixation dot was presented. The target rotated clockwise at a velocity of 23.4 r.p.m (2.56 s per rotation).

The target appeared at a random position along the trajectory of the circle and rotated randomly between 70° and 230° before the target changed its luminance. The target either changed its luminance from white (70.4 cd/m^2) to gray (24.1 cd/m^2) or from white (70.4 cd/m^2) to black (0 cd/m^2). After the change, the target continued to move randomly for 70° to 140°. Observers' task was to adjust the cursor to the position at which the small or large luminance decrement occurred.

The horizontal position of the left eye was monitored with a head-mounted, infrared, light-reflecting eyetracker (Skalar Medical B. V., IRIS Model 6500). The analog signal was bandpass, demodulated, and low-pass filtered (DC 100 Hz, 3 dB) and then digitized at a rate of 250 Hz by a DataTranslation A/D-D/A converter (DT 2821). Fixation had to be maintained within 1° of the centrally presented black (0 cd/m2) fixation dot.

Task and procedure Participants sat in a dimly lit room 50 cm from the screen. Head movements were restricted by a chin-forehead rest, and viewing was binocular. Each trial started with a brief (200 ms) broadening of the fixation dot as a warning signal. After 800 ms, the target appeared and started to rotate. Observers' task was to indicate where on the target's trajectory the visual or acoustic change occurred. After the target had vanished, the subject adjusted a cursor on the virtual circle until it appeared to be at the position of the change. For the adjustment procedure, the mouse was used. Participants initiated and terminated a trial by pressing the left mouse button. No feedback was provided. When a fixation error occurred, an error message appeared and the trial was repeated in the remainder of the experiment. The different change conditions were randomly interleaved and 36 repetitions were collected for each condition.
Results The angular deviation between the judged position of the luminance change and its actual position was calculated (see Figure 1). Positive deviations indicate that the judged position of the luminance change was displaced from the actual position in the direction of motion, whereas negative deviations indicated displacement opposite to the direction of motion. Angular deviation, α, was converted into time intervals ($\Delta t = \alpha * 360^{-1} * \text{r.p.m.}^{-1}$). Negative times indicate that perception of target motion was delayed with respect to perception of the luminance change. Positive times indicate that perception of the change was delayed relative to the target motion. As shown in Figure 1, perception of the luminance change was significantly delayed with the large luminance decrement, $M = 37$ ms, $SEM = 13.8$, $t(7) = 2.7$, $p < .05$, and with the small luminance decrement, $M = 116$ ms, $SEM = 16.4$, $t(7) = 7.08$, $p < .0005$. The two conditions differed significantly, $M = 79$ ms, $SEM = 14.3$, $t(7) = 5.52$, $p < .001$.

Discussion

Large errors occurred when the change of a continuously displaced luminance difference between target and background (a moving object) had to be localized. The luminance change was mislocalized in the direction of motion. This indicates that motion was perceived before the luminance difference: Before the luminance change reached conscious awareness, the target continued to move such that the target position associated with the luminance change was displaced in the direction of motion. The results show that the perception of first-order motion and luminance differences are not necessarily synchronous events. Even though the displacement of a luminance difference constitutes motion, the results suggest that luminance is treated similar to features that do not contribute to the perception of first-order luminance-defined motion, such as color or form. Surprisingly, the time-to-consciousness of changes in luminance is longer than the time-to-consciousness of motion. Previous research has shown that color and form had shorter times-to-consciousness than motion (Zeki & Bartels, 1998).

The present results are consistent with research on the flash-lag effect. In the flash-lag effect, a stationary luminance difference (a flash) is perceived later than a continuously displaced luminance difference (a moving object). Thus, motion appears to be processed faster than luminance differences per se. Experiment 1 shows that this finding extends to luminance differences within the object: A change of the luminance difference constituting the moving object is perceived after first-order motion.

Further, the time-to-consciousness was larger for a small luminance change than for a large luminance change. This finding is consistent with reaction time data. Simple reaction times to changes in luminance have been found to depend on the magnitude of the change (Burkhardt, Gottesman, & Keenan, 1987). Small changes yielded longer simple reaction times than large changes, suggesting that sensory latency increases with decreasing magnitude of the luminance change. Similarly, it took longer to process the small luminance change compared to the large luminance change which resulted in larger displacement of the small change compared to the large change.

Experiment 2

Experiments 2 and 3 were designed to validate the experimental procedure. In Experiment 1, observers had to indicate the position of the luminance change after the target had disappeared. Therefore, visual short-term memory was involved. It has been argued that the position of moving stimuli is extrapolated in visual short-term memory, resulting in a forward shift of the remembered position. This shift has been attributed to "representational momentum" (Freyd, 1987). Although there is evidence that eye movements may explain the forward shift (Kerzel, 2000; Kerzel, Jordan, & Müsseler, 2001), and representational momentum does not account for the effect of magnitude of the luminance change, Experiments 2 and 3 were run to rule out the possibility that a general forward bias explained the results. To this end, Experiment 2 tried to replicate (a) the results of the previous experiments and (b) results obtained with temporal order judgments (TOJ). A typical TOJ would require observers to indicate whether the onset of a moving stimulus in the visual modality succeeded or preceded a brief acoustic signal. Studies using TOJ have shown that the time-to-consciousness of acoustic stimuli is only slightly and not significantly shorter than the onset of visual motion (Aschersleben & Müsseler, 1999; Kerzel, 2000; Roufs, 1963). If the present procedure was a valid indicator of the time-to-consciousness of perceptual events, the slight precedence of acoustic over visual stimuli should be replicated.

Observers were asked to localize the position of a revolving target when one of two perceptual events occurred: A small luminance decrement of the target or an acoustic click sound. If the present procedure produced a general forward bias, both the visual and acoustic change should be mislocalized into the direction of motion. If the current procedure was a valid measure of the time-to-consciousness, the reverse should be observed: The acoustic tone should be localized before its true onset (i.e., opposite the direction of motion) and the luminance change should be localized after its true onset.

Methods

Participants Eight students fulfilling the same criteria as in Experiment 1 participated.

Apparatus, stimuli, procedure and task Apparatus, stimuli, procedure and task were the same as in Experiment 1 with the following exceptions: In the visual change condition, the target changed its color from white to gray (24.1 cd/m^2); in the acoustic change condition, a 2000 Hz beep was presented for 10 ms via loudspeakers. Eight fresh observers participated.

Results Perception of the visual change was significantly delayed, M = 134 ms, SEM = 25.7, $t(7) = 5.2$, $p < .005$, whereas the acoustic change was not, M = −46 ms, SEM = 35.2, $t(7) = -1.3$, $p > .2$. The visual and acoustic conditions differed significantly, M = 180 ms, SEM = 27.9, $t(7) = 6.42$, $p < .0005$.

Discussion

The visual change condition replicated the results of Experiment 1. The change of the luminance difference between target and background was localized after the true position of the change. In the acoustic change condition, no forward bias was observed: Numerically, the acoustic change was localized before the true position of the change. This difference was not significant as in previous studies that used TOJ (Aschersleben & Müsseler, 1999; Kerzel, 2000). Thus, the latency difference observed in Experiment 1 cannot be due to a general forward bias. If a general tendency to extrapolate the position of moving stimuli in the direction of motion had produced the pattern of results in Experiment 1, a similar tendency should have been observed for the acoustic change. However, a slight displacement of the perceived onset of the tone opposite to the direction of motion was observed.

Experiment 3

To further rule out the possibility that a general forward bias accounted for the results of Experiment 1, observers were asked to localize the first position of the moving object. With pointing movements and slow target velocities, it has been observed that the first position of a moving object is mislocalized opposite the direction of motion relative to the true first position (Kerzel, 2002a; Thornton, 2002). Maybe observers overcompensate for the distance the target traveled after it appeared because they consider the length of the trajectory as a whole (Kerzel, 2002a). With relative judgments and fast target velocities, the backward error is mostly reversed and the onset of the target is misperceived in the direction of motion (e.g. Fröhlich, 1923; Kirschfeld & Kammer, 1999). Current theorizing attributes the forward error to a lack of focal attention at target onset such that the initial part of the target's trajectory is missed (Kerzel & Müsseler, 2002; Kirschfeld & Kammer, 1999; Müsseler & Aschersleben, 1998). Presently, the experimental conditions meet those that have been shown to lead to the onset repulsion effect: The target velocity was slow (i.e., the tangential velocity was 8 °/s) and a variant of a pointing task was used. Thus, a bias to localize the target opposite the direction of motion should be observed here. In contrast, if a general forward bias was inherent in the experimental procedure, the opposite pattern should be observed.

Method

Participants Eight students fulfilling the same criteria as in Experiment 1 participated.

Apparatus, stimuli, procedure and task Apparatus, stimuli, procedure and task were the same as in Experiment 1 with the following exceptions: During the initial rotation of the target (between 70° and 230°), the target had the same color as the background, that is, no target was visible. Then, the target appeared either in gray (24.1 cd/m^2) or in black (0 cd/m^2). Observers' task was to indicate the initial position of the target. Eight fresh observers participated.

Results The judged onset preceded the actual onset in the low luminance condition, $M = -42$ ms, $SEM = 16.5$, $t(7) = 2.6$, $p < .05$, and in the high luminance condition, $M = -39$ ms, $SEM = 12.8$, $t(7) = 3$, $p < .05$. The difference between the two conditions was not significant, $M = 4$ ms, $SEM = 9.1$, $t(7) = 0.43$, $p > .6$.

Discussion

There was no indication of a forward shift when observers were asked to judge the first position of the moving stimulus. Rather, there was displacement opposite to the direction of motion. This result replicates previous studies (Kerzel, 2002a; Thornton, 2002) and provides further evidence against the assumption that a general forward bias explains the localization errors observed in Experiment 1. Nonetheless, the negative times-to-consciousness of about –40 ms pose a problem for the experimental logic: It seems highly implausible that the onset of the moving dot would reach consciousness *before* its actual onset. Also, unlike in Experiment 1, the luminance of the target did not affect localization. This should have been the case because luminance determines sensory latencies (Burkhardt et al., 1987).

The crucial difference between Experiments 1–2 and 3 may be that there was no motion preceding the event to be localized in Experiment 3. Perhaps this feature renders onset localization special: Observers may consider the complete trajectory length and calculate the first position relative to the final position. That is, they may subtract the estimated trajectory length from the final target position to determine the first position. There is reason to believe that distance is overestimated in this kind of distance-based (exocentric) localization (Kerzel, 2002b). This leads to an overestimation of the length of the trajectory (Kerzel, 2002a) such that displacement is opposite to motion. In contrast, if events along or at the end of the trajectory have to be localized, single positions and not the trajectory length as a whole are estimated. Consistent with this idea, localization of the end position of a smoothly moving object was not displaced when fixation was maintained (Eagleman & Sejnowski, 2000; Kerzel, 2000; Whitney et al., 2000). Thus, localization of the first position is special. Mechanisms unrelated to sensory latencies, such as distance estimation, may contribute to localization performance. Nonetheless, the results of Experiments 1 and 2 show that the localization task used here may be used as a measure of sensory latencies because results obtained with TOJ could be replicated for positions along the trajectory (Experiment 2).

General discussion

When observers were asked to indicate where the luminance of a moving object changed, they pointed to a location that was displaced in the direction of motion, indicating different perceptual times of luminance change detection and of motion perception. The difference of the time-to-consciousness was larger with a small luminance decrement (116–137 ms) than with a large decrement (37 ms) which is consistent with reaction time data (Burkhardt et al., 1987). In Experiments 2 and 3, the alternative explanation that the experimental procedure produced a general forward bias similar to a localization error known as "representational momentum" was ruled out. To this end, observers judged the position of the moving target relative to the onset of a tone in Experiment 2. No forward displacement occurred. In Experiment 3, observers' task was to judge the first position of the moving object. A bias opposite the direction of motion was observed. Thus, the forward displacement of the judged position of a luminance change cannot be accounted for by a general forward bias inherent in the procedure.

Rather, the results show that the perception of a continuously displaced luminance difference is not the same as the perception of first-order motion – even though displacement of a luminance difference essentially constitutes first-order motion. Rather, the perception of motion and the perception of luminance difference are dissociable events. It may be that motion is perceived when there is continuous displacement of some luminance difference that does not have to stay the same across successive positions. Only a crude correspondence of successive luminance differences would be sufficient to produce the perception of motion. In this view, the exact magnitude of the luminance difference between target and background would be but one of many features of target motion. Ecologically, such a mechanism appears highly plausible because moving objects may appear in front of varying backgrounds. Variations of background luminance would alter the target-background luminance difference. It may therefore be more important to establish a correspondence between successive displacements of a luminance difference while ignoring variations of this difference. Looked at in this way, *some* luminance difference establishes first-order motion, but its accurate representation is not necessary. Consistent with this idea, the present research shows that the processing of motion and luminance difference may dissociate in the temporal domain.

Neurophysiological considerations

The present study supports the notion of asynchronous and modular perception (Zeki & Bartels, 1998). The processing of visual information in the human brain is accomplished by numerous visual streams. Each stream is specialized to process different attributes of the visual scene (DeYoe & Van Essen, 1988; Livingstone & Hubel, 1988; Zeki, 1978). Two of the best-understood streams are the parvocellular and magnocellular pathways and the higher cortical areas they primarily project to. Typically, the parvocellular pathway is described as color-selective with low contrast and low temporal sensitivity. In contrast, the magnocellular pathway is color-blind and has a high contrast and temporal sensitivity (Livingstone & Hubel, 1988; Merigan & Maunsell, 1993). From V1, the magnocellular pathway projects primarily to area MT and the parvocellular pathway to V4. The former area is associated with motion processing (Dubner & Zeki, 1971), and the latter with color processing (Zeki, 1980). Because of the large number of specialized visual areas (Felleman & Van Essen, 1991) that process visual information in a distributed manner, the question arises of how the processing results from the different areas are integrated to form a unitary percept.

It was already demonstrated that perceptual times for form, color, and motion differ, although the neurophysiological distinction between form and motion as well as form and color is not very clear-cut (for a discussion see Moutoussis & Zeki, 1997). Form was perceived before motion by about 50 ms, and color was perceived before orientation by about 60 ms (Moutoussis & Zeki, 1997). In the present study, it was investigated whether there is a time difference in the perception of motion and of luminance change. Both the detection of luminance change and the perception of motion are assumed to be functions of the magnocellular stream and the associated parietal areas in the visual cortex (MT) because of the fast response characteristics of the magnocellular stream and its high contrast sensitivity (Merigan & Maunsell, 1993). Although motion and contrast are predominantly processed in the magnocellular pathway, and the associated cortical area MT, the results suggest that these two features may reach conscious perception at different times. Motion and luminance change may be perceived in an asynchronous manner.

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References

Aschersleben, G., & Müsseler, J. (1999). Dissociations in the timing of stationary and moving stimuli. *Journal of Experimental Psychology: Human Perception and Performance, 25*(6), 1709–1720.

Braddick, O. J. (1980). Low-level and high-level processes in apparent motion. *Proceedings of the Royal Society of London Series B-Biological Science, 290*(1038), 137–151.

Brenner, E., Smeets, J. B., & van den Berg, A. V. (2001). Smooth eye movements and spatial localisation. *Vision Research, 41*(17), 2253–2259.

Burkhardt, D. A., Gottesman, J., & Keenan, R. M. (1987). Sensory latency and reaction time: dependence on contrast polarity and early linearity in human vision. *Journal of the Optical Society of America [A], 4*(3), 530–539.

Cavanagh, P., & Mather, G. (1989). Motion: the long and short of it. *Spatial Vision, 4*(2–3), 103–129.

DeYoe, E. A., & Van Essen, D. C. (1988). Concurrent processing streams in monkey visual cortex. *Trends in Neuroscience, 11*(5), 219–226.

Dubner, R., & Zeki, S. M. (1971). Response properties and receptive fields of cells in an anatomically defined region of the superior temporal sulcus in the monkey. *Brain Research, 35*(2), 528–532.

Eagleman, D. M., & Sejnowski, T. J. (2000). Motion integration and postdiction in visual awareness. *Science, 287*(5460), 2036–2038.

Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex, 1*(1), 1–47.

Freyd, J. J. (1987). Dynamic mental representations. *Psychological Review, 94*, 427–438.

Fröhlich, F. W. (1923). Über die Messung der Empfindungszeit. [On the measurement of sensation time]. *Zeitschrift für Sinnesphysiologie, 54*, 58–78.

Hazelhoff, F. F., & Wiersma, H. (1924). Die Wahrnehmungszeit. Erster Artikel: Die Bestimmung der Schnelligkeit der Wahrnehmung von Lichtreizen nach der Lokalisationsmethode. [The time to perception: First article: The determination of the speed of perception of light stimuli with the localization method]. *Zeitschrift für Psychologie, 96*, 171–188.

Kerzel, D. (2000). Eye movements and visible persistence explain the mislocalization of the final position of a moving target. *Vision Research, 40*(27), 3703–3715.

Kerzel, D. (2002a). Different localization of motion onset with pointing and relative judgements. *Experimental Brain Research, 145*(3), 340–350.

Kerzel, D. (2002b). Memory for the position of stationary objects: Disentangling foveal bias and memory averaging. *Vision Research, 42*(2), 159–167.

Kerzel, D., Jordan, J. S., & Müsseler, J. (2001). The role of perception in the mislocalization of the final position of a moving target. *Journal of Experimental Psychology: Human Perception and Performance, 27*(4), 829–840.

Kerzel, D., & Müsseler, J. (2002). Effects of stimulus material on the Fröhlich illusion. *Vision Research, 42*(2), 181–189.

Kirschfeld, K., & Kammer, T. (1999). The Fröhlich effect: a consequence of the interaction of visual focal attention and metacontrast. *Vision Research, 39*, 3702–3709.

Krekelberg, B., & Lappe, M. (2001). Neuronal latencies and the position of moving objects. *Trends in Neurosciences, 24*(6), 335–339.

Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science, 240*(4853), 740–749.

Lu, Z. L., & Sperling, G. (1995). The functional architecture of human visual motion perception. *Vision Research, 35*(19), 2697–2722.

Mateeff, S., & Hohnsbein, J. (1989). The role of the adjacency between background cues and objects in visual localization during ocular pursuit. *Perception, 18*(1), 93–104.

Mateeff, S., Yakimoff, N., & Dimitrov, G. (1981). Localization of brief visual stimuli during pursuit eye movements. *Acta Psychologica, 48*(1–3), 133–140.

Merigan, W. H., & Maunsell, J. H. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience, 16*, 369–402.

Moutoussis, K., & Zeki, S. (1997). Functional segregation and temporal hierarchy of the visual perceptive systems. *Proceedings of the Royal Society of London Series B-Biological Science, 264*(1387), 1407–1414.

Müsseler, J., & Aschersleben, G. (1998). Localizing the first position of a moving stimulus: the Frohlich effect and an attention-shifting explanation. *Perception & Psychophysics, 60*(4), 683–695.

Neuhaus, W. (1930). Experimentelle Untersuchung der Scheinbewegung [Experimental investigations of apparent motion]. *Archiv für die gesamte Psychologie, 775*, 315–458.

Nijhawan, R. (1994). Motion extrapolation in catching. *Nature, 370*(6487), 256–257.

Patel, S. S., Ogmen, H., Bedell, H. E., & Sampath, V. (2000). Flash-lag effect: differential latency, not postdiction. *Science, 290*(5494), 1051a.

Ramachandran, V. S., & Anstis, S. M. (1986). The perception of apparent motion. *Scientific American, 254*(6), 102–109.

Roufs, J. A. J. (1963). Perception lag as a function of stimulus luminance. *Vision Research, 3*, 81–91.

Thornton, I. M. (2002). The onset repulsion effect. *Spatial Vision, 15*(2), 219–244.

Whitney, D., & Murakami, I. (1998). Latency difference, not spatial extrapolation. *Nature Neuroscience, 1*(8), 656–657.

Whitney, D., Murakami, I., & Cavanagh, P. (2000). Illusory spatial offset of a flash relative to a moving stimulus is caused by differential latencies for moving and flashed stimuli. *Vision Research, 40*(2), 137–149.

Zeki, S. (1980). The representation of colours in the cerebral cortex. *Nature, 284*(5755), 412–418.

Zeki, S., & Bartels, A. (1998). The autonomy of the visual systems and the modularity of conscious vision. *Proceedings of the Royal Society of London Series B-Biological Science, 353*(1377), 1911–1914.

Zeki, S. M. (1978). Functional specialisation in the visual cortex of the rhesus monkey. *Nature, 274*(5670), 423–428.