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Forward displacements of fading objects in motion: The role of transient signals in perceiving position

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Abstract

Visual motion causes mislocalisation phenomena in a variety of experimental paradigms. For many displays objects are perceived as displaced ‘forward’ in the direction of motion. However, in some cases involving the abrupt stopping or reversal of motion the forward displacements are not observed. We propose that the transient neural signals at the offset of a moving object play a crucial role in accurate localisation. In the present study we eliminated the transient signals at motion offset by gradually reducing the luminance of the moving object. Our results show that the ‘disappearance threshold’ for a moving object is lower than the detection threshold for the same object without a motion history. In units of time this manipulation led to a forward displacement of the disappearance point by 175 ms. We propose an explanation of our results in terms of two processes: Forward displacements are caused by internal models predicting positions of moving objects. The usually observed correct localisation of stopping positions, however, is based on transient inputs that retroactively attenuate errors that internal models might otherwise cause. Both processes are geared to reducing localisation errors for moving objects.

Introduction

Visual motion can influence the perceived position of objects as shown in various experimental paradigms. In representational momentum observers perceive the final position of a moving object as shifted in the direction of motion (Freyd & Finke, 1984; Hubbard, 1995). In the Fröhlich effect the position of the sudden onset of a moving object is misperceived; the object seems to appear at a later point of the trajectory (Fröhlich, 1923; Kirschfeld & Kammer, 1999). When observers view moving elements contained within the boundaries of static windows, a motion-induced positional bias is observed such that the windows appear displaced in the direction of motion (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990). Flashes can be mislocalised in the direction of motion when they are presented near a moving object (Whitney & Cavanagh, 2000). In the flash-lag effect a moving object is perceived to be ahead of a flashed stationary object, although both are physically aligned in space (Hazelhoff & Wiersma, 1924; Nijhawan, 1994). A common feature in all these studies is that motion causes a mislocalisation in the ‘forward’ direction; i.e. the displacement occurs in the direction of future positions of the moving object.

Given these findings it is surprising to find some displays in which this expected forward shift is not observed. These displays involve unpredictable events such as moving objects abruptly stopping, changing direction and/or speed. When a moving object unpredictably stops, it does not appear to overshoot its final position. This has been observed in experiments using flashes for the relative judgement of the stopping position (Eagleman & Sejnowski, 2000; Nijhawan, 1992), using pointing movements

(Kerzel, 2000) and static probe stimuli (Kerzel, Jordan, & Müsseler, 2001). When a moving object abruptly changes direction, then the perceived position at which the object reverses is not displaced forward (Whitney & Murakami, 1998). However, recently some conditions have been found, in which similar stimuli do produce ‘overshoots’. If abruptly stopped moving objects are blurred (Fu, Shen, & Dan, 2001) or presented in the retinal periphery (Kanai, Sheth, & Shimojo, 2004) a forward displacement is reported.

Why is the forward displacement of abruptly stopped moving objects sometimes not observed? We suggest that whether a given stimulus will produce the forward displacement or not depends on the relative operational strength of two opposing mechanisms. The first mechanism uses information from the earlier part of the moving object’s trajectory to accurately predict its position, possibly to compensate for the spatial lag in position that would otherwise be expected due to delays in the neural processing between the photoreceptors and higher visual areas. However, when abrupt events cause transient neural signals, strongly stimulating the visual system, a second mechanism is engaged that acts like a ‘correction’ overriding the output of the first mechanism.

Our thesis is based on well known psychophysical and physiological facts. Events occurring later in time can change the perception of earlier events (Breitmeyer, 1984; Dennett & Kinsbourne, 1995; Kolers, 1972; Libet, 1981; Ross, 1972; van der Waals & Roelofs, 1931). For example, in backward masking a briefly presented visual stimulus can be rendered invisible, if it is followed by another stimulus nearby

(Alpern, 1953; Breitmeyer, 1984). More importantly for the present experiments, stimulus offsets per se can reduce the visibility of a previously presented target (Breitmeyer & Kersey, 1981). Temporal transients like stimulus onsets and offsets elicit strong neural responses, both excitatory and inhibitory, that can suppress the perception of other stimuli (Macknik, Martinez-Conde, & Haglund, 2000). Here we explore the possibility that the strong transient neural signal associated with the disappearance of a moving stimulus provides the visual system with a cue that allows for the localisation of the vanishing position without a forward displacement. Analogously to backward masking this transient might influence perception retroactively and facilitate the perception of the correct vanishing position (Nijhawan, 2002).

In this study we test our thesis by manipulating the transient at the offset of a moving object. We employed a *gradually fading* moving object that initially appeared bright and then disappeared for the observer without a strong transient. Does this object disappear at the position in its trajectory where its luminance is at detection threshold, or does it overshoot this point and will be visible in positions where retinal input per se can no longer sustain perception of the object?

Experiment 1

The purpose of this experiment was to measure the luminance at which a fading moving object is seen as disappearing by the observer, and determine whether this luminance is above or below detection threshold for the same moving object without the same motion history. We used two conditions: In the ‘long-trajectory motion’ condition a small dot moved on a circular trajectory while continuously becoming dimmer. Observers judged whether the dot disappeared before or after a radial reference line presented adjacent to the moving dot (Fig. 1C). In the ‘short-segment motion’ condition the same dot was presented moving for only a short trajectory at different luminances. The observers reported whether they perceived the dot or not. We predicted that the long-trajectory dot would perceptually disappear in a forward-displaced position, i.e. at luminance levels where the short-segment dot was not detectable.

Methods

Participants

Eight observers participated in the experiment. Two observers (including author GM) were informed, while six were naïve about the hypothesis. All had normal or corrected to normal visual acuity.

Apparatus and Stimuli

The stimuli were shown in a dimly lit room on a CRT computer monitor (Sony CPD-E500) at 1280 x 1024 pixel resolution and 85 Hz refresh rate. Stimuli were generated using Matlab and the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). The observer viewed the screen from a distance of 80 cm with the head stabilised by a chin rest. The stimulus consisted of a small white dot (3 x 3 pixels, 0.06° x 0.06°) moving counter-clockwise on a circle (radius 2.8°). Analogue fading of the dot was achieved by hardware: a variable neutral density filter (Edmund Optics Inc.; range of neutral density 0 – 4; range of transmission 1 – 0.0001; see Fig. 1A) was mounted between the observer and the screen. In this experiment the filter was fixed in the position shown in Fig. 1A. A fixation LED was presented at the centre of the circular trajectory using a beam splitter (Fig. 1B). To the observers the dot appeared to fade as it moved (see Fig. 1C). Using this physical setup rather than changing the dot's luminance in the software had several advantages. In software luminance can only be changed in steps of finite size. This confines experimenters' control over stimuli, especially for luminance contrasts close to the detection threshold[1]. This method also makes correction for non-linearities in the monitor's luminance function unnecessary.

[Figure 1 here]

Procedure

This experiment consisted of two conditions. In the 'short-segment motion' condition we measured the dot luminance, at which observers were able to detect the dot's presence with 50% probability. In the 'long-trajectory motion' condition we measured the luminance at which the same fading moving dot was seen as disappearing. Note

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[1] The ability to rotate the filter with a micro stepper motor (see Experiment 2) also enables us to change the luminance of a moving object with any continuous function.

that different luminances of the dot were achieved by presenting the dot behind different regions of the filter, therefore larger angular positions directly correspond to lower luminances. All the analysis was carried out in terms of positions.

The stimulus in the short-segment motion condition consisted of five screen refresh frames (58.8 ms at 85 Hz refresh rate), during which the dot rotated for about 12° (arc distance 0.6° visual angle) at an angular velocity of $204°s^{-1}$ (tangential velocity $10.4°s^{-1}$ visual angle). During this motion the dot's luminance decreased by a factor[2] of 0.7. To achieve different intensity levels the stimulus was presented at one of ten different positions behind the filter. A radial line (length 1.6°) presented adjacent to the filter precued the starting position of the dot. At the starting position of each trial the dot appeared brightest, so this position and luminance were used to work out the actual detection performance. Trials were structured as follows: First the cue line appeared, 400 ms later the stimulus was presented for 58.8 ms. After another 300 ms the cue line was turned off and the observer was prompted to press one of two keys to report whether they saw the stimulus or not. To counteract observers simply learning the position where the stimulus was visible, on 20% of the trials the cue line was presented, but was not followed by the stimulus. Observers were not informed about the presence of these 'catch' trials.

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[2] $\text{factor} = \frac{\text{luminance in last frame}}{\text{luminance in first frame}}$

In the long-trajectory motion condition the dot started moving from the 6 o'clock position (0°), where the filter's transmission was 1, and moved counterclockwise into the darker parts of the filter. The dot's velocity was the same as in the short-trajectory motion ($204°s^{-1}$; $10.4°s^{-1}$ visual angle). Although the dot on the screen completed a whole circular trajectory, it was typically perceived to disappear at about 220° (Fig. 1C). While the dot was moving a radial reference line was shown adjacent to the filter, randomly at one of ten different positions. Observers pressed one of two keys, indicating whether they saw the dot disappear 'ahead of' or 'before' the line. On 20% of the trials the dot actually vanished from the screen at a position where it was still clearly visible, 10° (angular position) before the line. These trials prevented observers from learning about the vanishing positions.

An initial experimental session was used to a) familiarise observers with the stimuli, and b) select the ten positions where the short-segment motion would be presented to each observer because of individual differences in absolute thresholds. Following this each observer performed a block of 250 trials of the short-segment motion condition and 250 trials of the long-trajectory motion condition. Twenty measurements were made for each data point in both conditions (20 trials x 10 data points + 50 catchtrials = 250 trials). In three short breaks the main room lights were turned on to avoid dark adaptation of the observers. Psychometric functions were fitted to the data using probit analysis (Finney, 1971; McKee, Klein, & Teller, 1985) to obtain 50%-thresholds. Confidence intervals for these thresholds were computed using a bootstrap method (Foster & Bischof, 1991). Responses on the catch trials in both conditions were used to measure ‘false alarm’ rates and to compute a bias measure (Macmillan & Creelman, 1991). Observers that showed a response bias in their decisions on the catch trials of more than one standard deviation unit in either direction were excluded from the analysis.

Results

[Figure 2 here]

All observers reliably reported that the moving dot in the long-trajectory motion condition was visible at luminances, at which they were unable to detect the short-segment motion dot. However, two observers were excluded from the analysis because of large biases in their responses on the catch trials. These observers were unable to reliably detect the disappearance of the dot even at relatively high luminances. For the remaining six observers biases were smaller than one standard deviation.

The difference between the two thresholds in every single remaining observer was at least four times the size of the 95%-confidence intervals for the thresholds. The raw data and fitted psychometric functions for one naïve observer are shown in Fig. 2. The average rotation angle between thresholds across all observers was 35.8° (sd = 6.3°; arc distance 1.8° visual angle, sd = 0.3°). The distance measure was translated into a time measure, describing for how long the dot was visible after it passed the detection threshold measured in the short-segment motion condition. On average this time was

175.4 ms (sd = 30.8 ms). Fig. 3 shows the threshold differences for all six observers and the group mean. The slopes of all psychometric functions were similar and showed no significant differences between conditions (dependent test: t(5) = 2.32, p = 0.068; data not shown).

[Figure 3 here]

Discussion

All observers showed a robust difference between the thresholds for the long-trajectory motion and the short-segment motion conditions. Observers were unable to detect the short-segment dot at luminance levels (and positions) at which they still reliably saw the long-trajectory dot. We interpret this as a forward displacement of the dot's vanishing position in the long-trajectory condition. In this condition the dot disappears without providing a strong transient signalling its offset. Therefore the proposed correction mechanism for the perceived final position is not operational, and the dot is visible in positions at which retinal input alone is insufficient to reliably yield a percept, as in the short-segment motion condition.

Two factors unrelated to our hypothesis could have contributed to the results. The visibility of the dot in the short-segment motion condition could be diminished as the dot was presented at different locations. Although the position of the dot was cued, it might be argued that the spatial uncertainty is greater in the short-segment motion condition than in the long-trajectory motion condition. This could allow observers to deploy attention to 'track' the long-trajectory dot, leading to better detection performance. In addition, probability summation might contribute to the better visibility of the long-trajectory stimulus. The short-segment dot is presented for only five refresh frames, whereas the long-trajectory is presented for longer after it passes the reference line. Because more frames are presented in the long-trajectory condition (although in each frame the dot will be dimmer than in the previous one), probability summation predicts better detection of the dot that is presented for more discrete frames. Experiment 2 addresses these *attention* and *probability summation* hypotheses.

Experiment 2

This experiment measures the detection threshold for the short-segment motion dot in a different way. Again the dot's luminance was changed from trial to trial, but it was now presented in one position. Furthermore, the stimulus was presented repeatedly until the observer gave her response. In a second condition the length of the trajectory was approximately doubled to check if more discrete presentation frames increased the dot's detectability. If the higher detection threshold for the short-segment dot in Experiment 1 is based on observers' uncertainty about its presentation position or attentional disadvantages over the long-trajectory dot, it is expected that these modifications will eliminate the difference in thresholds. Furthermore, if the difference in thresholds in Experiment 1 depended on the longer presentation of the long-trajectory dot at sub-threshold luminances, the extension of the trajectory length in this experiment is expected to lead to significant differences in detection thresholds.

Methods

Participants

Four observers from Experiment 1 took part in this study. Three observers were naïve about the purpose of this experiment.

Apparatus and stimuli

Most of the apparatus was the same as in Experiment 1. A micro stepper motor (Parker Hannifin Corp.) controlled by the experimental software was used to rotate the filter disk. Now the dot was always presented in the 12 o'clock position, 2.8° above the fixation point. Rotation of the filter changed the dot's luminance. In an additional condition the trajectory length of the stimulus was increased from 12° to 26.4° (arc distance 1.3° visual angle; 11 refresh frames, i.e. 129.4 ms at 85 Hz refresh rate). On the extended trajectory the dot's luminance decreased by a factor of 0.45.

Procedure

To alert the observer an acoustic beep signalled the start of a trial. The stimulus was repeatedly presented until the observer made a response. Again the response was a key press, indicating whether the observer saw the stimulus or not. After the response the screen turned black and the motor moved the filter to the next position. For each of the two segment lengths there were 120 trials, ten trials at twelve different luminance levels. The trial order was randomised for each observer for a total of 240 trials.

Results

The thresholds measured for the two motion segment lengths did not differ significantly from each other, as confidence intervals for both thresholds overlap for every single observer. Fig. 4 shows the data of Experiment 1 and Experiment 2. The detection performance improved for three observers compared to the short-segment condition of Experiment 1. However, all four observers still showed a large difference between the new detection thresholds and the disappearance threshold for the dot in the long-trajectory condition of Experiment 1.

[Figure 4 here]

Discussion

Probability summation would predict that increasing the trajectory length of the short-segment dot would lead to its greater detectability. Experiment 2 shows that the longer short-segment stimulus is not detected significantly better than the original stimulus. It can be concluded that probability summation cannot be the sole contributor to the difference in thresholds measured in Experiment 1.

Experiment 2 eliminated spatial uncertainty for the short-segment stimulus by presenting it repeatedly in the same position. These manipulations did improve detection performance in three out of four observers. Nonetheless there remains a wide gap between the thresholds for short-segment motion (of Experiments 1 and 2) and long-trajectory motion (Experiment 1). We interpret this difference as a forward displacement due to the dot's motion history.

General Discussion

Close examination of the studies that do not show a forward displacement for moving objects (Eagleman & Sejnowski, 2000; Kerzel, 2000; Nijhawan, 1992; Whitney & Murakami, 1998) points to one potential common denominator for correct object localisation: a strong transient signalling an abrupt change in the moving object. We hypothesised that this transient carries accurate positional information, which is used by the visual system to enable the perception of the correct position (Nijhawan, 2002). Although this transient arrives at relevant cortical areas after a significant delay following retinal stimulation, the transient is able to influence the perceived position of the object in a retroactive manner. Similar retroactive effects are evident in backward masking and other phenomena (Breitmeyer, 1984; Dennett & Kinsbourne, 1995; Kolers, 1972; Libet, 1981; Ross, 1972; van der Waals & Roelofs, 1931).

In the present experiments we tested this hypothesis by removing the retinal transient elicited by the moving object's offset. This was achieved by using a gradually fading object (Experiment 1). We expected that a fading moving object that does not provide a transient signal would show a forward displacement; i.e. it would be visible at luminances lower than the detection threshold for motion over short segments. Experiment 1 confirmed this expectation. In Experiment 2 we confirmed that this result cannot be attributed solely to probability summation depending on the length of the motion sample or to greater deployment of spatial attention in the long-trajectory motion condition.

Our results are particularly noteworthy as similar non-fading stimuli, where a transient does signal the abrupt offset, have previously been shown to be localised correctly or mislocalised in the opposite direction (Kerzel, 2000; Stork & Müsseler, 2004). Kanai, Sheth, and Shimojo (2004) described a set of conditions where an overshoot of the moving object can be found with abrupt offsets. One of these conditions used a very low-contrast moving object. The off-transient of a low-contrast object is weaker than of a high-contrast object. Our interpretation of their finding would be that the weak transient signal is not able to trigger the correction mechanism described here; therefore the moving object is perceived to overshoot.

The present study manipulated the transient related to the offset of a moving object. To apply to experimental paradigms where there is an abrupt change in the direction of motion (Whitney & Murakami, 1998) our findings have to be extended to transients related to direction changes. It is known that the visual system responds strongly to such unpredictable events. For example, EEG studies have shown event-related potentials in response to the onset of motion and changes in the direction of motion (Clarke, 1972; Hoffmann, Unsold, & Bach, 2001; Pazo-Alvarez, Amenedo, & Cadaveira, 2004). These signals seem to originate from higher visual areas, and may signal the change of the direction of motion to areas coding for object position, contributing to the accurate perception of the position of such events. This would extend our hypothesis to explain the lack of a perceptual overshoot in paradigms where moving objects stop without disappearing (Eagleman & Sejnowski, 2000) or abruptly change direction (Whitney & Murakami, 1998).

Our interpretation of the forward displacement for moving objects found in the present study and in the various other paradigms is as follows. There are non-trivial neural delays in the transduction, transmission and processing of information within the nervous system. It has been suggested that there are mechanisms to compensate for these delays, otherwise it would not be possible to successfully interact with a dynamic environment (De Valois & De Valois, 1991; Ghez & Krakauer, 2000; Lacquaniti & Maioli, 1989; Nijhawan, 1994; Wolpert, Ghahramani, & Jordan, 1995). Especially the interaction with moving objects would pose a severe problem, because the position information available to the system would always lag behind the position the object presently occupies. Possible neural mechanisms for the anticipation of moving objects in the visual system have been identified, including local lateral interactions in the retina (Berry, Brivanlou, Jordan, & Meister, 1999) and later levels (Baldo & Caticha, 2005; Jancke, Erlhagen, Schoner, & Dinse, 2004; Kanai et al., 2004; Kirschfeld & Kammer, 1999), and/or internal models that facilitate extrapolation by top-down influences on early cortical representations. Internal forward models have been proposed previously to account for forward displacements found in experiments involving limb movements (Miall & Wolpert, 1996; Wolpert et al., 1995). The visual nervous system might generate an analogous internal model for the processing of moving visual stimuli (Erlhagen, 2003; Miall & Wolpert, 1996; Nijhawan & Kirschfeld, 2003).

On this view, our present findings suggest that neural processes underlying the perception of a moving object can be maintained with weaker neural activity due to an internal model. The perceived position is to some degree independent from bottom-up stimulation. Motion in the model cannot be stopped instantaneously. However, when motion in the outside world is stopped with a strong transient this generates a strong neural response, which carries accurate position information. This transient overrides the neural activity that is otherwise maintained by the internal model. When the transient input is weakened (for example due to gradual fading) the internal model runs unhampered for longer.

It seems to be necessary that the correcting transient stems from the moving object itself and not from neighbouring objects. Other transients (like flashes nearby) do not usually reset the predicted position of a moving object, but lead to a spatial offset between moving object and flashes (the flash-lag effect). However, recently conditions have been found, in which flashes can lead to a reconstruction of the veridical position of the moving object. Kanai and Verstraten (2006) observed that, additionally to the forward displaced position of a moving object, a second instance of the same object in its veridical position can be seen when flashes are positioned suitably to trigger filling-in processes.

In contrast to our view described above, Eagleman and Sejnowski (2000) proposed that in the flash-lag effect “the flash resets motion integration”, and later the newly integrated position of the moving object is “postdicted to the time of the flash”. The general principle of a subsequent event influencing the perceived position is compatible with our proposed retroactive correction mechanism. However, Eagleman and Sejnowski claimed that the flash-lag effect is caused exclusively by retroactive (or 'postdictive') mechanisms. Our interpretation of the flash-lag effect would be different: The position of the moving object is constantly predicted by an internal model to compensate for delays in the neural pathways (Nijhawan, 1994). The flash does not interfere with this prediction, therefore an offset between the moving object and the flash is perceived in standard flash-lag displays. In the case of the abrupt stopping of motion (e.g. the flash-terminated flash-lag display) the transient signal associated with this abrupt event does interfere with ongoing motion processing and retroactively influences the perceived position of the moving object. We use both predictive and retroactive mechanisms in this explanation, which might at first seem unparsimonious. However, we assume that whenever the brain can use predictive mechanisms, it will do so to benefit from a more 'up to date' world model. Confronted with unpredictable, sudden events, the brain will employ retroactive mechanisms to come up with the most reasonable interpretation of the sensory input. This interaction of two opposing mechanisms is advantageous to an animal because it maximally reduces localisation errors of moving objects.

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Figure 1

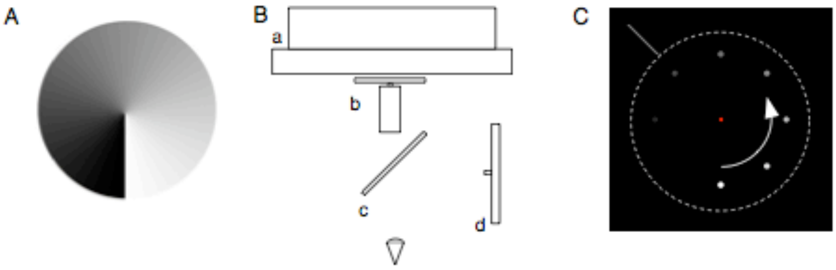

Figure 2

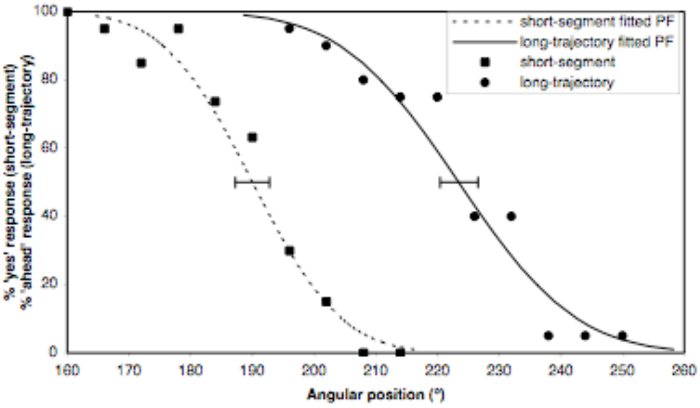

Figure 3

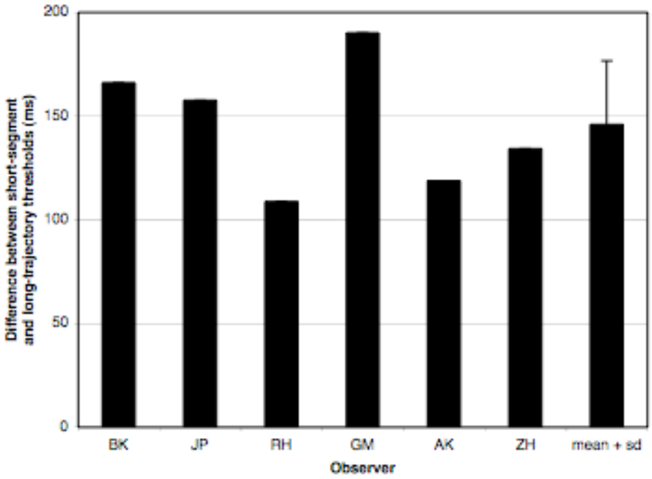

Figure 4

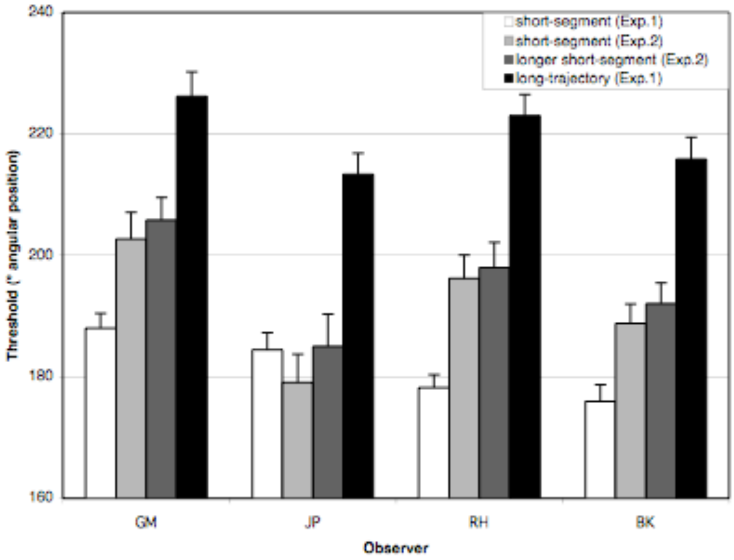

Figure 1 **A)** The variable neutral density filter that was mounted between observers and the screen. **B)** The apparatus: In front of the computer screen (a) the neutral density filter was mounted on a rod (a micro stepper motor in Experiment 2; b). A beam splitter (c) was used to present a fixation LED (d) in the plane of the screen. **C)** Stimulus in the 'long-trajectory motion' condition: observers viewed a white dot moving behind the filter on a counterclockwise trajectory starting at 0° (6 o'clock position). The dot appeared to fade as it moved until it disappeared at around 220°. The dotted line depicts the outline of the filter disk in front of the screen. A grey radial line was presented at different positions.

Figure 2 Raw data and fitted psychometric functions from Experiment 1 for naïve observer ZH. The abscissa denotes the angular position of the reference line where the dot was presented (short-segment motion) or where observers made the decision ('dot disappeared ahead of/before the line'). Higher angular positions correspond to lower stimulus luminances. The ordinate denotes percent 'yes' responses (short-segment motion) and percent 'ahead' responses (long-trajectory motion). The horizontal error bars represent 95%-confidence intervals for the 50%-thresholds.

Figure 3 Difference (in units of time and rotation) between the thresholds for the long-trajectory motion and the short-segment motion conditions for each of the 6 observers and the group average (with standard deviation).

Figure 4 Absolute thresholds from Experiments 1 and 2 for four observers who participated in both experiments (including author GM). Bigger angular position denotes lower luminance of the stimuli. The white bar represents the detection threshold for the short-segment stimulus from Experiment 1; the two grey bars depict thresholds for the two short-segment stimuli in Experiment 2; the black bar shows the disappearance threshold of the long-trajectory stimulus from Experiment 1. Errorbars show 95%-confidence intervals for each threshold.