The Position of Moving Objects.

Markus Lappe and Bart Krekelberg[*]
Ruhr University Bochum,
Allg. Zoologie & Neurobiologie ND7/30,
44780 Bochum, Germany
Tel: +49 234 700 4369
Fax: +49 234 709 4278
Email: {lappe,bart}@neurobiologie.ruhr-uni-bochum.de

Abstract

Moving objects occupy a range of positions during the period of integration of the visual system. Nevertheless, a unique position is usually observed. We investigate how the trajectory of a stimulus influences the position at which the object is seen. It has been shown before that moving objects are perceived ahead of static objects shown at the same place and time. We show here that this perceived position difference builds up over the first 500ms of a visible trajectory. Discontinuities in the visual input reduce this build-up when the presentation frequency of a stimulus with a duration of 42ms falls below 16 Hz. We interpret this relative mislocalisation in terms of a spatio-temporal filtering model. This model fits well with the data given two assumption. First, the position signal persists even though the objects are no longer visible and secondly, the perceived distance is a 500ms average of the difference of these position signals.

1 Introduction

Determining the position of moving objects is not an easy task. There are several well known properties of the visual system that can interfere with this task in non-trivial ways. First, the (long) integration time of the system which gives it its sensitivity at low luminance levels, would lead to a blurred image if left unchecked (Burr, 1980). How does the visual system assigns a unique position to such blurred objects? A second problem is caused by the delays present in the visual pathways. These delays are normally expected to lead to delayed perception; we perceive the world not as it is now, but as it was some 80ms ago. Nijhawan (1994) suggested, however, that perception uses the predictability of the trajectories of moving objects to correct for the visual latency. This poses the question: “At any particular point in time, which snapshot of the world is perceived?” Let us consider these two problems in more detail.

---

[*] Corresponding author

Fast moving objects occupy a range of positions during the time over which the visual system is commonly thought to integrate ($\sim$ 100ms (Barlow, 1958; Burr, 1981)). Nevertheless, often moving objects do not appear to be smeared out (Burr, 1980). Previous work on this so-called suppression of visible persistence has tried to find out which factors are relevant to the *amount* of suppression. The relevant factors that have been identified are the speed (Burr, 1980; Hogben & Di Lollo, 1985), interstimulus interval (Castet, 1994), spatial separation and retinal eccentricity of the stimuli (Di Lollo & Hogben, 1985; Chen, Bedell, & Öĝmen, 1995). Those authors measured the amount of blur as a function of the various parameters of the stimulus. Even though the removal of blur necessarily involves the assignment of a unique position to an object, the final (de-blurred) position was not measured by those authors. In this paper we consider de-blurring as one aspect of the more general process of the localisation of moving objects and specifically measure the perceived position of moving objects. This complementary approach is made necessary by the observation that even when the amount of suppression is known, the percept has not uniquely been identified yet. One could imagine, for instance, a localisation mechanism that reduces blur by removing all activity but the activity arising from the last few milliseconds. Alternatively, a localisation mechanism could determine the position by calculating the centroid of the current activity. Both mechanisms would reduce motion blur by a large amount, but they predict a very different perception of the position of moving objects.

The fact that humans can correct for the latencies of their information processing system is demonstrated by our ability to catch a fast moving ball. This, however, only demonstrates the correction for latencies at the action end of the perception-action pathway. There is no logical need to *perceive* the ball where it is now rather than where it was 80ms ago as long as you stretch out your arm to the position where the object is now. Nevertheless, latency correction could operate in perception, and this has been suggested by Nijhawan (1994). He investigated the position of a moving object by probing its perceived position with a static, briefly flashed object. He observed that, although the static and moving object were in reality in the same position, the position of the moving object was perceived to be shifted forward along the trajectory. Nijhawan interpreted this as showing that the position of a continuously visible object is extrapolated along its path to correct for the visual latency.

We consider motion-deblurring and a possible latency correction or extrapolation mechanism as two aspects of the more general problem of the localisation of moving objects. In that view, the setup as used by Nijhawan shows a localisation mechanism at work on stimuli with different trajectories. First, the mechanism extracts the position of the continuously illuminated objects from a continuous stream of visual information. Secondly, the mechanism localises a static stimulus with a brief exposure. Thirdly, the difference between these two positions is determined. In our view, a non-zero difference in position shows that *trajectory information affects the operation of the localisation mechanism*.

The set-up as used by Nijhawan represents only one end of the spectrum: it provides information about the difference in the perception of the position of static versus continuously visible, moving objects. To investigate the dynamics of the process of localisation, we will investigate the difference in perceived position of two moving objects. One of these is continuously visible, while the other is seen only intermittently. By changing the parameters of the latter stroboscopic motion sequence (the duration and the frequency of the stations), we can determine the way in which the visibility of an object over time influences its perceived position. This allows us to answer questions such as: “for how long should an object be visible before the localisation mechanism is affected by the trajectory?” or “how frequently should an object be visible to allow its trajectory information to be used by the localisation mechanism?". At the other end of the spectrum, we also compare the perceived position of objects that are all continuously visible. This answers the question whether any parameter apart from the visibility of the trajectory influences the localisation mechanism.

In the first experiment we show that objects in stroboscopic motion are perceived to lag behind objects in continuous motion. Secondly, we argue that a latency-correction mechanism as proposed by (Nijhawan, 1994) cannot be held responsible for the effect. In search for an alternative mechanism, we then probe the dynamics of the localisation process by comparing the position of stroboscopic with that of continuous motion. Our data show that the lag-effect decreases exponentially with both frequency and duration of the stroboscopic motion sequences. In other words, the perceived difference in position of moving objects compared to static objects increases as a function of the amount of visible trajectory. Visibility of the trajectory, however, is not the only relevant factor. In a final experiment we compare the perceived position of two continuously visible objects that move at different velocities. We find that a difference in velocity leads to significant lag and even lead effects.

2 Materials and methods

Stimuli

Following the experiments in (Baldo & Klein, 1995) we use the stimulus shown in figure 1. The stimulus consist of one set of three dots rotating about a fixed point and two sets of two dots that are repetitively flashed for brief periods of time on either side of the rotating dots. In our setup the outer dots move along with the inner dots when they are visible. A further difference compared to (Baldo & Klein, 1995) is that, depending on the flash-frequency, the outer dots can be flashed multiple times per turn. This stimulus is designed to compare the position of objects in stroboscopic with those in continuous motion. From the experiments in (Nijhawan, 1994; Baldo & Klein, 1995) we expect the flashed dots to lag behind the continuously visible dots: a *flash lag-effect*. We define the 'lag-angle' as the angle between the inner, continuously moving dots and the outer, stroboscopically moving dots (see figure 1: the angle α).

Single dots subtend 0.4 degrees of the visual field and their centres are separated by 1.5 degrees. The whole stimulus of seven dots measures 9 degrees across and rotates at 25 rotations per minute.

The outer dots always have a luminance of 57.8 cd/m^2, and the background is always at 0.05 cd/m^2. In the frequency experiment the duration of the outer dots is fixed at 42ms while in the duration experiment the outer dots are flashed with a frequency of 1 Hz. In the luminance experiment, the outer dots' frequency and duration were fixed at 4 Hz, 42ms respectively. The inner dots are always shown at the screen refresh-rate (72 Hz), their luminance was the same as that of the outer dots except in the luminance experiment where it was varied.

In the high-frequency experiments, all dots are flashed at the screen refresh rate of 72 Hz. The definition of the lag-angle is kept as the angle between the inner and the outer dots. To test the influence of eccentricity, an extra separation between the inner and outer dots of 3 degrees is introduced. These experiments were done in a lit room.

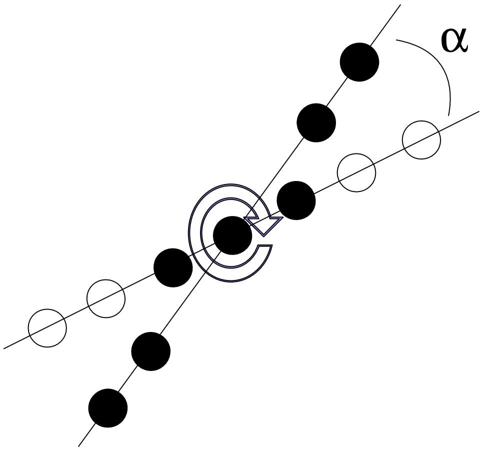

Figure 1: The flash-lag illusion. Seven dots rotate rigidly around a common centre. The three inner dots are shown continuously, while the outer dots are repetitively flashed for brief periods of time. Subjects report that the outer dots appear to lag behind the three inner dots. The unfilled dots show the position at which the outer dots are "flashed", the filled dots show the percept. The angle α is called the lag-angle. The arrow denotes the rotation direction.

Apparatus

Stimuli were generated on a Silicon Graphics Indigo2 system and rendered on a monitor with a 72 Hz vertical refresh rate. Using a monitor rather than a real-time system with light emitting diodes (as in (Nijhawan, 1994)) restricts the choice of durations of the stimuli to integer multiples of the duration of a single frame. Furthermore, the maximum flash-frequency is restricted by the duration of a frame. Significant effects, however, can be found in the temporal range accessible to this method.

Procedure

Subjects were seated at a distance of 70cm in front of the monitor. They fixated the central dot of the stimulus which coincided with the centre of the screen.

A method of adjustment was used to determine the perceived lag-angle. Subjects could introduce an offset angle between the inner and outer dots by pressing left and right mouse buttons. They adjusted this angle until they perceived the inner and outer dots to be in perfect alignment (See figure 1). After confirming this percept by pressing the middle mouse button, the offset angle was stored. There was no time pressure; subjects were free to adjust the stimuli to their satisfaction. The next trial was started immediately afterwards. The order of presentation of trials was randomised across all parameters within an experiment and left and rightward rotations were chosen at random. Moreover, to prevent the possibility of memorising the number of mouse-clicks needed to align the dots, a random initial offset angle between the inner and outer dots was chosen for each trial.

Data Analysis

The stored offset angles are the angles needed to null the lag-effect and are therefore interpreted as the negative of the real flash-lag angles. The angles were averaged over trials. Note that these angles are angles of orientation, *not* angles of the visual field. The figures show mean values with error bars representing ± 1 standard error. A measure of the sensitivity of the subjects is given by the standard deviation of the lag angles obtained for one particular stimulus.

Significant trends and significantly different means were tested with one way ANOVAs and Student's t-tests where appropriate. The Pearson Product Moment was used as a measure of correlation.

Subjects

Subjects were five volunteering researchers and students from the department (including the two authors). All subjects except the authors were naive with respect to the particular hypotheses being tested in the experiments although RK was aware of the general background of the experiment.

3 Results

To test our setup, we performed some experiments analogous to those of Nijhawan (1994). A clear flash lag-effect could be measured for all subjects with stimuli generated on a monitor rather than with the continuous light of LEDs. Moreover, the dependence on the angular velocity is similar to what has been shown for continuous light. That is, the lag-angle between continuous and stroboscopic objects increases roughly linearly with angular velocity. The presence of a lag-effect in our setup is not entirely a straightforward consequence of the LED experiments in (Nijhawan, 1994). Due to the finite refresh rate of a monitor, objects in this setup are never “continuously lit”. In our experiments the inner three dots (see figure 1) are flashed too, albeit at the high rate of 72 Hz. These preparatory experiments show that the effect we study on a monitor is comparable with that seen in experimental set-ups under continuous illumination. Therefore we will continue to refer to the dots shown at the screen refresh rate as being in continuous motion.

As discussed in the introduction, Nijhawan (1994) interpreted the lag-effect as the result of a latency correction mechanism. This hypothetical mechanism would extrapolate the position of continuously moving objects in order to compensate for the latency that the visual signal incurred on its way from the eye to the cortex. Such an extrapolation would displace continuously visible objects by an amount equal to the latency times the velocity thus giving rise to a perceived separation when compared to static objects that are presented at that position at the same time. A prediction of this hypothesis is that the lag-effect should increase when the latency of the inner dots increases. We tested this prediction by decreasing the luminance of the inner dots. This is known to increase the latency (see for instance (Roufs, 1963)).

Figure 2 shows that, in contradiction to the latency-correction hypothesis, the lag-effect decreases when the inner dots have an increased latency. This means that the dots are not

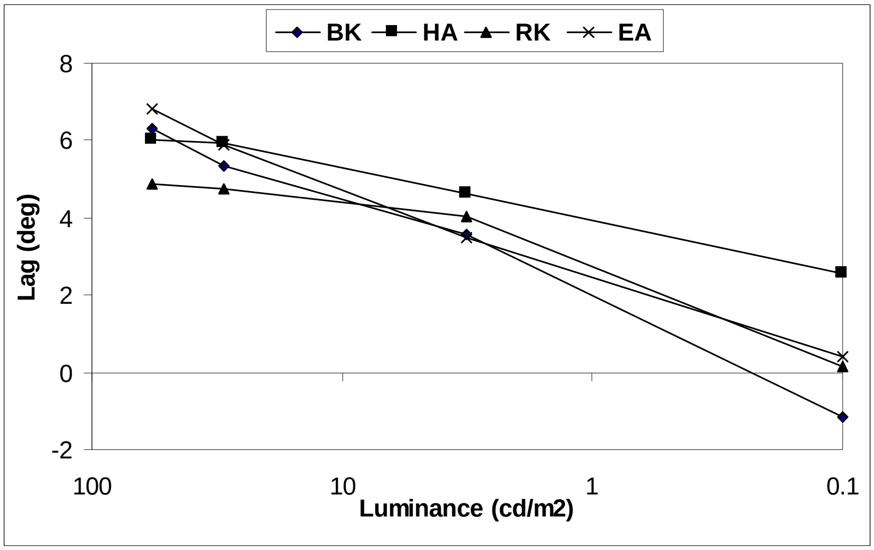

Figure 2: Luminance experiment. Contrary to the prediction of a latency-correction hypothesis, an increase in the latency due to a decrease in luminance decreases the lag between the inner and the outer dots.

extrapolated more when they move more during the time when the signal travels from eye to cortex. Although this does not disprove the possibility of an extrapolation mechanism for moving objects, it does show that this mechanism does not adapt its extrapolation to the changing latencies in the visual system. (For another interaction between luminance and lag-effect, see (Purushothaman, Patel, Bedell, & Öĝmen, 1998)).

This motivates our attempt to find another explanation for the lag-effect. As discussed in the introduction we believe that such an explanation can be found in a mechanism that extracts and compares position information from moving objects and is affected by the trajectory of these objects. We pursue this hypothesis by investigating lag effects between stroboscopically and continuously moving objects. Varying the temporal properties of the stroboscopic motion stimuli allows us to investigate the temporal dynamics of the localisation mechanism.

3.1 Temporal Dynamics of Localisation

In this section we will discuss the influence of the duration (figure 3) and the frequency (figure 4) of the stroboscopic motion sequences on the perceived lag with respect to continuous motion. Three aspects of the localisation are discussed. First, the dependence of the lag-effect on the parameters duration and frequency. To stress the similarity in the parameter dependencies rather than the absolute sizes of the effect, the data for the various subjects are normalised to one at the briefest of durations or lowest frequency, respectively. Secondly, the lag angles used for this normalisation are shown in the bar charts in figures 3 and 4. This shows the variation among subjects as well as the absolute size of the effect. A third interesting aspect of the localisation mechanism is its sensitivity: how consistently can subjects attribute a lag to objects with different degrees of visibility? This question is addressed by plotting the standard deviations of the subjects lag-angles in figure 5. The following describes the experiments and results in more detail.

In the duration-experiment we determined the influence of the duration of a trajectory on the perceived position. Figure 3 shows how a change in the duration of the outer dots, which are flashed at a frequency of 1 Hz, affects the lag angle as perceived by 5 subjects.

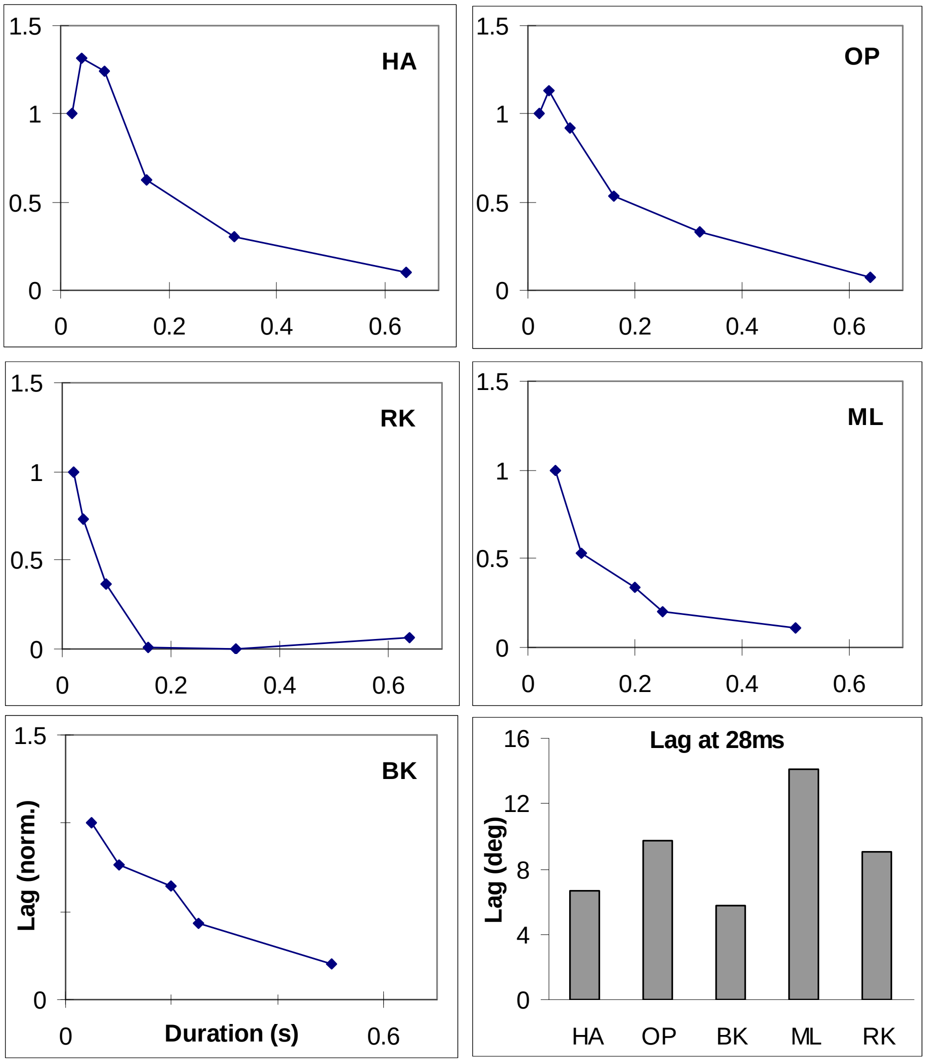

Figure 3: Duration-experiment. The dependence of the lag angle on the duration of single flashes which are shown repetitively at a frequency of 1 Hz. The curves are normalised with respect to the lag angle that is found for the briefest duration. The axis labels in the bottom left figure apply to all figures showing individual data. The absolute size of the lag angle (in degrees of orientation) corresponding to a normalised lag of one is shown in the bottom-right figure.

The lag angle decreases as a function of the duration of the flashes. This effect is significant for all subjects ($p < 0.05$) and can be described by an exponential. Differences in the perceived position between continuously shown objects and flashed objects only disappear when the duration of the flashed objects is above 500ms. One can also interpret these figures as showing the dynamics of the localisation mechanism. At the onset of a motion stimulus its position is the same as that of a static stimulus. When the stimulus starts moving, however, its position is perceived slightly beyond the position of a static stimulus shown at that position, at that time. This discrepancy increases with time; the localisation mechanism progressively adds a perceived difference. For trajectories of 500ms a further increase in duration has no significant effect; the position of the stroboscopic stimulus is now the same as that of the continuous stimulus and maximally different from that of the static stimulus.

As the bar-chart in figure 3 shows, there is considerable variation among subjects. The absolute lag angles perceived by subjects vary from 6 to 14 degrees of orientation. The subjects' sensitivities are discussed below, together with the sensitivities in the frequency-experiment.

In the previous experiment the frequency of the stroboscopic motion stimulus was constant (1 Hz). In the present frequency-experiment we wish to determine the effect of bringing the stations of the motion sequence nearer together while duration and speed are kept constant. This provides information on the position-extraction mechanism's ability to extract information from a discontinuous stream of input. The presentation frequency of the outer dots is varied while their duration is kept constant (at 42ms). Figure 4 shows that the lag angle falls off exponentially with the flash-frequency. This effect is significant for all subjects ($p < 0.05$). For frequencies above 16 Hz the lag-effect is almost zero. The effect of frequency shows that the localisation mechanism is affected by the separation between stations in the apparent motion trajectory. The nearer the stations are, the smaller the perceived difference with a continuously visible object becomes. Looking forward to the experiment in the next section, we can see that the lag at 16 Hz is not significantly different from that at 72 Hz (where both inner and outer dots are continuously visible). This is so for all subjects ($p > 0.05$) and shows that, as far as the localisation mechanism is concerned, a trajectory which is visible for 42ms every 63ms (=16Hz) is equivalent to a continuously visible trajectory. Hence, the mechanism can combine information from trajectories sampled at 16Hz.

A second interesting aspect of the frequency dependence is that the lag angle is not zero at the high flash frequencies of 16 Hz. Moreover, two subjects show a lead effect: the outer, flashed dots are seen ahead of the inner, continuously moving dots. As these 16Hz stimuli are almost continuously visible, these observations suggest that there could be lag and lead effects between continuously moving objects. This is investigated in section 3.2.

The third aspect of the localisation mechanism we wish to discuss is its sensitivity. How well can subjects distinguish the position of moving objects? We use the standard deviation of a number of repeated measurements, a measure of the subjects' uncertainty, as a measure of the sensitivity. The smaller the standard deviation, the higher the sensitivity. The median of the sensitivities averaged over all subjects and experiments is 2.4 degrees. More detailed information on the sensitivity is shown in figure 5. There we show the sensitivities of each subject in the duration and frequency experiments. To investigate the influence of the size of the lag effect on the sensitivity we divided the experiments in two groups. The first contains stimuli with brief flash durations or low flash-frequencies and is called the 'large lag' group. The second group consists of the stimuli that lead to small lags: the stimuli with long durations or high flash frequencies. As figure 5 shows, subjects' sensitivities improve with smaller lag-angles. Moreover, experienced subjects (BK,ML) reach somewhat better sensitivities than naive subjects (HA,OP,RK).

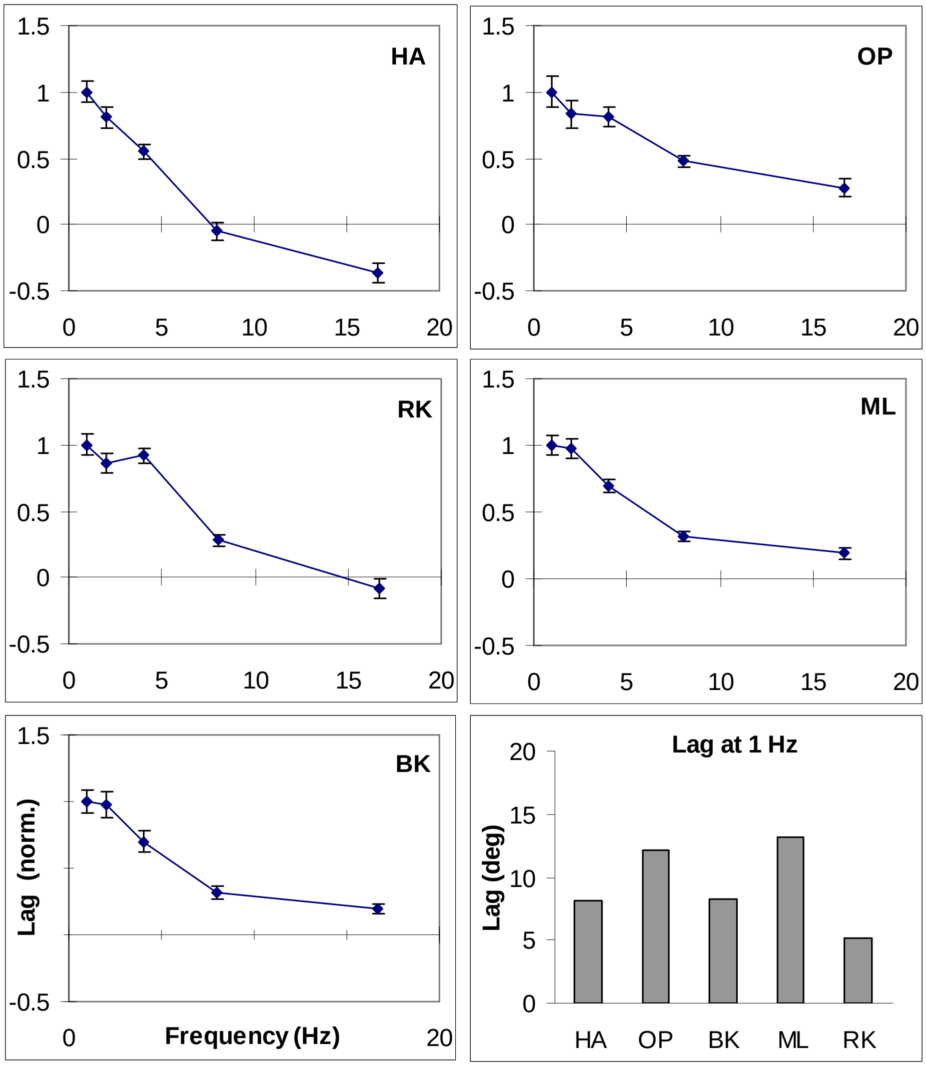

Figure 4: Frequency-experiment. The dependence of the lag angle on the frequency of flashes whose individual duration is 42 ms. The angle is normalised with respect to the lag angle at the lowest frequency (1 Hz). The axis labels in the bottom left figure apply to all figures showing the individual data. The bar chart shows the absolute lag angles at 1 Hz.

3.2 Localisation of Two Continuously Moving Objects

The results in the previous section hinted at a possible influence of parameters other than those determining the visibility of the trajectories on the lag-effect. To investigate this we set up an experiment in which the inner as well as the outer dots were flashed at the maximum screen refresh rate (72 Hz). To the observers this looks as if all seven dots are continuously lit and, if continuity of observation is the only important factor, one would expect these objects to be in perfect alignment. To our surprise, this high-frequency limit of the lag-effect was significantly different from zero for some subjects (Figure 6). Moreover, one of the subjects showed a significant *lead*-effect: the outer dots were seen *in front of* the inner dots.

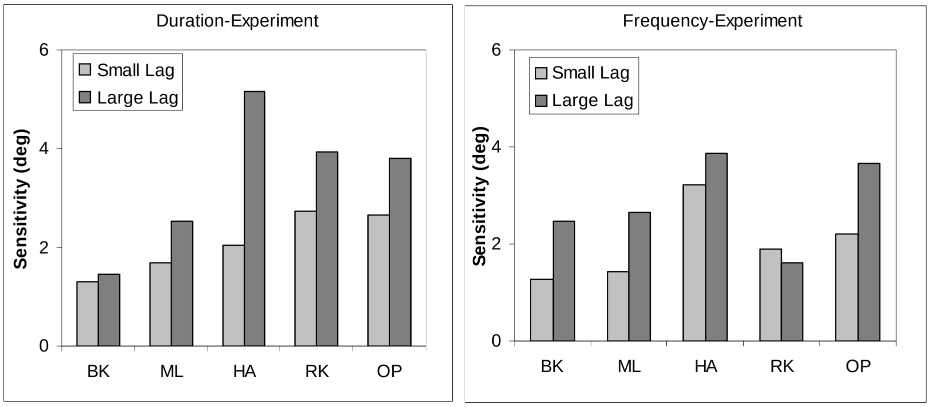

Figure 5: Subjects' sensitivities. The sensitivities of the subjects are shown for the frequency and duration experiment. The 'small lag' group represents the sensitivities obtained with long duration or high frequency stimuli. The 'large lag' group consists of the stimuli with a brief duration or a low frequency. Sensitivities were recorded in the experiments reported in figures 3 and 4.

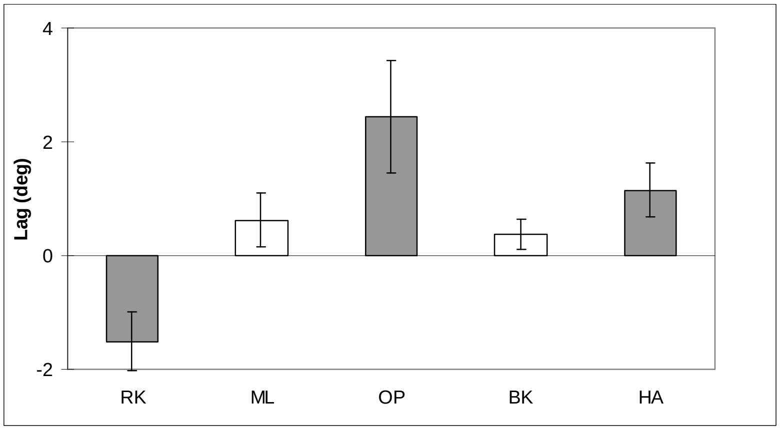

Figure 6: High frequency Limit experiment. Inner and outer dots were shown with equal frequency. (72 Hz; the monitor refresh rate). The filled bars represent values which are significantly different from zero ($p < 0.05$, Student t-test).

Duration, frequency and angular velocity of inner and outer dots are identical in this stimulus, hence this shows that other properties must also play a role in the localisation of the objects. The only factors that could be responsible for this effect are the higher (tangential) velocity of the outer dots, or their increased eccentricity on the retina. We measured the influence of these parameters in an experiment in which four of the six subjects participated. The effect of eccentricity was studied by adding an extra separation of 3 degrees between the inner and the outer dots. The measured lag-effect for three angular velocities is shown for the original stimulus and the stimulus with added eccentricity in figure 7. A two-way ANOVA showed that for all subjects except ML, the effect of both angular velocity and eccentricity are significant ($p < 0.05$), but that there are no significant interactions between the two parameters.

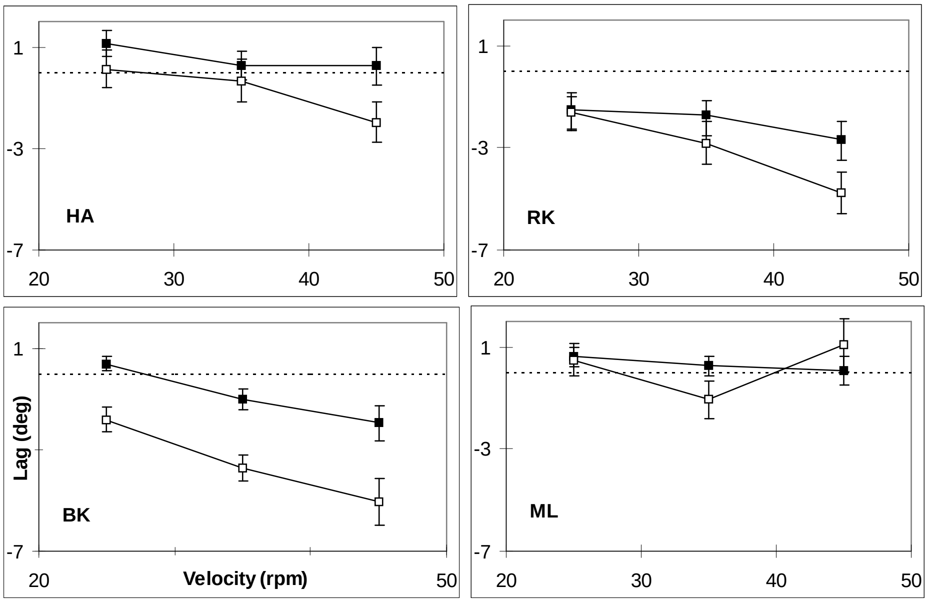

Figure 7: Tangential velocity and eccentricity experiment. The effect of increasing angular velocity and eccentricity when both inner and outer dots are shown at the maximum frequency (72 Hz). Solid squares: the standard stimulus as shown in figure 1 is used. Open squares: an extra separation between the inner three and outer four dots is introduced to increase the retinal eccentricity of the outer dots.

The geometry of our stimulus results in an inevitable confounding of tangential velocity with angular velocity and eccentricity. The parameters can be chosen, however, to create outer dots with different eccentricity but equal tangential velocity. Such is the case for the stimuli with an extra separation between inner and outer dots of 3 degrees and an angular velocity of 25rpm compared to the stimuli without extra separation and an angular velocity of 45rpm. The outer dots in these stimuli move at approximately the same tangential velocity even though their light reaches the retina at different eccentricities. If eccentricity per se were a determining factor in the lag-effect, one would expect a different lag-effect for these stimuli.

Figure 7 shows, however, that the lag angle for these stimuli is approximately the same. This indicates that not the eccentricity, but the tangential velocity is the relevant factor in this experiment. In other words, the tangential velocity of the outer dots affects the localisation mechanism. For low velocities, the fastest stimulus lags somewhat behind the slow stimulus, whereas for higher velocities the fast moving stimulus overtakes and leads the slow moving stimulus. Note that such an effect can only be measured in circular motion, where objects with different velocities can move “side by side”.

As an aside; the tangential velocity is not responsible for the lag-effect as shown in figures 3 and 4. This can be tested by reversing the stimulus such that the outer dots are shown continuously, while the inner dots are flashed. Baldo and Klein (Baldo & Klein, 1995) showed that this leaves the effect intact: the flashed dots still lag behind even though their tangential velocity is smaller than the continuously visible dots.

3.3 Visibility Fraction and ISI

In this section we regroup our data to find the stimulus parameters that best account for the dependencies we found.

The experiments have shown the dependencies of the lag-effect on two of the temporal properties of the stimulus. To relate our results to that on visible persistence we combine and replot the data from the frequency-, duration- and high-frequency limit experiments in terms of the parameters that have been found to be important in visible persistence. Specifically, both the temporal interval (ISI) as well as the spatial distance (dx) between two successive presentations of stimuli are known to have an influence on the perception of (stroboscopic) motion (Castet, 1994; Di Lollo & Hogben, 1985; Chen et al., 1995). In our setup these parameters covary with changes in duration and frequency. Due to the constant angular velocity of our stimuli in the first three experiments, the dependence on dx is identical with that on ISI.

Our data from the duration-, frequency- and high-frequency limit experiments can also be expressed in terms of the dependence on a parameter we call the visibility fraction (VF). This quantity denotes the fraction of the time during which a stimulus is visible and is given by the product of flash-duration and frequency. Figure 8 shows the data of the three experiments shown in figures 3,4,6 pooled over all subjects and expressed in terms of ISI and VF.

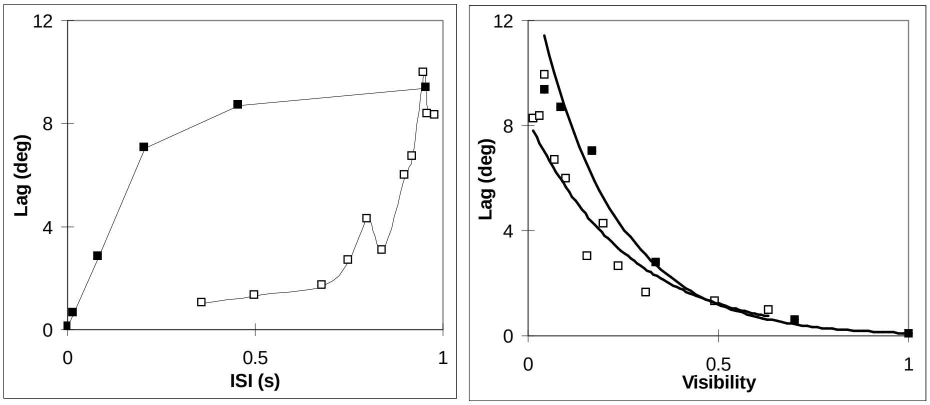

Figure 8: **Left)** Lag effect as a function of ISI. **Right)** Lag effect as a function of the visibility fraction. Curves show best-fitting exponential functions. Filled squares represent the data from the frequency-experiment, open squares those of the duration-experiment.

This representation of the data shows that the ISI is a bad predictor of the lag-effect whereas the visibility fraction can account for most of our data. Nevertheless, data obtained in the duration experiments generally lie somewhat below the data obtained in the frequency experiment; especially when the VF is small. Hence, the localisation primarily depends on the fraction of time during which a stimulus is visible. This suggests that the (mis)-localisation is due to a process that averages over longer periods of time. The difference in lag between duration and frequency experiments for small VF can then be interpreted as the (partial) failure of this averaging mechanism when it has to average over multiple disconnected parts of a trajectory. This idea is formalised in the next section.

3.4 Theoretical Analysis

In this section we apply a model to our data that was developed for the description of spatio-temporal interpolation in dynamic vernier alignment (Morgan & Watt, 1983). The latter is a technique that has been used to study the perceived position of objects in stroboscopic motion. This technique allows one to determine the position that stroboscopically moving objects "occupy" between the stations of the motion sequence (Morgan, 1979). In other words, it probes the interpolation process by which human observers come to interpret stroboscopic motion as continuous motion. Interpolation of motion trajectories is perfect for stroboscopic motion whose stations are separated by less than 3 minutes of arc in space and less than 30ms in time (Fahle & Poggio, 1981; Morgan & Watt, 1983). Such objects are perceived at the position they would have been if they were in continuous motion. For larger spatial or temporal separations the interpolation breaks down and the objects are seen at the positions of the stations of the stroboscopic motion sequence. In (Morgan & Watt, 1983) a model of this interpolation process based on spatio-temporal filters is presented. The model consists mainly of two components. First, the position signal is temporally low-pass filtered. In other words, the activity representing the presence of an object at a particular location leaves behind a trace of activity after the object has disappeared. Secondly, the perceived position is determined by a spatial average of this activity. To be precise, the temporally filtered signal is spatially filtered with a Difference-Of-Gaussians filter, and the zero-crossings of this spatio-temporally filtered signal are identified with the position of the object.

For our purposes this model can be simplified. First, for the flashed dots in the duration and frequency experiment, the spatial separation between stations (flashes) is so large that the spatial filter's influence is most likely negligible. Secondly, due to the temporal persistence of the position signal, the zero-crossings of the flashed dots stay at their last shown position, even after the dots have been turned off. This simplifies matters considerably and the position as given by the zero-crossings follows the trajectory shown in figure 9.

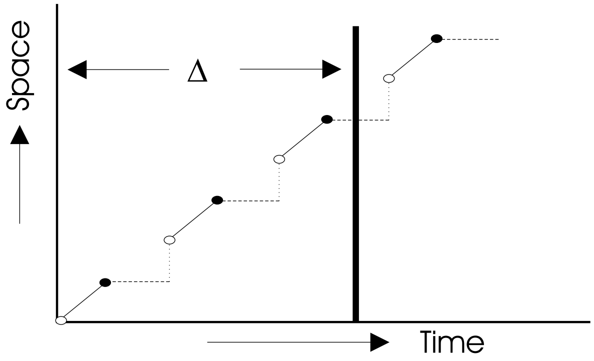

Figure 9: Zero-crossing trajectory of a flashed dot without spatial interactions. The open circles denote position and time when a flash is turned on. The solid lines show the physical trajectories; where the dots actually moved. These lines have a temporal extent that represents the parameter 'duration'. The dashed lines show the model trajectories after the dot is turned off: this is due to the temporal persistence of the activity in the model. The length of these lines equals the IFI. The vertical line at time $t = \Delta$ represents the putative averaging period. In this case, the averaging includes two completed flash periods ($N = 2$) plus some lag in the third period.

It should be noted that the trajectory of figure 9 is not what subjects report. The flashed dots are not perceived at all between their two stations. There is no logical reason, however, why their position signal could not still be present. It means that the position signal is available for comparison with other position signals, but not for direct perception of an object.

Based on the observations in section 3.3 we hypothesise that subjects adjust the offset-angle based not on the instantaneous, but rather on an averaged lag. In other words, we suggest that the measured lag corresponds to the *average* difference between the trajectories that are predicted by the zero-crossing model. This hypothesis can be tested with the data at hand. Let the parameter Δ denote the time over which the lag is averaged. An analytic expression for the lag averaged over Δ can easily be derived. First, observe that the total lag in a single period (from flash n to flash $n+1$) is $\frac{1}{2}IFI^2 * speed$ (the surface of one of the triangles in figure 9). The total lag in a time-period of Δ can be calculated by counting the number of flashes completely visible within this period (N), multiplying this by $\frac{1}{2}IFI^2 * speed$ and finally adding the total lag observed in the last flash-period, which will be somewhat less than $\frac{1}{2}IFI^2 * speed$, depending on Δ. This results in the following formula for the lag-effect:

$$Lag = \alpha * (N * IFI^2 * speed + (\Delta - N/frequency - duration)^2 * speed)$$

The parameter α is introduced as an extra degree of freedom to catch the effects that are ignored in this simple model. The distance between the stations of the stroboscopic motion sequence, for instance, is not explicitly included in the model even though this parameter is not constant in the frequency-experiment. We used a non-linear least-squares fit to the data to determine the parameters α and Δ for the duration and frequency data.

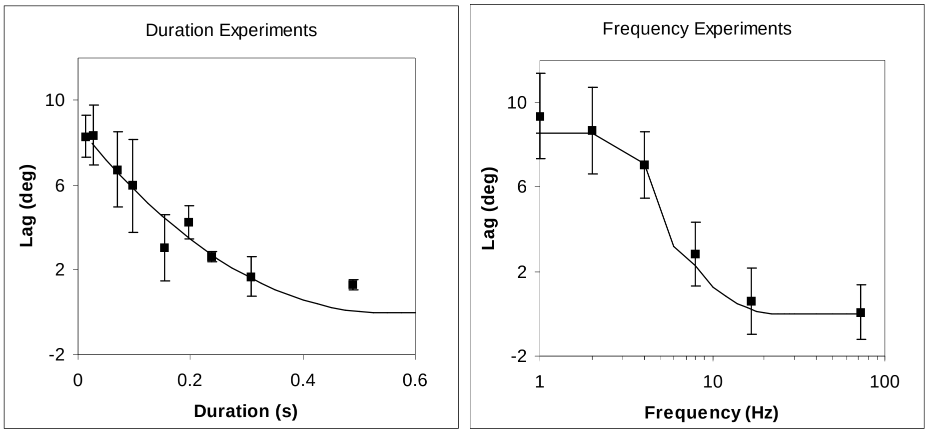

Figure 10: Fitting the model to the data. The solid squares represent the duration and frequency data averaged over all subjects. The lines show the good fit of the model to both experiments.

Figure 10 shows how well the model fits the data. For the frequency experiment $r^2 = 0.99 (p < 0.001)$ while for the duration experiment $r^2 = 0.94 (p < 0.001)$. These good fits of the model to the data support our hypothesis that the relative position of two moving objects is determined by a slow averaging process. The best-fitting averaging period Δ for the duration experiment is determined as 0.54s, while the frequency data require a Δ of 0.27s. We interpret the difference between these time constants as showing that the localisation mechanism averages over a period of 540ms but that this averaging is imperfect for trajectories that are only intermittently visible.

4 Discussion and Conclusion

Our experiments shed a light on the dynamics of the mechanism that localises moving objects. We compared the perceived position of stroboscopically and continuously moving objects to find out how the relative position of two moving objects changes when more of their respective trajectories becomes visible. Our data show that the localisation mechanism is affected by the trajectory over a period of up to 500 ms and that it can combine information from successive short (42ms) "views" as long as these follow each other with a frequency not below 16 Hz. At frequencies below 16 Hz, the objects are increasingly perceived to be at the position where static objects would be perceived. The strong predictive value of the visibility fraction suggest that a low-level temporal averaging mechanism could be responsible for these effects. As a simplified model we suggest that the lag is the average difference between the zero-crossings of a spatio-temporally filtered position signal. The lag occurs first because the activity representing the flashed object persists after the object is turned off and secondly, because the difference in position is averaged over a long (~ 500ms) time period. Visibility of the trajectory, however, is not the only factor determining the localisation of moving objects. This is most clearly shown by our finding that, depending on their (tangential) velocity, continuously visible objects can be seen to lag or lead other continuously visible objects.

Baldo and Klein (1995) interpreted the flash-lag phenomenon as showing a gradient in attention: the flashed objects were hypothesised to warrant a lower degree of attention and would therefore be delayed in their processing. This begs the question why the flashed objects would warrant a lower degree of attention. Moreover, it has been shown that different "amounts of attentional resources" allocated to the flashed objects fail to influence the lag effect (Khurana & Nijhawan, 1995; Khurana, Cavanagh, & Nijhawan, 1996). Analogous, but based on low level properties of the visual system, one could hypothesise that the shorter duration of the outer dots leads to an increase in their latency. If, however, the results on duration dependent latencies obtained in cat visual cortex (Duysens, Gulyás, & Maes, 1991) transfer to humans, the opposite seems to be true.

The simplified zero-crossing model we used is relevant only in the range where spatial averaging of position of successive flashes plays no role. This is not the case for the localisation of (almost) continuously moving objects. There, successive flashes are within the range of effective spatio-temporal interpolation. An avenue for future research is to calculate the zero-crossing trajectories (or another determinant of the position such as the maximum in the energy (Morrone & Burr, 1988)) while including spatial interactions. This may lead to an explanation of the lag and lead effects discussed in section 3.2. Moreover, it will allow us to include the possible role of parameters such as the distance between the stations in motion sequence without resorting to the ad hoc parameter α.

Concluding, the perceived relative position of objects is not akin to a snapshot of the retinal image, but rather the result of a dynamic process that combines position and possibly motion signals over a period of approximately 500ms.

Acknowledgements

We thank the subjects for their patience, Michael Morgan and an anonymous referee for helpful comments and the Human Frontier Science Project for financial support.

References

Baldo, M. V. C., & Klein, S. A. (1995). Extrapolation or attention shift? *Nature*, *378*, 565-566.

Barlow, H. B. (1958). Temporal and spatial summation in human vision at different background intensities. *Journal of Physiology*, *141*, 337-350.

Burr, D. C. (1980). Motion smear. *Nature*, *284*, 164-165.

Burr, D. C. (1981). Temporal summation of moving images by the human visual system. *Proceedings of the Royal Society of London, B*, *211*, 321-339.

Castet, E. (1994). Effect of the ISI on the visible persistence of a stimulus in apparent motion. *Vision Research*, *34*, 2103-2114.

Chen, S., Bedell, H. E., & Öĝmen, H. (1995). A target in real motion appear blurred in the absence of other proximal moving targets. *Vision Research*, *16*, 2315-2328.

Di Lollo, V., & Hogben, J. H. (1985). Suppression of visible persistence. *Journal of Experimental Psychology*, *11*, 304-316.

Duysens, J., Gulyás, B., & Maes, H. (1991). Temporal integration in cat visual cortex: a test of Bloch's law. *Vision Research*, *31*, 1517-1528.

Fahle, M., & Poggio, T. (1981). Visual hyperacuity: spatiotemporal interpolation in human vision. *Proceedings of the Royal Society of London, B*, *213*, 451-477.

Hogben, J. H., & Di Lollo, V. (1985). Suppression of visible persistence in apparent motion. *Perception and Psychophysics*, *38*, 450-460.

Khurana, B., Cavanagh, P., & Nijhawan, R. (1996). Are moving objects 'corrected' or flashed objects attentionally delayed? *Investigative Opthalmology and Visual Science*, *37*, 529.

Khurana, B., & Nijhawan, R. (1995). Reply to Baldo and Klein. *Nature*, *378*, 566.

Morgan, M. J. (1979). Perception of continuity in stroboscopic motion: a temporal frequency analysis. *Vision Research*, *19*, 491-500.

Morgan, M. J., & Watt, R. J. (1983). On the failure of spatiotemporal interpolation: a filtering model. *Vision Research*, *23*, 997-1004.

Morrone, M. C., & Burr, D. C. (1988). Feature detection in human vision: a phase-dependent energy model. *Proceedings of the Royal Society of London, B*, *235*, 221-245.

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

Purushothaman, G., Patel, S., Bedell, H. E., & Öĝmen, H. (1998). Perceived spatial lag of flashed vs. moving lines varies with relative luminance and timing. *Investigative Opthalmology and Visual Science*, *39*(4), S1077.

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