



Temporal recruitment along the trajectory of moving objects and the perception of position

Bart Krekelberg ^{*}, Markus Lappe

Department of Zoology and Neurobiology ND7/30, Ruhr-Universität Bochum, 44780 Bochum, Germany

Received 6 May 1998; received in revised form 25 September 1998

Abstract

The trajectory of a moving object provides information about its velocity, direction and position. This information can be used to enhance the visual system's ability to detect changes in these parameters. We show that the visibility of the trajectory of a moving object influences the perception of its position. This form of temporal recruitment builds up on a long timescale of approximately 500 ms. Temporary occlusion of the trajectory during this time period reduces recruitment, but does not abolish it. Moreover, we found no spatial restrictions on recruitment on the scale of 10° of arc. When the position of objects on trajectories with different degrees of visibility are compared, this recruitment effect causes spatial offsets. This leads to a visual illusion in which the position of moving objects is misperceived. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Recruitment; Stroboscopic motion; Perceptual illusion; Alignment; Human visual psychophysics

1. Introduction

The information provided by the trajectory of a moving object influences the perception of velocity and direction as well as its detectability. In information processing terms, one can look upon this as demonstrating that the information about velocity, direction and position present in the history of a stimulus is used to enhance the perceiving system's performance. Consider for instance the perception of direction. Snowden and Braddick (1989a) found that the discrimination threshold for the direction of an apparent motion stimulus improves with increasing number of stations in a trajectory. A similar temporal recruitment was found for the discrimination of velocity (Snowden & Braddick, 1991) as well as the detection of a trajectory on a noisy background (Watamaniuk, McKee & Grzywacz, 1995). In all three cases trajectory-information is accumulated over time and used to enhance the observer's sensitivity. At the neural level this enhancement may be implemented by spatio-temporal interactions between neurons with their receptive fields along the trajectory.

A network of neurons with spatially separated receptive fields but similar direction selectivity and mutual facilitation, for instance, could enhance the detection of the direction of motion (Watamaniuk et al., 1995).

Here we will study temporal recruitment in the context of position perception. We will use temporal recruitment as a purely descriptive term for the effect of the history of a stimulus on the current percept. In other words, if the percept is influenced by more than the instantaneous stimulus, some form of temporal recruitment is present. This claim is independent of any hypotheses about the underlying mechanisms. The existence of temporal recruitment is not surprising given the long integration time of the visual system. In fact, an integration time on the order of 100 ms (Barlow, 1958) leads to a significant uncertainty in the position of fast moving objects. The fact that such objects are nevertheless perceived to occupy only a single position has been noted and investigated (Burr, 1980). Some authors have suggested that spatio-temporal interactions deblur the position of moving objects (Di Lollo & Hogben, 1985; Hogben & Di Lollo, 1985; Castet, 1994). In this view the activity of a current stimulus suppresses the activation corresponding to its previous positions. Such competitive interactions would suppress the inte-

^{*} Corresponding author. Tel.: +49-234-7004369.

E-mail address: bart@neurobiologie.ruhr-uni-bochum.de (B. Krekelberg)

gration mechanism and lead to the percept of a single crisp rather than smeared-out object. This process, called suppression of visible persistence, sharpens the perceiver's perception of position (for an alternative view, see Burr & Morgan, 1997). Purushothaman, Öğmen, and Chen (1998) recently suggested a model that uses spatio-temporal interactions to achieve deblurring. In our terminology, their model shows a possible mechanism underlying a form of temporal recruitment that leads to deblurring.

The examples above show that temporal recruitment exists in the perception of direction, velocity, and the detection of trajectories. In this paper we investigate the spatio-temporal properties of temporal recruitment in the perception of position. Nijhawan (1994) showed that a briefly flashed object is perceived behind a continuously visible, moving object at the same position. This *lag-effect* shows that seeing a trajectory leading to the current position affects the perception of the current position. Hence we refer to this as temporal recruitment in the perception of position. It is not known what mechanism is responsible for this form of temporal recruitment, but hypotheses based on motion extrapolation (Nijhawan, 1994), attention (Baldo & Klein, 1995) and temporal pooling (Lappe & Krekelberg, 1998) have been suggested. We will discuss these as well as some alternatives in Section 4.

In the first two experiments we show that recruitment is constrained by temporal rather than spatial factors and is limited to approximately 500 ms. This is in rough agreement with the limit on the improvement of trajectory detection found by Watamaniuk et al. (1995). In a third experiment we extend the analysis to trajectories which are visible only intermittently and determine the influence of the number of stations in the trajectory. We find that the effect of recruitment extends over multiple stations, but asymptotes at approximately four stations. In two further experiments we determine that this limitation is not spatial but temporal in nature: the recruitment in discontinuous trajectories is also limited by an horizon of 500 ms.

Our analysis extends the results and interpretation in Lappe and Krekelberg (1998) to a situation in which the number of stations in a trajectory is controlled. Some of these results have been presented in abstract form (Krekelberg & Lappe, 1998a,b).

2. General methods

2.1. Stimulus

We use a stimulus consisting of a set of seven dots that rotate about a fixed point (Baldo & Klein, 1995). The outer four dots are turned off after a short period of time while the inner three keep on turning. Khurana

and Nijhawan (1995) introduced this so called flash initiated cycles paradigm for the comparison of the position of static and moving objects. We extend this here to a set-up in which all dots move, albeit for varying durations. The results of Khurana and Nijhawan (1995) lead us to expect that the briefly shown outer dots should appear to lag behind the continuously visible inner dots (Fig. 1).

The lag-effect will be expressed as the angle between outer and inner dots (α in Fig. 1). To allow a comparison of the lag-effect at different velocities, we will also express the lag-angle as an equivalent delay, given by the lag-angle divided by the angular velocity.

The outer dots are shown on continuous or on interrupted trajectories. On a *continuous trajectory*, the outer dots move along with the inner dots for a specified duration at the onset of a stimulus. *Discontinuous trajectories* on the other hand show multiple subtrajectories of a specified duration, separated by an interflash interval. Unless otherwise mentioned the IFI is 140 ms. The number of subtrajectories is also referred to as the number of flashes. Note that, during these flashes, the outer dots rotate around the fixation point. This means that whenever both inner and outer dots are visible, their trajectories are identical.

The dots in the stimulus subtend 0.5°, the whole stimulus 11° of the visual field. The luminance of all dots is kept at 56 cd/m², the background of the screen 0.05 cd/m² (Minolta 1° luminance meter). Unless otherwise stated, the angular velocity is 30 rpm or 180 deg/s, clockwise. For the outermost dot this corresponds to a tangential velocity of 17° of *visual angle* per s, while the outermost continuously lit dot moves at 6 deg/s.

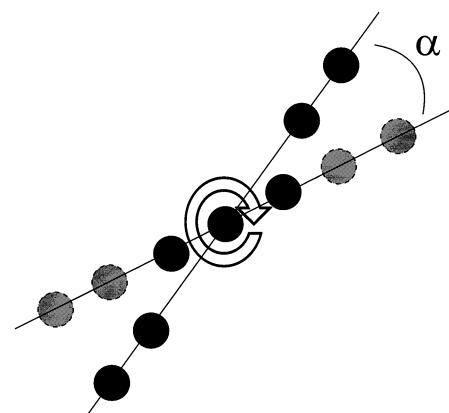


Fig. 1. The lag-effect stimulus, adapted from Baldo and Klein (1995). The inner three dots are continuously visible, whereas the two sets of two outer dots are briefly flashed. The whole stimulus rotates around its centre which is also the fixation point. The grey dots show the actual position of the flashed outer dots. The black dots represent the percept observers report. The angle α is referred to as the lag-angle.

2.2. Apparatus

Stimuli are 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 restricts the temporal resolution of the stimuli, but it is adequate for our purposes. Moreover, as we have shown in (Lappe & Krekelberg, 1998), the results with this set-up are comparable with those obtained with the continuous light of diodes.

2.3. Procedure

Participants are seated in a darkened room, in front of the monitor at a distance of 0.5 m. They are instructed to keep their heads in the same position and to fixate the centre of the screen, which coincides with the rotation axis of the seven dots.

Eye position is not monitored. Nijhawan (1997) reported that the lag-effect disappears when the participants pursue the moving objects with their eyes. As we do not record the eye movements in our experiments, this could influence our data. However, the inner dots are lit continuously in all experiments, pursuit should therefore be equally successful in all conditions. If occasional involuntary pursuit actually leads to a reduction of the lag-effect, this could at most reduce the overall lag-effect. We therefore expect no effect of imperfect fixation on the pattern of results we found.

An offset angle is introduced between the inner and outer dots under the control of an adaptive parameter estimation method. Participants indicate the percept of a lag or a lead by pressing left or right mouse buttons (2AFC). The next trial is started immediately after an answer has been given or, if the participant's attention lapses, after 7 s. In the latter case the missed trial is repeated at some later time in the same experiment. This guarantees a minimum of 25 repeats per condition per experiment. Within a single experiment the order of presentation of trials is randomised across all parameters.

2.4. Data analysis

To determine the perceived lag-angle we use an adaptive threshold estimation procedure based on a maximum-likelihood method (Harvey, 1986). The answers (lag or lead) are used on-line to determine the most likely psychometric curve representing this participants responses from a sigmoid family parameterised by a threshold a and a slope b : $e[b(x - a)]/(1 + e[b(x - a)])$. The maximum likelihood psychometric response curve is used to generate the next stimulus; the 25 and 75% points on the psychometric curve are chosen with equal probability. This method allows us to determine both

the point of subjective equivalence (PSE; the 50% point and in this parameterisation also the parameter a) and the slope of the psychometric function with reasonable efficiency. The slope is used off-line to estimate the confidence intervals for the threshold. If the confidence intervals extend beyond the parameterised region, the parameter estimation has failed. In such a case the experiment is repeated. If the same occurs again, the data are discarded. Non-convergence of the method in this way indicates that the percept is unstable. Such pruning was seldom necessary and is noted in the text.

The maximum likelihood method estimates the complete probability distribution of the lag-angle over a range of values. As such it automatically gives access to the confidence intervals of the thresholds. The 95% confidence intervals are used as errorbars in the figures showing the results of individual participants. In figures depicting the mean across participants, however, errorbars represent the standard error in the mean (± 1 S.E.), providing information about the variability across experiments and participants.

2.5. Participants

A total of 10 members of the department (including the two authors) participated in the experiments. Not all participants participated in all experiments.

3. Experiments

3.1. Flash duration

Temporal recruitment in the perception of position has been demonstrated by contrasting the perceived position of briefly flashed static objects with that of continuously visible moving objects (Nijhawan, 1994). We want to determine the influence of the duration of a trajectory. For this purpose, we compare the position of an object whose trajectory is visible infinitely long (i.e. until an answer is given) with one whose trajectory is cut short after a variable amount of time (duration). Changes in the perceived position between these objects are due to a process of recruitment that is not yet complete for the objects with a brief duration.

3.1.1. Methods

The stimulus described in Section 2 starts to rotate clockwise at 30 rpm from the horizontal position. Initially both the inner and the outer dots are visible, but the outer dots are turned off after a variable duration. Three participants performed three experiments each, resulting in 600 datapoints per participant; 75 repetitions per condition.

The lag-angle as a function of the duration is fitted to an exponential function with a least-squares method.

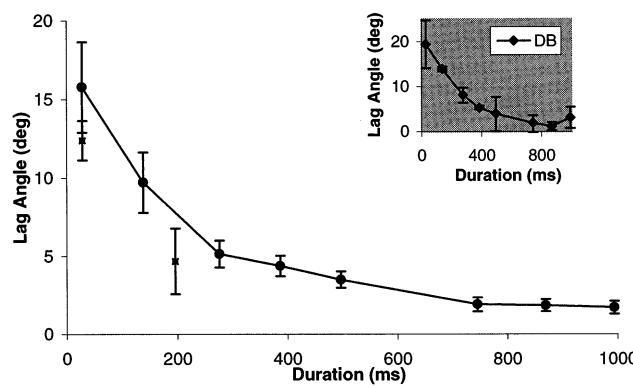


Fig. 2. The lag-angle as a function of the duration of the trajectory of the outer dots. The main figure shows the pooled data with errorbars representing ± 1 S.E. while the inset shows the data of a single experiment and a single participant. Here the errorbars signify the 95% confidence intervals as determined with the maximum likelihood method. The datapoints represented by squares stem from the experiment in Section 3.2 and are explained in Section 3.2.

The Pearson product moment correlation coefficient is determined as a measure of the goodness-of-fit.

3.1.2. Results

The lag-angle decreases exponentially when the duration of the trajectory increases. The lowest correlation in a single experiment was 0.88 while the correlation of the pooled data is 0.93. There is no sign of any discontinuity in this dependence. For durations above 500 ms, the outer and inner dots are seen at the same position (Fig. 2).

In our set-up an increase of the duration of the outer dots, inevitably increases the spatial extent of their trajectory. The next experiment determines which of these parameters is responsible for the increase in recruitment.

3.2. Velocity

To disentangle the influence of spatial extent and temporal duration of the trajectory, the angular velocity of the stimulus must be varied. Nijhawan (1994) found that, for the lag-effect between static and moving stimuli, the dependence on velocity was linear. He used this to argue in favour of the latency correction hypothesis (see Section 4). The current experiment extends these results to the velocity dependence of the lag-effect between moving stimuli with different trajectory durations.

3.2.1. Methods

Four participants performed an experiment in which three angular velocities (5, 15, 35 rpm) were combined with two durations of the outer dots (28, 196 ms). The outer dots were shown only once per condition. The six conditions were presented interleaved. Each participant repeated the experiment three times.

The datapoints at the lowest speed for the long duration and the highest speed for the short duration are chosen such that the spatial extent of the trajectory was identical.

Linear least-mean-squares regressions were performed on the individual participants' data as well as on the pooled data. Effects and interactions were tested with a standard two-way ANOVA.

3.2.2. Results

The pooled results are shown in Fig. 3. There is a significant effect of duration, speed as well as an interaction ($P < 0.05$). The dependence of the lag-angle on the velocity is highly linear for either duration: the Pearson correlation averaged over all participants is 0.95 ± 0.05 .

Moreover, the lag-angles for the datapoints with differing duration but identical spatial extent of the trajectory, are significantly ($P < 0.01$) different. From this we conclude that the temporal and not the spatial extent of a trajectory determines the recruitment effect for continuous trajectories. In an environment with trajectories of different temporal extent this effect will lead to spatial mislocalisation.

The linear dependence on velocity shows that the perceived position of an object whose trajectory is partially visible lags behind by an amount of $\delta \times \text{speed}$. Leaving open the interpretation of the parameter δ , we will refer to it as the (equivalent) delay (see Section 4.2). The equivalent delay is defined by the lag-angle divided by the velocity and can be determined from the slope of the velocity dependence curves. The experiment shows that, for a continuous trajectory, the equivalent delay is independent of velocity. This will be used in Section 3.5. The equivalent delays, determined from the individual participants' curves of the velocity dependence, are shown in Fig. 4. All participants show a significant decrease in equivalent delay associated with an increase in the duration of the stimulus ($P < 0.05$).

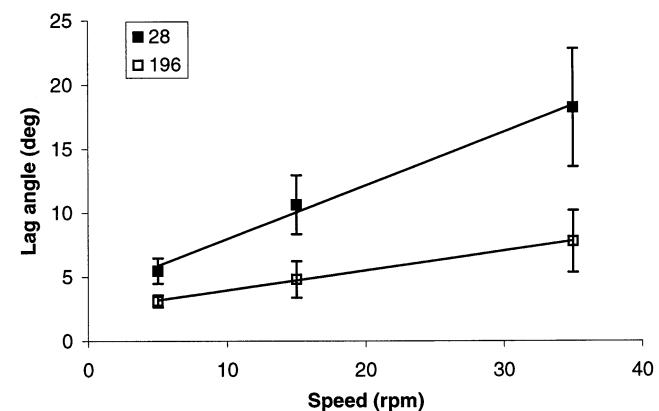


Fig. 3. The dependence of the lag-angle on the velocity for two durations of the trajectory of the outer dots (28 and 196 ms). The data are pooled across four participants. Errorbars represent the standard error in the mean of four participants.

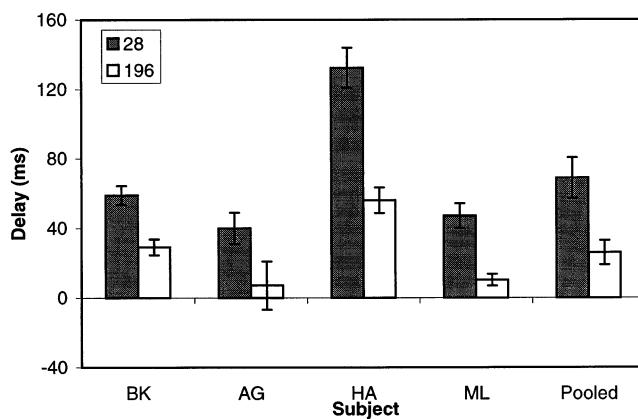


Fig. 4. The equivalent delays for two durations of the flashes. A longer duration leads to a reduced equivalent delay and hence a reduced spatial lag. Errorbars represent standard errors in the estimated regression slopes.

To see that the results are consistent over time and between experiments, one can calculate lag-angles from the equivalent delays measured in this experiment. These lag-angles can then be compared with the data in Fig. 2. For an angular velocity of 30 rpm, the incurred delay of 26 ms at a duration of 196 ms should lead to a lag angle of $0.026 \text{ s} \times 30 \text{ rpm} \times 6 \text{ deg/rpm} = 5^\circ$. Similarly, the 69 ms equivalent delay at a flash duration of 28 ms results in 12° of lag. These two indirectly calculated lag-angles are shown as squares in Fig. 2.

3.2.3. Discussion

These results extend the findings of Nijhawan (1994), who showed a linear velocity dependence of the lag between static and moving objects. Because a method of adjustment was used in those experiments, the percept was based on multiple flashes of the static object (at the same position). In our experiment participants see a single continuous trajectory of variable duration and both inner and outer dots move. In this experiment the lag can be ascribed uniquely to the duration of the trajectory.

Summarising the results of the experiments of Sections 3.1 and 3.2, we conclude that for continuous trajectories, a recruitment effect can be observed. This recruitment effect can be expressed in terms of an equivalent delay. This delay is independent of the velocity of the stimulus, but depends exponentially on the duration of a trajectory. The recruitment asymptotes for a trajectory duration of more than 500 ms.

3.3. Number of stations

The dependence on the duration of continuous trajectories is similar to the dependence we discussed in Lappe and Krekelberg (1998). There, however, the outer dots were repetitively flashed at a fixed interval

while the participants adjusted an offset angle to cancel the perceptual lag-effect. In that set-up we could not know how many flashes the participants saw, although we can be sure that they saw more than one. A comparison of the data shows that the lag-effect is generally much larger for a single flash (Fig. 2) than for a large number of flashes (Lappe & Krekelberg, 1998). This indicates that the recruitment effect may survive temporary interruptions of a trajectory.

In this section we investigate this. We want to determine whether the recruitment effect builds up, not only over a single continuously visible trajectory, but also when only fragments of a trajectory are visible.

3.3.1. Methods

Four participants perform an experiment in which the number of flashes is varied (1, 2, 3, 4, 10). Each participant performs the experiment three times, resulting in 75 datapoints per condition and a total of 375 datapoints per participant.

The stimulus starts to rotate clockwise from the horizontal position. The outer dots are shown for 28 ms, every 140 ms starting from $t = 0$. The inner dots are visible until an answer is given. After the specified number of stations has been shown, a red dot appears in the top-right edge of the screen to signal that a response can be made. Responses before the appearance of the red dot are ignored.

3.3.2. Results

The expectations based on a comparison of the data in Section 2 and the data in (Lappe & Krekelberg, 1998) are fulfilled. We find that recruitment summates over interrupted trajectories and becomes more efficient with a larger number of stations. For the spatial and temporal parameters used in this experiment, this summation saturates at approximately four to six stations: a further increase in stations no longer leads to a decrease in equivalent delay (Fig. 5).

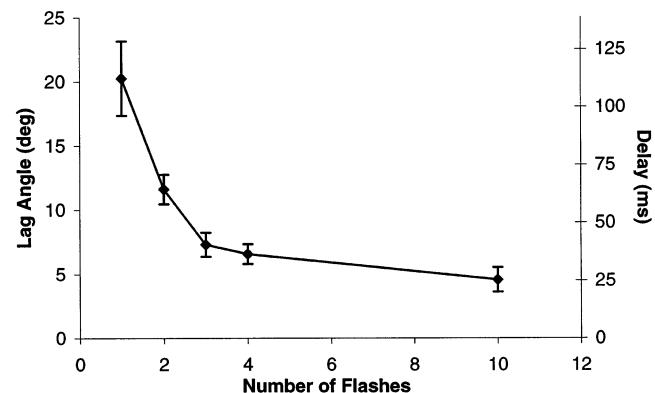


Fig. 5. Increasing the number of flashes reduces the perceived spatial offset. The axis on the right shows the equivalent delay of the flashed dots. The data are pooled across four participants.

The asymptotic value of the lag-angle corresponds to the situation where a brief flash is shown repetitively for a large number of times. This is roughly equivalent to using a method of adjustment to study the lag-effect as in (Lappe & Krekelberg, 1998). The fact that the lag-effect does not asymptote to zero shows that the summation over time is hampered by the interruptions in the trajectory. In (Lappe & Krekelberg, 1998) we showed that the fraction of time during which the trajectory is visible (visibility fraction) to a large extent determines the remaining lag-angle for a large number of flashes.

Even though answers received before the last flash, are not accepted by the computer, we cannot be sure as to the moment when the participants reach their decision about the answer. The participants are instructed, however, to look at the whole stimulus and only decide upon an answer when the red dot appears. The fact that a dependence on the number of dots is found, makes it likely that the participants indeed follow these instructions.

3.4. Limits of recruitment

Fig. 5 shows that the recruitment asymptotes well before ten flashes have been presented. We define the limit of recruitment as the number of flashes after which a further increase in flashes no longer significantly decreases the lag-angle. In our experiments this limit lies at approximately four flashes. In other words, information present in the first flash affects the perceived position in the fourth flash, but not the fifth flash. It is not clear, however, whether this limit is determined by the spatial range over which these four flashes were shown, the time between the last and the first flash of the motion trajectory, or the number of flashes. The next two experiments address this question.

3.5. Spatial limits

If the dependence on the number of flashes is in fact due to a spatial limit to the recruitment, an increase in speed for a high number of flashes will push some of the objects outside the recruitment region. In other words, a four-flash stimulus at high speed would effectively be a three flash stimulus. Fig. 6 illustrates this. The results in Fig. 5 show that such a decrease in the effective number of flashes should lead to an increase in the equivalent delay. This means that a spatial limitation to the recruitment predicts a velocity dependent equivalent delay. Such a dependence would show up as a non-linear dependence of the lag-angle on the velocity for a large number of flashes (see Fig. 3 for comparison). The current set-up, in which we can control the number of flashes the participants see, can test this hypothesis.

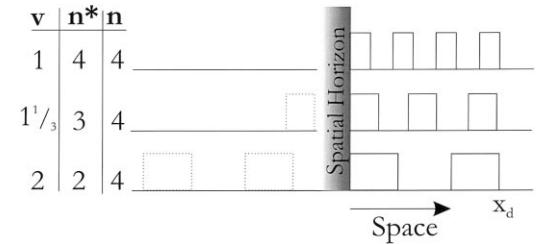


Fig. 6. The spatial horizon hypothesis. x_d is the position of the last flash in a stimulus sequence. Participants respond after the stimulus has been shown at this position. The first row shows the experiments of Fig. 5 with four flashes ($n = 4$): all four fall within the spatial horizon. By increasing the angular velocity (v), one of the flashes is moved over the horizon. The effective number of flashes (n^*) is now reduced to three. Note that space, not time is on the horizontal axis.

The following numerical example may clarify the argument. Seven flashes at 30 rpm cover nearly 11° of visual angle, while four flashes at 30 rpm go through 7° . The fact that the equivalent delay barely decreases from four to seven flashes (see Fig. 5) could be interpreted as showing that recruitment is limited to a spatial region of approximately 7° . When four flashes rotate at 50 rpm, only 2.7 flashes fall within this hypothetical horizon of 7° . According to Fig. 5 this should result in an equivalent delay of 41 ms: more than the equivalent delay of four flashes at 30 rpm (36 ms). In other words, if recruitment is limited spatially, a velocity dependent equivalent delay would be expected for multiple flashes.

3.5.1. Methods

The same four participants as in the previous experiment participated in an experiment in which four flashes were shown with variable angular velocity (5, 10, 15, 25, 35, 45, 50 rpm), duration 28 ms, IFI 140 ms. Data were pooled across participants.

3.5.2. Results

Contrary to the prediction of the spatial recruitment region the results in Fig. 7 show that the lag-angle

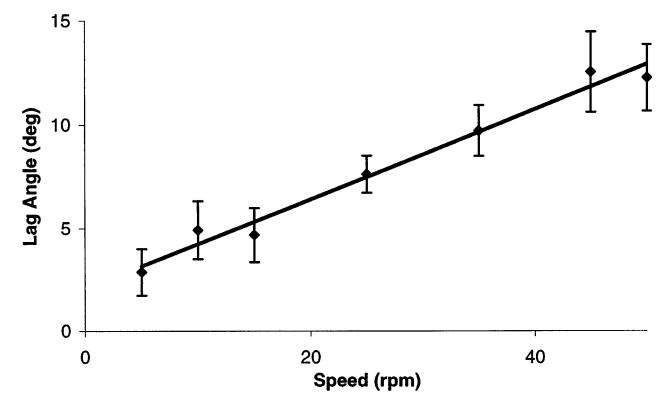


Fig. 7. The dependence of the lag-angle on the angular velocity when four flashes are shown. The slope of this curve represents the equivalent delay. The data are pooled over four participants.

depends linearly on the velocity. The mean of the (Pearson) R -squared over all experiments is 0.92 ± 0.04 . The (constant) slope of the curve represents the equivalent delay. The delay, as determined from Fig. 7 is 36 ms. This is the same as the equivalent delay measured for a stimulus with four flashes in the previous experiment (see Fig. 5). This allows us to conclude that the equivalent delay does not depend on the velocity and hence the dependence on the number of flashes cannot be explained by a spatially limited region of recruitment.

It is unlikely that stimuli at arbitrary large distances influence each other, hence there must be some spatial limitation to the recruitment effect. Our experiments only show that this limitation is larger than 10° of visual angle, the maximum extent of the trajectory of the four dots in this experiment. This already is a very significant spatial range; much wider than spatio-temporal interactions are often thought to span (Morgan & Watt, 1982). To test even larger spatial scales we would have to enlarge the radius of the stimulus. This not only moves the dots onto the peripheral retina, it also increases their tangential velocity. Both eccentricity (Baldo & Klein, 1995) and tangential velocity (Lappe & Krekelberg, 1998) have been shown to affect the lag-effect. Moreover, with highly eccentric outer dots, the participants find it difficult to determine whether the outer dots lag or lead the inner dots. A different stimulus geometry may be more suitable to determine the large spatial limits to recruitment.

3.6. Temporal limits

An alternative hypothesis for the limit to recruitment is that recruitment stops at four stations due to the long time period between the first and last station. In the experiment in Section 3.3 this time was 440 ms. If the recruitment were limited by a fixed temporal horizon, it should be possible to disrupt it by increasing the time between the flashes (interflash interval; IFI). This is analogous to the test we performed for the spatial hypothesis in Section 3.5. There we moved the dots over the hypothetical spatial horizon and showed that this had no effect. Here we investigate what happens when the dots are shifted over the hypothetical temporal horizon (see Fig. 8).

The numerical example of the previous section can be restated as follows. The time between the first and last of ten flashes with an IFI of 140 ms and a duration of 28 ms is more than 1 s. The time between the first and last of four flashes, however, is only 440 ms. The fact that the equivalent delay barely decreases from four to ten flashes (see Fig. 5) could be interpreted as showing that the recruitment is limited to a *temporal* region of approximately 440 ms. This would tally well with the finding that increasing the duration of a continuous

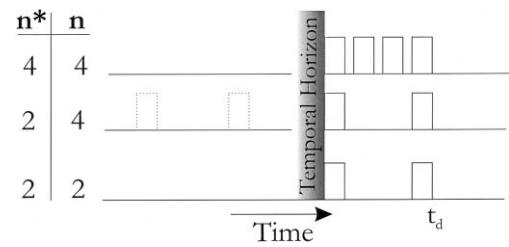


Fig. 8. The temporal horizon hypothesis. The top row shows the experiment whose results are described in Section 3.3. That experiment provides us with an estimate of the temporal horizon of approximately 440 ms. By increasing the IFI we can now present two rather than four flashes within this horizon. The middle row shows an experiment in which four flashes ($n=4$) are shown of which only two are within the horizon ($n^*=2$), the bottom row is the control experiment in which only two flashes are shown. Note that the stimuli represented by the middle and bottom row are identical inside the horizon.

trajectory beyond approximately 500 ms has no effect on the lag-angle (see Fig. 2). When the IFI of a four-flash stimulus is increased to 384 ms, only two flashes fall within the hypothetical horizon of 440 ms. If the temporal horizon hypothesis is correct, these two flashes should result in an equivalent delay of 64 ms (from Fig. 5). If, on the other hand, only the *number* of flashes is relevant, we expect a delay of 36 ms even with this extended IFI.

3.6.1. Methods

The temporal horizon estimated from Fig. 5 is used to generate stimuli with one, two or three flashes that are pairwise identical within the horizon. Seven participants perform this experiment, their results are averaged.

In order to test our hypothesis more stringently, we also determine the individual temporal horizons for three participants who performed the experiment in Section 3.3. We then present stimuli that are identical *within the temporal horizon* but not beyond (see Fig. 8).

Two participants have a recruitment limit of four stations; they can be tested on stimuli with one, two, or three flashes inside the horizon (and three, two or one beyond the horizon). One participant has a recruitment limit of three stations and can only be tested on stimuli with one or two flashes inside the horizon (and two or one beyond). The lag-effect for these stimuli is compared to lag-angles for stimuli with one, two, or three flashes inside the horizon and none beyond. The parameter n refers to the number of flashes shown, while n^* refers to the number of flashes inside the temporal horizon, which we call the virtual number of flashes.

Presenting these stimuli in a completely randomised fashion leads to considerable confusion in the participants. We therefore resort to presenting these stimuli in blocks in which the parameters (n, n^*) are kept con-

stant. Due to the randomised choice of 25 and 75% points on the best-fitting psychometric curve, participants are still not able to anticipate the next stimulus in the adaptive threshold estimation.

3.6.2. Results

The temporal horizon hypothesis predicts that the presence or absence of stimuli beyond the horizon is irrelevant. Hence, the lag-effect for stimuli with one flash in all (real 1) or one flash within the horizon but three beyond (virtual 1) should be the same. Fig. 9 shows examples of the individual results as well as the pooled data. Both agree with the temporal horizon hypothesis. The lag-angles for real and virtual number of flashes are not significantly different ($P > 0.05$). DB's data for a single flash (both virtual and real) had to be discarded for the reasons mentioned in Section 2.

We conclude that the perceived lag-angle only depends on the number of flashes within the temporal horizon and hence that the limit of recruitment over discontinuous trajectories is given by a temporal window of approximately 500 ms.

4. General discussion and conclusion

The visible trajectory of a moving object influences the perception of its position. The results of Nijhawan (1994) showed this by comparing the position of static to moving objects. We have extended this here to a comparison of objects whose motion trajectories have varying degrees of visibility. The main findings are that this recruitment takes place over a long timescale of approximately 500 ms. Temporary occlusion of the trajectory during this time period reduces the recruitment, but does not abolish it. Moreover, we have not

found any spatial restrictions on recruitment on the scale of 10° of the visual field.

The above summary is a description of what we, and others, have observed, not an interpretation of the possible underlying mechanisms. We devote the rest of this section to a discussion of the hypothetical mechanisms.

4.1. Latency correction

Nijhawan (1994) proposed that the lag-effect between static and moving objects is caused by a mechanism for latency correction. In this view, moving objects are predicted ahead along their trajectory to correct for the latency the signal must have incurred on its way from the eye to the retina. When comparing a moving and a static object, this leads to a spatial offset (the lag) because the moving object is seen where it is now rather than where it was 100 ms ago.

The fact that the equivalent delay as measured in Section 3.2 does not depend on the velocity has been used as an argument in favour of this view (Nijhawan, 1994). The equivalent delay between static and moving objects can, in this view, be interpreted as the signal latency that has been corrected. If this latency does not change with velocity, one would expect a constant equivalent delay or a linear dependence of lag-angle on the velocity, which has been found by (Nijhawan, 1994) and confirmed here. Moreover, the corrected signal latencies found in this way are of the right order of magnitude (20–100 ms) to correct for processing latencies in early cortical areas.

The latency correction hypothesis predicts that the amount of lag depends on the latency of the signal. To be precise, one would expect that an increase in the latency of the inner dots, would lead to an increase in

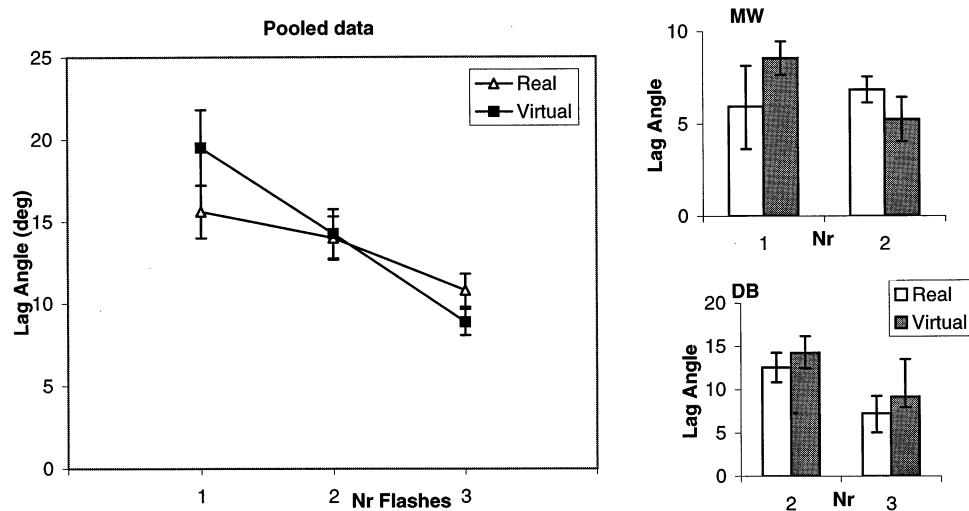


Fig. 9. A test of the temporal horizon hypothesis. The two figures on the right show the individual data for two participants, the figure on the left the results after pooling over seven participants. Flashes outside the temporal horizon have no significant ($P > 0.05$) influence on the lag-effect.

their forward prediction, hence an increase in the lag-effect. In (Lappe & Krekelberg, 1998) we tested this by reducing the luminance of the inner dots, which increases their latency (Roufs, 1963). The prediction of latency correction is not fulfilled. On the contrary, the lag-effect is *reduced* when the luminance of the inner dots is decreased (Lappe & Krekelberg, 1998).

This shows that latency correction in the strict sense cannot be responsible for the recruitment effect. Whatever mechanism is responsible for recruitment, it does not have access to accurate estimates of the latency of visual stimuli. The reduced hypothesis, that recruitment is due to prediction without explicit reference to the visual latency is explored in the next section.

4.2. Extrapolation

Given that the position of static objects is accurately perceived, the data of Nijhawan (1994) clearly show that the position of moving objects is extrapolated along their trajectory. In this statement extrapolation is used to describe a purely spatial relationship. Extrapolation, however, has the connotation that knowledge of the trajectory (such as its speed) is used to achieve this. In this section we discuss an extrapolation mechanism in this sense. Clearly, the value of such a mechanism would be that the animal could anticipate and therefore react more quickly to (predictable) changes in the environment. To obtain an estimate of the future position, an extrapolation mechanism would need to estimate the velocity of a stimulus and multiply this by some amount of time, the extrapolation period.

The linear dependence of the lag-effect on velocity (Nijhawan, 1994) shows that the extrapolation period of this hypothetical mechanism is independent of the velocity. This is confirmed in Section 3.2 for the lag-effect between two moving objects. Section 3.1, however, showed that the lag-effect between two moving objects depends on the duration of their trajectory. Moreover, Lappe and Krekelberg (1998) showed a similar decreasing dependence of the lag-effect on the temporal frequency of the stations in an stroboscopic motion sequence. There, we also showed that these two dependencies can be summarised as a dependence on the visibility fraction; the relative fraction of time that a trajectory is visible.

An extrapolation mechanism could explain this dependence on the visibility fraction in two ways. First, the velocity estimate used by the mechanism could underestimate the velocities of briefly shown objects. To explain the data in Fig. 2 the velocity estimates for the briefly shown objects would have to be underestimated by a factor of seven. (Snowden & Braddick, 1991) showed, however, that Weber fractions for velocity discrimination of trajectories with durations above 30 ms start at 0.5 but rapidly decrease to 0.06 for dura-

tions longer than 100 ms. Even though (Snowden & Braddick, 1991) used random dot patterns, we think this shows that it is unlikely that the perceived velocity was misjudged enough to change the extrapolation by a factor of seven. Moreover, the results of Katz, Gizzii, Cohen and Malach (1990) indicate that perceived speed *increases* when the duration of a trajectory is decreased.

If a misjudgement of the velocities of the two stimuli cannot explain the duration dependence of the lag-effect, then the prediction period must depend on the duration of the trajectory. This is peculiar. Given the purported behavioural advantage of extrapolation, why would an extrapolation mechanism reduce the period over which it extrapolates when less of the trajectory becomes visible? Although peculiar behaviour is not evidence against a mechanism, it seems likely that the smooth dependence of the lag-effect on low level properties of trajectories points to a low level explanation of the lag effect.

4.3. Attention

An attentional hypothesis for the lag-effect was put forward by Baldo and Klein (1995). They hypothesised that briefly shown, static dots were delayed in their perception with respect to the moving dots. During this delay, the moving dots would move on, which would cause a spatial lag. The underlying cause of this delay was thought to be attentional in nature. The effect can then be interpreted as a variant of the Fröhlich effect: a suddenly appearing object needs time to reach awareness (Müsseler & Ascherleben, 1998). To support this link with attention, however, one would have to show that the time to awareness depends on parameters such as duration and frequency in the way we have shown here. Moreover, one would expect an interaction of the lag-effect with the classical attentional paradigms such as pop-out in visual search. Reportedly this has not been found (Khurana, Cavanagh & Nijhawan, 1996).

4.4. Facilitation along a trajectory

An explanation along the lines of (Baldo & Klein, 1995), but without reference to attentional processing, is that the outer dots in Fig. 1 have a longer visual latency. Such an increased visual latency would lead to a spatial offset with the inner dots due to the fact that the inner dots keep on turning while the outer dots have not been processed yet.

An increase of the visual latency for shorter durations, however, would seem inconsistent with the properties of single cells in cat V1 (Duysens, Gulyás & Maes, 1991). A possible alternative is that the latency of the inner dots is decreased due to a form of facilitation along the trajectory. Allik and Kreegipuu (1998) presented evidence that could support this view. They

showed that the reaction time for the detection of the direction of motion decreases when a two-station apparent motion sequence is perceived as real motion. In their set-up this was the case when the two stations were presented within 60 ms of each other, but not with an IFI of 600 ms. One could hypothesise that the first station of the 60 ms apparent motion sequence facilitated the processing at the second station. Such facilitation was absent in the 600 ms sequence because the second station was beyond the temporal horizon. To support this hypothesis, it would be interesting to see whether an increase in the number of stations within the temporal horizon leads to a further decrease of the reaction time in the experiment of Allik and Kreegipuu (1998). This would supplement the finding of Snowden and Braddick (1989b) who showed that the detection threshold for the direction of motion decreased with the number of stations. The hypothesis of 'facilitation along a trajectory' predicts that the direction should not only be detected more easily, but also more rapidly.

Baldo and Klein (1995) showed that the lag-effect increases when the outer dots are moved to a more eccentric position. Within the facilitation framework this could be interpreted as showing that the facilitation is reduced in the periphery. To test this directly, the experiments of Allik and Kreegipuu (1998) could be repeated at different eccentricities.

Arguments against a process of facilitation are that the interactions would have to operate on a much larger spatial scale than hitherto assumed possible. If there indeed is a form of facilitation over a range of many degrees of arc (as would follow from Section 3.5), one would expect this to show up in processes of spatio-temporal interpolation. Good interpolation, however, is generally assumed to be restricted to scales on the order of minutes of arc (Fahle & Poggio, 1981; Morgan & Watt, 1982).

4.5. Temporal pooling

All experiments considering the lag-effect and its variants, measured the perceived distance between objects. In Lappe and Krekelberg (1998) we proposed that the lag-effect is the consequence of a temporal pooling process that determines the perceived distance between moving objects. For objects that have disappeared, this pooling process is hypothesised to have access to a position signal that persists at the last visible position.

Nijhawan (1994) discarded an explanation along these lines based on the finding that participants perceive a lag-effect at strobe-onset: when the flashed and the moving object are turned on (the flash-initiated cycles paradigm). If the percept were formed and measured at strobe-onset, this would indeed be evidence against a role for the persistence of a position signal. It seems obvious though that it takes time before the

distance percept reaches awareness. During this time an averaging process along the lines described in Lappe and Krekelberg (1998) could operate. This is confirmed by the experiments in Section 3.1 which show that the percept is influenced by visual stimuli up to 500 ms after stimulus onset. Note that this does not require *visible* persistence of the stimuli for 500 ms. The close fits of data and a model based on persistence of the position signal in Lappe and Krekelberg (1998) are promising, and further work extending this is currently in preparation.

Concluding, we established that a recruitment process operates along the trajectory of moving objects in the perception of position. It is not entirely clear, however, which mechanisms underlie this phenomenon. Even though further experimental as well as theoretical work is clearly required, we believe that an explanation can be based on purely low-level spatio-temporal interactions between the representations of the stimuli.

Acknowledgements

We thank Maike Warnstedt and Daniela Bonacker for their diligent help with the experiments.

References

- Allik, J., & Kreegipuu, K. (1998). Multiple visual latencies. *Psychological Science*, 9, 57–60.
- 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., & Morgan, M. J. (1997). Motion deblurring in human vision. *Proceedings of the Royal Society of London, B*, 264, 431–436.
- Castet, E. (1994). Effect of the ISI on the visible persistence of a stimulus in apparent motion. *Vision Research*, 34, 2103–2114.
- 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.
- Harvey Jr., L. O. (1986). Efficient estimation of sensory thresholds. *Behavior Research Methods: Instruments and Computers*, 18, 623–632.
- Hogben, J. H., & Di Lollo, V. (1985). Suppression of visible persistence in apparent motion. *Perception and Psychophysics*, 38, 450–460.
- Katz, E., Gizzii, M., Cohen, B., & Malach, R. (1990). The perceived speed of an object is affected by the distance it travels. *Perception*, 19, 387.
- Khurana, B., Cavanagh, P., & Nijhawan, R. (1996). Are moving objects corrected or flashed objects attentionally delayed? *Investigative Ophthalmology and Visual Science*, 37, 529.

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

Krekelberg, B., & Lappe, M. (1998). Position of stroboscopically moving objects: lag and lead effects in the perception of motion. *European Journal of Neuroscience*, 10(10), 259.

Krekelberg, B., & Lappe, M. (1998b). Temporal recruitment in the localisation of stroboscopically moving objects. *Society for Neuroscience Abstracts*, 24, 1399.

Lappe, M., & Krekelberg, B. (1998). The Position of Moving Objects. *Perception* (in press).

Morgan, M. J., & Watt, R. J. (1982). Effect of motion sweep duration and number of stations upon interpolation in discontinuous motion. *Vision Research*, 22, 1277–1284.

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

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

Nijhawan, R. (1997). Visual decomposition of colour through motion extrapolation. *Nature*, 386, 66–69.

Purushothaman, G., Öğmen, H., & Chen, S. (1998). Motion deblurring in a neural network model of retino-cortical dynamics. *Vision Research*, 38, 1827–1842.

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

Snowden, R. J., & Braddick, O. J. (1989). The combination of motion signals over time. *Vision Research*, 29, 1621–1630.

Snowden, R. J., & Braddick, O. J. (1989). Extension of displacement limits in multiple-exposure sequences of apparent motion. *Vision Research*, 29, 1777–1787.

Snowden, R. J., & Braddick, O. J. (1991). The temporal integration and resolution of velocity signals. *Vision Research*, 31, 907–914.

Watamaniuk, S. N., McKee, S. P., & Grzywacz, N. M. (1995). Detecting a trajectory embedded in random-direction motion noise. *Vision Research*, 35, 65–77.