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A model of the perceived relative positions of moving objects based upon a slow averaging process

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Abstract

We extend the local energy model of position detection to cope with temporally varying position signals and the perception of relative position. The extension entails two main components. First, a form of persistence for the position signal based on the temporal impulse response function of the visual system. Secondly, we hypothesise that the perceived relative position of two objects is determined by a slow average of the difference of the objects' position signals. The model explains why briefly flashed static dots are perceived to lag behind continuously visible moving dots, without the need for a motion extrapolation process [Nijhawan, R. (1994). *Nature*, *370*, 256–257]. The dependence of this illusion on parameters such as the velocity, duration, frequency and number of flashes of the motion trajectories is accurately captured by the model. Furthermore, the model makes two predictions. First, briefly flashed dots on a staircase trajectory should lead dots with a long duration. Secondly, it should be possible to abolish the lag-effect between continuously visible and stroboscopically moving objects by halting the continuously visible dots during the interflash interval of the stroboscopic dots. Both predictions are corroborated in experiments.

Keywords: Local energy; Perceptual illusion; Visual psychophysics; Model; Visual motion; Motion extrapolation

1. Introduction

The perception of position is a basic building block for the construction of visual percepts. Many known properties of the visual system, however, could contribute to an uncertainty in the position of moving objects. Consider for instance the long ($\sim$120 ms) integration time of the visual system; although this is useful when trying to detect faint objects (Barlow, 1958), for moving objects it could lead to a smearing of the position. The variability in the latency of the visual system introduces further uncertainty. A reduction of the luminance of an object, for instance, increases the visual latency. Because objects move during the latency period, perceived position at some time t could depend on the latency. Under some circumstances, this shift of the position due to a reduced luminance can indeed be observed (Pulfrich, 1922).

The perceived position of moving objects has recently been the subject of a large number of experiments. Nijhawan (1994) quantified MacKay's stroboscopic illusion (Mackay, 1958) and showed that moving and static objects presented at the same retinal location at the same time are not perceived at the same position. Assuming that the position of static objects is accurately perceived, this so called flash-lag illusion has been interpreted as a misperception of the position of the moving dots.

Nijhawan (1994) interpreted the lag-effect as the result of a process of motion extrapolation. He hypothesised that the visual system uses the predictability of the path of moving objects to correct for the latency the signal must have incurred on its way to cortex. This would allow observers to perceive the object where they are 'now' rather than where they were some 80 ms ago. In Lappe and Krekelberg (1998) we showed that, given the influence of luminance on the lag-effect, an accurate process of latency correction cannot be responsible for the lag-effect. This, however, still left the possibility that the position of moving objects is extrapolated to

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some constant degree (i.e. independent of the visual latency of the signal). In a purely geometric interpretation this certainly is the case; given that the static object is seen at the (correct) retinal position, the lag-effect shows that the moving object's position is extrapolated along the motion trajectory. The word 'extrapolation', however, has a further connotation: it suggests that a mechanism estimates the objects' trajectory and uses this information to predict its future position. We disagree with the latter interpretation.

As we have pointed out in Lappe and Krekelberg (1998), there is no logical necessity to interpret the lag-effect as a mislocalisation of the moving dots. The alternative interpretation acknowledges that all flash-lag experiments of Nijhawan (1994), Baldo and Klein (1995), Khurana and Nijhawan (1995) and Lappe and Krekelberg (1998) provide access to the distance subjects perceive between static and moving objects, not their individual positions. In earlier work, the perception of distance between moving objects has been studied with a Vernier alignment method in which two lines in stroboscopic motion are phase-shifted. That is, one of the Vernier lines is delayed with respect to the other. The main finding has been that brief temporal offsets are perceived as spatial offsets (Morgan, 1980; Morgan & Watt, 1982). When the two lines are presented dichoptically, the spatial offset results in a disparity offset and a percept of stereoscopic depth (Burr & Ross, 1979; Morgan, 1979). When the time and distance between successive stations in the stroboscopic motion sequence are small enough, the spatial offset equals the distance the object would have travelled during the temporal delay. In other words, the object is seen at the position where it would have been if it were in continuous motion. This led to the proposal that the offset is due to a process of spatio-temporal interpolation (Morgan, 1979). Fahle and Poggio (1981) and Morgan and Watt (1983) have shown that spatio-temporal interpolation is perfect for small stimuli on trajectories with inter-flash intervals less than 30 ms and a spatial separation of the stations less than 4 min of arc. Although spatial blurring can increase the temporal limits of integration (Burr, 1981; Fahle & Poggio, 1981), the trajectories we consider fall outside this range and are at best partially interpolated. Our results are therefore complementary to those obtained with the (dynamic) Vernier method and show what happens to the position signal when interpolation fails.

In previous work (Lappe & Krekelberg, 1998; Krekelberg & Lappe, 1999) we have shown that the perceived relative position of moving objects depends on their trajectory over a time window of approximately 500 ms. The fraction of time during which the trajectory is visible was shown to be the most important factor. The fact that the overall visibility fraction rather than the precise make up of the trajectory is relevant, led us to hypothesise that a temporal averaging process underlies these effects. In this paper we wish to quantify this hypothesis. We present a model of the perception of distance based upon existing models of position perception, combined with data on the temporal impulse response function of the visual system and our averaging hypothesis.

Section 2 presents the details of a model of relative position perception that includes spatial and temporal interactions. When describing the performance of the model we will often refer to experimental data. Details of the experimental methods can be found in Lappe and Krekelberg (1998) and Krekelberg and Lappe (1999), but see also Section 4.2. We discuss the model's properties and show that a computer simulation reveals stimulus-parameter dependencies that closely match those found in the experimental data. In Section 3 we make two simplifying assumptions which allow us to derive an analytic expression of the relation between perceived distance and the spatio-temporal properties of the stimuli. We use this analytic model to fit the three free parameters of the model to the experimental data. The close fit we find supports our averaging hypothesis which we can now state as: 'perceived distance is based on an averaging period on the order of 600 ms.'

In Section 4 we report on two experiments that test the model. First, the model predicts that of two objects on a staircase trajectory, the one with the briefer duration will lead in front of the other. This prediction is confirmed. In a second experiment we directly test the assumption that position signals of temporarily occluded objects persist at the last seen position. This assumption is also confirmed by the data.

2. Model

To compute the distance between two objects an algorithm first has to determine the positions of the individual objects. In a further stage these signals need to be compared. The possible mechanisms of the first stage of this process have received a considerable amount of attention in the vision literature. Two main views have emerged. Marr and Hildreth (1980) and Morgan and Watt (1983) have propounded the view that the position of an edge is determined by the zero-crossing of the spatially filtered luminance distribution. When a difference of Gaussians filter is used, this roughly corresponds to the maximum change in luminance. This is rather intuitive and almost seems a definition of an edge. One should be aware though that the definition of the position of an edge need not corresponds to the perceived position of an edge.

The alternative view, developed by Morrone and Burr (1988), states that the position of edges and lines

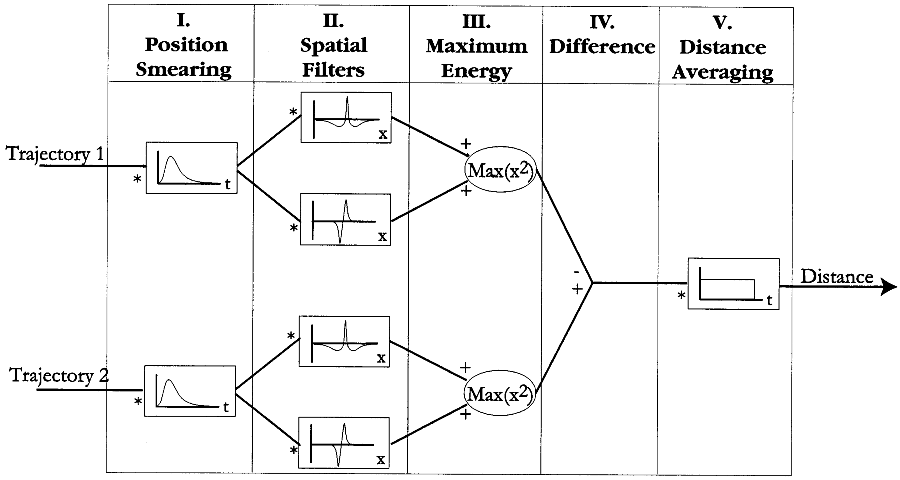

Fig. 1. The model. Input signals representing the retinal luminance distribution of two objects enter on the left. The signals are convolved with a temporal filter (stage I), then by two spatial filters in quadrature (stage II). The filter outputs are summed and squared. The location at which this filtered signal is maximal corresponds to the location of the object (stage III). To obtain a measure of the perceived distance, the positions are subtracted in stage IV and this difference is averaged over time in stage V. The signs next to the arrows denote the operation taking place in that module (*, convolution; +, −, ×, addition, subtraction and multiplication). See Appendix A for mathematical details.

corresponds to those positions where the local energy in the luminance distribution reaches its maximum. The local energy is a non-linear function of the luminance distribution, which makes its interpretation less intuitive. Calculations of the local energy distributions of simple luminance patterns, however, show that peaks in the energy correspond to edges or lines (Morrone & Burr, 1988). The psychophysical evidence presented by Morrone and Burr (1988) showed that the local energy definition of position corresponds more closely to perceived position than the zero-crossing definition. Based on this, and the smoothness of the local energy, which makes the computation of position easier, we have chosen the local energy model as the position component in our model. As it turns out, however, the differences between the models of edge detection leave many of our results unaffected.

Morrone and Burr (1988) applied their model to the perception of long duration, static stimuli. Therefore, there was no need to take the temporal response of the visual system into account. For moving or briefly flashed stimuli, however, the influence of the temporal response of the visual system is crucial, as has been shown by Morgan and Watt (1983). Similar to the model of Morgan and Watt (1983), we therefore precede the local energy calculations with a temporal low pass filter. This can be thought of as a persistence of the activity representing the position of a stimulus after that stimulus is extinguished. The position of an object is re-defined as the location of the maximum in the local energy after the temporal low-pass filter. We will refer to this localisation model as the extended local energy model.

Fig. 1 shows the hypothesised algorithm as a block diagram. A mathematical description of the model can be found in Appendix A. In the block-diagram processing flows from left to right. In stage I a luminance distribution is temporally low-pass filtered (appendix, Eq. (1)). Then, the signal is filtered spatially by two difference-of-Gaussians filters in quadrature (stage II, Eq. (3)). Stage III determines the local energy by squaring and summing the filtered signals. The position of an object is the location where the local energy attains its maximum (Eq. (4)). The localisation part (stages I–III) of the model is completely specified by the parameters of the spatial and temporal filters.

Intuitively, the scale parameter α of the spatial filter determines the range over which stimuli can interact. Morrone and Burr (1988) used four spatial scales for their model, but, given the size of our stimuli, we will focus our attention on a model with a single spatial scale: $\alpha = 1$ cpd. The temporal filter (Eq. (2)) is determined by the time-constant β, and gain g, which Roufs and Blommaert (1981) measured as 12 ms and 0.7, respectively. Unless otherwise mentioned we use these values in the model simulations.

The calculation of perceived distance or relative position of objects has received little attention. Presumably, the reason for this is that the computation seems trivial; need one not only determine the difference between the positions, as shown in stage IV in Fig. 1? For static objects, we know of no evidence to the contrary, but the distance between static and moving (Nijhawan, 1994; Baldo & Klein, 1995; Khurana & Nijhawan, 1995) or between two moving objects (Bachmann & Kalev, 1997; Lappe & Krekelberg, 1998; Krekelberg & Lappe, 1999) is not given by the difference in their

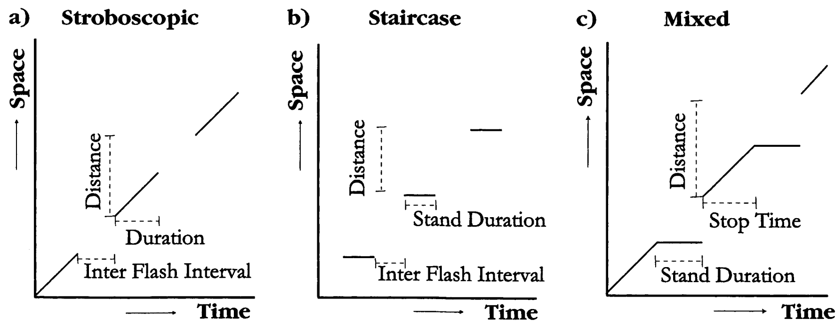

Fig. 2. (a) Definition of the parameters of stroboscopic motion trajectories. (b) Definition of staircase motion trajectories. (c) Definition of mixed staircase and stroboscopic trajectories. Solid lines show when and where the stimuli are visible.

perceived instantaneous positions calculated by either of the position models suggested above. This follows from calculations of model trajectories we performed (not shown), but it can also be deduced from the trajectories shown in (Morgan & Watt, 1983, Fig. 13). Moreover, it seems clear that the 500 ms recruitment effect discussed in Krekelberg and Lappe (1999) cannot be explained by means of a temporal impulse response function with a time-scale on the order of 12 ms.

The simplest hypothesis that makes the perception of relative position dependent on the trajectory is that the perceived distance is the temporal average of the difference in position. This hypothesis is implemented in stage V of the model (Eq. (5)). A similar averaging hypothesis was discussed but not formalised by Morgan (1977) as an explanation of the Pulfrich effect. In this paper we discuss in detail how this hypothesis is able to explain perceived distance.

2.1. Methods

The trajectories of the objects whose distance we wish to determine play an important role in the model as well as in the experiments of Section 4. Therefore, we briefly summarise the definitions and the parameters as we will be using them. Non-smooth motion trajectories consist of stations. The stimuli are shown at successive stations separated by a *period* of time, which leads to a presentation- or flash-frequency = 1/period. Furthermore, objects in stroboscopic motion move visibly and smoothly for a specific flash-*duration*, then disappear for a certain *inter-flash interval* (IFI, see Fig. 2a). The sum of duration and IFI equals the period. For staircase trajectories, which are shown in Fig. 2b, motion is always in jumps. The objects stand still for a specific *stand duration*, followed by a period of invisibility (IFI), then a jump to the next position. On a mixed staircase-continuous trajectories, finally, the object is visible all the time, but, in a single period it moves only until *stop-time*, after which it stands still for stand duration (Fig. 2c). Spatially, the parameter *distance* refers to the distance between stations in the sequence.

In the simulation model we implement the averaging hypothesis as follows. A fixed number of stations of a stroboscopic motion trajectory with a particular duration and frequency are calculated by the extended local energy model. Next, the difference between this trajectory and a trajectory which is continuously visible is determined and averaged over the whole simulated period of time. This means that we assume that the averaging period encompasses the whole trajectory. The calculated average is interpreted as the model equivalent of the perceived distance.

The model is implemented in Matlab. Stimuli are simulated on a spatio-temporal grid with a small enough resolution (dx, dt) such that a further decrease of the gridsize has no significant influence on the calculated trajectories. The model implements one-dimensional spatial filters only and as such can only deal with one-dimensional stimuli. To extend the model to two-dimensions we would not only need more extensive computational resources, but also a detailed knowledge of the structure of the two-dimensional spatial filters (see Section 3). Unless otherwise mentioned, a stroboscopic motion trajectory of five stations was simulated and the speed of the objects was kept constant at 15 degrees of the visual field per second.

2.2. Results

When comparing stroboscopic to continuous trajectories, we find that the objects in stroboscopic motion lag behind. Hence, a correlate of the experimental lag-effect exists in the model. Section 2.2.1 shows that the dependence of the model-lag on the stimulus parameters (velocity, duration and frequency) is similar to that of the experimental lag-effect. Section 2.2.2 investigates the dependence of the model lag on the model parameters α and β, as defined in Eqs. (2) and (3).

2.2.1. Stimulus parameter dependence

Nijhawan (1994) showed that the lag-effect depends linearly on the angular velocity of the stimuli. He used

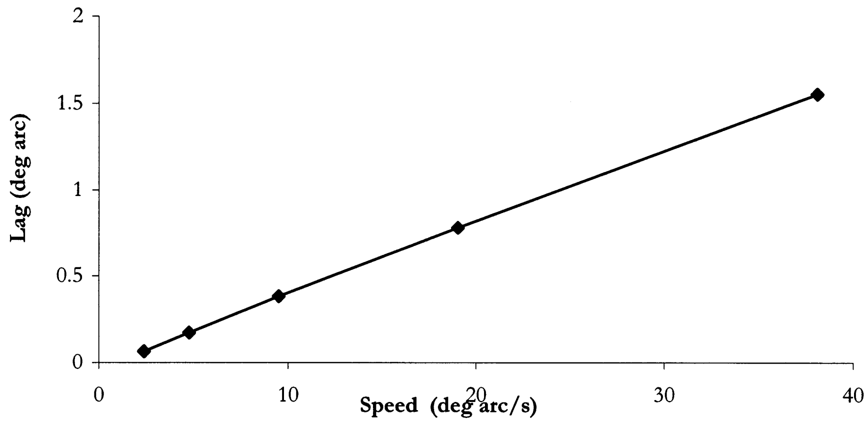

Fig. 3. Velocity dependence in the model. The lag-effect increases linearly with the velocity of the stimulus.

this as an argument in favour of the latency correction hypothesis: if the continuously visible, moving dots are extrapolated in time to correct for their (constant) latency, an increase in their velocity should lead to a linearly increased extrapolation. This should be observable as a lag-effect that increases linearly with angular velocity.

The duration and frequency are constant at 14 ms and 24 Hz, respectively. Fig. 3 shows the dependence of the retinal lag on the velocity. This highly linear dependence shows that the linear velocity dependence found in experiments need not be a consequence of latency correction.

In the experiments discussed in detail by Lappe and Krekelberg (1998), the frequency and duration of the stations in the stroboscopic motion sequence were varied. This had a significant influence on the perceived distance between moving objects; the distance decreased when more of the trajectory became visible. We test whether this behaviour is found in the model as well.

First, the frequency was varied from 2 to 32 Hz, while the duration was kept at 28 ms. Secondly, the duration was varied from 56 to 450 ms, while the frequency was 2 Hz. Fig. 4 shows that the model lag-effect rapidly decreases when more of a trajectory becomes visible with either a longer flash-duration (Fig. 4a) or a higher flash-frequency (Fig. 4b). The time-constant of the decrease with duration is approximately 500 ms. The maximum frequency for which an effect can still be observed is 30 Hz, this is somewhat higher than the 16 Hz asymptote we found in experiments (Lappe & Krekelberg, 1998, Figs. 4 and 6).

2.2.2. Model parameter dependence

In the original local energy model of Morrone and Burr (1988), four spatial filters were used rather than the single one we use. To investigate the possible influence of the other spatial filters, we run simulations in which the filter parameter α is varied over the range $\alpha \in [0.25-2]$ cpd. Fig. 4a shows that, for high frequencies, the lag increases slightly with α. Over the simulated range, however, the effect is smaller than 0.1 degrees of arc.

The relatively small effect of α is a consequence of the fact that most stations in the trajectories we studied are separated by far more than the range of effective spatial interpolation. In other words, as far as these trajectories are concerned, the spatial filters operating in human vision are effectively delta functions. Trajectories for which spatial-interpolation is negligible will be called 'wide' trajectories and figure prominently in Section 3. The simulations show that the influence of α is small even when the successive stations of the trajectories are near enough to cause spatial interactions (high frequency or long duration trajectories). This is presumably due to the non-linear way in which position is determined in the local energy model: spatial interactions lead to spatial spreading of the signal, but this does not affect the position of the maximum in the energy in this simple stimulus.

The parameter β, the scale of the temporal impulse response function, has a somewhat larger influence on the calculated lag. Fig. 5 shows the results of simulations in which duration and frequency were varied over the same range as in Fig. 4, but now for three values of β, while α was kept at the standard value of 1 cpd. An increase in the time-scale β leads to a small decrease of the lag-effect for low frequencies (at all durations), but an increase for higher frequencies. These effects are due to the fast rise and slow fall of the temporal impulse response function. Even though the effects are small, they can lead to measurable perceptual effects, as shown in Section 4.

2.3. Discussion

The simulations show that the model captures the essential properties of the data: a linear velocity dependence, and an exponential decay of the lag-effect with duration and frequency that saturates near 500 ms and

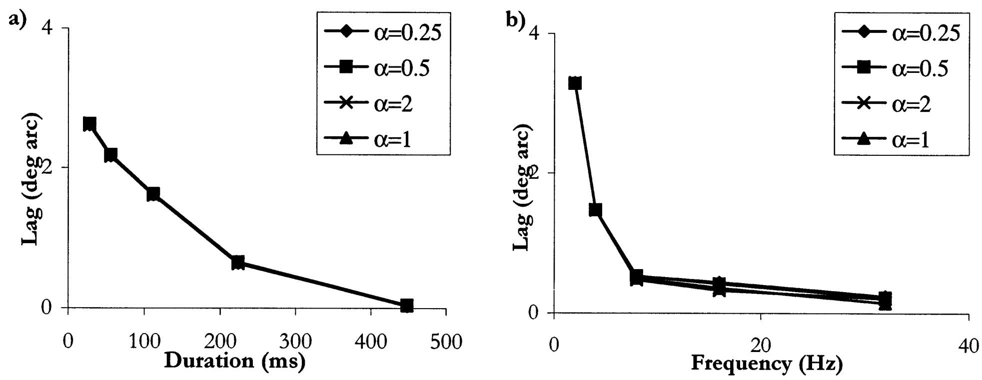

Fig. 4. Distance between objects calculated by the model as a function of stimulus parameters. (a) The influence of the flash-duration: asymptote near 500 ms. (b) The role of the flash-frequency; exponential decrease to an asymptote near 30 Hz. The (partially overlapping) curves show the minimal influence of the spatial-scale α on the calculated lag-effect (see Section 2.2.2).

30 Hz, respectively. These particular numbers depend somewhat on the temporal filter parameter β, but not on the spatial filter parameter α.

It should be noted that Figs. 3 to 5 show the model lag in degrees of the visual field as a function of the stimulus parameters. This lag is between two objects moving in one dimension. The figures in, for instance, (Lappe & Krekelberg, 1998) report the lag in terms of degree of orientation between two objects on a two-dimensional trajectory (see Fig. 12 for an example of the stimulus we used). Consequently, the absolute sizes of these lags cannot be compared. When we compare data to the simulation model, we can only compare the way in which the lag-effect depends on the stimulus parameters. To overcome this limitation, the next section uses the finding that the spatial interactions are unimportant for wide trajectories. This allows us to derive a simplification of the model, which can be applied to two-dimensional trajectories and makes a direct comparison of data and model feasible.

3. Restriction to wide trajectories

Most experiments in (Lappe & Krekelberg, 1998; Krekelberg & Lappe, 1999) used trajectories in which the spatial interactions among flashed objects was negligible. In the sense defined above, the trajectories were wide. For such retinal trajectories the model predicts position trajectories of a staircase shape. As long as the object is visible, the position trajectory will follow the retinal trajectory, albeit with some delay. When the object disappears, however, the position signal will persist at the last seen position. In other words, the position signal of the objects in stroboscopic motion is a combination of smooth trajectories combined with staircase parts (see Fig. 6).

Formally, this result can be obtained by assuming that the objects in our experiments are sufficiently small to avoid spatial interactions between their representations, even after temporal smearing. In such a model without spatial interactions the difference between a one-dimensional model and a two-dimensional model disappears. To describe our experimental data we merely frame the model in terms of angular coordinates. In other words, we assume that the mechanism that calculates the perceived distance has access to the angle at which an object is seen. For the task our subjects perform, such coordinates seem to be the natural ones (see Fig. 12). In these coordinates, the retinal input signals can be written as in Eqs. (6) and (7). Setting the spatial filters to delta-functions then allows us to derive an analytic expression for the perceived distance (Eq. (8)).

We introduce the parameter Δ to denote the time over which the average position difference is calculated. In the simulation model of Section 2 we effectively assumed that Δ is large enough to contain all of the simulated trajectory. Owing to the reduced complexity of the analytic model, we can now leave Δ as a free parameter. The aim of this section is to estimate this parameter from the experimental data. Two additional parameters are introduced. First, a scaling parameter γ that simply translates the numbers in the model to the appropriate experimental units. The setup of some of our experiments requires that we introduce a third parameter. As described in Krekelberg and Lappe (1999), subjects viewed a variable number of stations in the trajectory of the outer dots in Fig. 12. Then a go-signal appeared which informed the subjects that they were now allowed to answer the 2AFC question: 'did the outer dots lag or lead?' We assume that the subjects' answer was based on the distance percept at some point after the go-signal. How long after the go-signal, we do not know. As it seems reasonable that this time is not zero, however, we introduce the free parameter τ that allows us to fit these experimental circumstances. Note however that this parameter is not

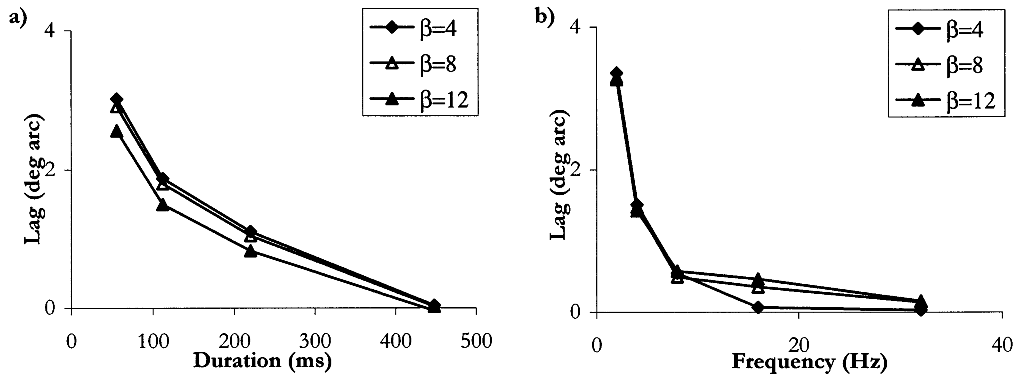

Fig. 5. The influence of the time-scale β on the calculated lag-effect. The (small) effect of β clearly depends on the frequency (a) and duration (b) of the trajectories.

an essential parameter of the distance perception model. The model predicts a distance percept $d^*(t)$ at time t, without reference to the τ parameter. We believe, however, that our 2AFC experiments give access to the perceived distance at time $t = t_{go} + \tau$, where t_{go} represents the time that the go-signal is presented. In experiments without a go-signal (i.e. a cancellation method as in Lappe and Krekelberg (1998) we arbitrarily assume that the go-signal is the offset of one of the flashes. This choice does not influence the best-fitting parameters.

We use the data from Lappe and Krekelberg (1998) and Krekelberg and Lappe (1999). In these experiments the duration, speed, frequency and the number of flashes of the stroboscopic motion sequences were varied over a wide range. To obtain a dataset to fit the model parameters, we average the measured perceived lag-angles for each stimulus parameter configuration over all subjects, determining the mean lag-effect and the standard deviation. This results in a total of 69 datapoints, whose lag-angles vary from 0.6 to 24° of orientation.

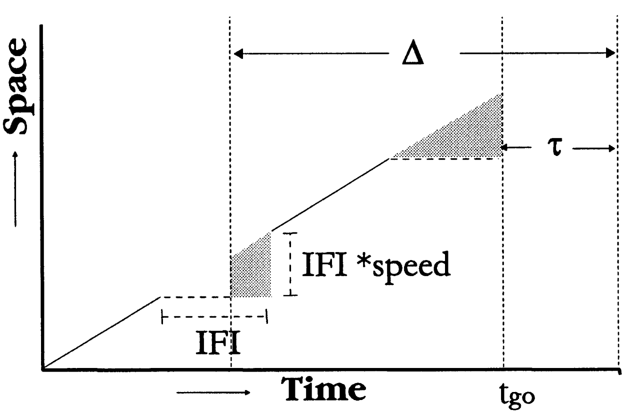

Fig. 6. Path predictions for wide trajectories in the experimental setup of Krekelberg and Lappe (1999). If spatial interactions can be ignored, the position signal of an object in stroboscopic motion will consist of continuous segments (while the object is visible) and segments in which the object stands still (while the object is hidden from view). The go-signal arrives at t_{go}. We assume that subjects report the distance perceived some τ seconds after the go-signal. The model averages the distance over Δ seconds preceding $t_{go} + \tau$. For the data at hand, position in space is given by a polar angle. Solid lines: visible position, dashed lines: persistent position. Shaded areas are position differences that contribute to the distance perceived at $t_{go} + \tau$

The parameters Δ, γ and τ are fitted to this dataset by means of a non-linear least squares method based on the Levenberg–Marquardt algorithm that compares $d^*(t_{go} + \tau)$ to the experimentally determined lag-effect. To determine a goodness-of-fit, we use the median of the standard deviation obtained in all experiments as a measure of the inherent variability in the data. This estimate is robust against outliers in the distribution of standard deviations that could be caused by the small number of subjects performing some of the experiments. The details of subjects sensitivity to the lag-effect, discussed in Lappe and Krekelberg (1998) are, however, ignored by this averaging procedure. With this estimate of the expected variability, we can determine the χ^2 statistic of the model. Constant χ^2 boundaries are used to determine the 95% error bounds on the fitted parameters.

3.1. Results

The best fitting model has the following parameters: $\gamma = 0.28 \pm 0.02$, $\Delta = 630 \pm 45$ ms and $\tau = 250 \pm 30$ ms. The goodness of fit as given by the χ^2 value is 41.7. Given the large number of degrees of freedom (df = 66) this is a very good fit ($P < 0.01$). The Pearson correlation $R^2 = 0.81$ is statistically highly significant ($P < 0.001$).) To show the overall fit of the model, Fig. 7 shows a scatter plot of all our data and the predictions of the model. As a further, somewhat informal test of the model, we use stimulus parameter values supplied in Nijhawan (1994), Baldo & Klein (1995) and Khurana and Nijhawan (1995) as input to the model and determine the predicted lag. Fig. 7 also shows a comparison of our prediction and the data in those publications.

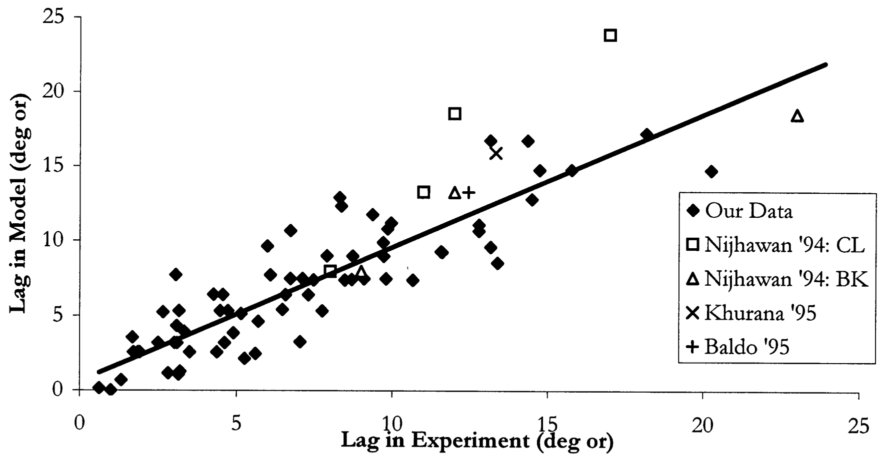

Fig. 7. A scatter plot of model versus experimental data. The abcissa shows the lag-effect as measured in experiments, the ordinate the lag-effect calculated by the model. The lag as seen by our subjects (triangles) is to a large amount (81%) predicted by the calculations of the model. The data from earlier publications are included to show the agreement even with data obtained in different laboratories under (presumably) different circumstances.

Apart from the data of subject CL in Nijhawan (1994), the agreement between our model and their data is good. The following section shows that the model accurately captures the stimulus parameter dependencies.

3.1.1. *Stimulus parameter dependence*

We now proceed to compare the predictions of the model defined by the three parameters with the results from the experiments reported previously. The figures below contain datapoints from Lappe and Krekelberg (1998) and Krekelberg and Lappe (1999); for details of the experimental procedures the reader is referred to those publications, but see also Section 4.2. The lines in the figure represent the predictions of the model. Error-bars show the standard deviation across subjects.

Fig. 8 shows a comparison for experiments in which the duration was varied. In Fig. 8b a method of adjustment was used to measure the lag-effect (Lappe & Krekelberg, 1998). As a consequence, the number of flashes seen by the subjects was large. In the experiment shown in Fig. 8a, a 2AFC method was used and the number of flashes seen by the subject was restricted to one (Krekelberg & Lappe, 1999).

The next comparison considers the speed dependence. We tested the dependence of the lag-effect on the angular velocity of the stimulus in two situations. In the first, the inner dots moved continuously while the outer dots were visible once, for either 28 or 196 ms, at stimulus onset. In the second situation, the outer dots were flashed four times with a duration of 28 ms each and at an interflash interval of 140 ms. Clearly, the speed dependence in the model is highly linear, both for single flashes and for multiple flashes. This extends the result discussed for the full spatiotemporal model in Section 2.2.1 and confirms that a linear velocity dependence need not be the consequence of latency-correction as has been argued by Nijhawan (1994).

Apart from the dependence of the lag-effect on the parameter on the abcissa, Figs. 8 and 9 also show that the lag-effect decreases with the number of flashes seen by the observer. This dependence was made explicit in an experiment discussed by Krekelberg and Lappe (1999). Fig. 10a shows that the model behaves similarly. The final test of the model is the dependence on the frequency of flashes. In previous work we showed that there is an exponential decrease of the lag-angle with the frequency of flashes that asymptotes near 16 Hz. Fig. 4b shows that the full spatio-temporal model shows similar behaviour. Fig. 10b demonstrates that the analytic model captures this dependence more accurately.

3.2. *Discussion*

An object whose trajectory is only intermittently visible lags behind an object on a continuously visible trajectory. A model, based on the assumption that spatial interactions are negligible in our particular setup, can be compared directly with the experimental data. With only three free parameters the model agrees closely with the experimental data. From the fits we deduce that the time period over which a distance percept is built up, is on the order of 600 ms.

The fact that the model without spatial interactions in the perception of position can account for the data shows that the essential elements in the model are first, the persistence of the position signal after the disappearance of the object and secondly the slow averaging procedure. Nevertheless, it is expected that spatial interactions will play a role for trajectories whose stations are nearer to each other. This may be the case for the

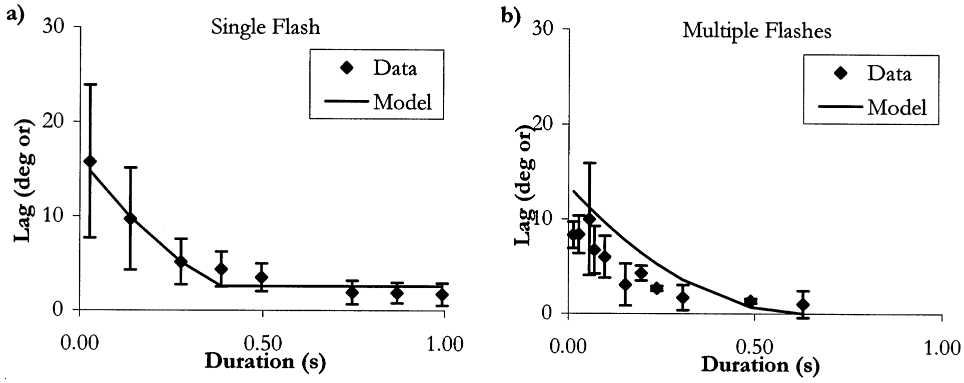

Fig. 8. A comparison of duration dependence in model and data. (a) Subjects determine the distance between a continuously moving object and an object in stroboscopic motion that is seen only once, for 28 ms. (b) Stroboscopic motion trajectories with a large number of flashes, shown with a flash-frequency of 1 Hz, are compared to continuous motion.

high-frequency experiments in (Lappe & Krekelberg, 1998, Figs. 6 and 7). There we measured the lag-effect between inner and outer dots when all dots were shown at the screen refresh rate (72 Hz). A significant lead effect was found for high velocities. That is, the outer dots were perceived ahead of the inner dots. We have not found this behaviour in either the simplified or the full spatio-temporal model under these circumstances. One reason for this could be that complex spatial interactions not captured by the Mexican Hat spatial filters play a role in this setup. Another reason could be that the model does not use the motion signals that would be generated by these smoothly moving stimuli. Further evidence for the importance of pure motion signals in the perception of position has recently been provided by Snowden (1998) and Nishida and Johnston (1999). Both used the motion after-effect to show that the position of moving objects is also misperceived in a stimulus in which movement is illusory.

The model of Morgan and Watt (1983) calculates position trajectories much like ours. Morgan and Watt developed this spatio-temporal interpolation model to explain the properties of dynamic Verniers. Their first aim was to explain why a temporally delayed stroboscopic motion sequence is seen at a spatial offset. Secondly, Morgan and Watt wanted to explain why the threshold for detecting such an offset rises rapidly when the stations in the sequence are separated by more than 4 min of arc. Their explanation of the first finding was that, for small distances between stations, the paths are interpolated. Between these interpolated paths, a spatial offset exists which is detected by the visual system. To explain the second finding, they proposed a 'consistency rule': a spatial offset between interpolated paths is only perceived if it is consistent over time. Because the distance between two poorly interpolated paths with a temporal offset is not consistent over time (see Morgan & Watt, 1983, Fig. 13), poor interpolation would prevent the subjects from seeing the spatial offset. Our model suggests a different interpretation. In our view, the perceived distance is the average over time of the difference in position. For poorly interpolated position signals with a temporal delay this difference is non-zero only during the time of the delay. The averaging over time reduces the effective, perceived distance to a small and possibly subthreshold spatial effect. For well interpolated paths, on the other hand, the distance is constant over time and the averaging procedure does not change the percept. Hence, for well interpolated paths, the thresholds for perception should be the same whether the offset is caused by a temporal delay or a spatial offset. This has indeed been found by Morgan and Watt (1983). We propose therefore that the consistency rule, as proposed by Morgan and Watt, be interpreted as a consequence of the slow averaging procedure that underlies the perception of distance.

4. Experiments

After showing that the model agrees closely with existing experimental data, we now wish to test two somewhat counterintuitive predictions of the model. The temporal interactions between stimuli are most easily understood in the regime where spatial interactions play no role. This is the case for many of our experiments; as long as the stations of the sequence are apart by more than $\sim 1°$ of the visual field. In this regime we can derive the following two predictions from the model.

4.1. Model predictions

The full spatio-temporal simulation model can be used to derive a prediction for the perceived distance between two objects on a staircase trajectory. Consider the time at which the stimulus jumps to the next position for a staircase trajectory with zero IFI. Due to

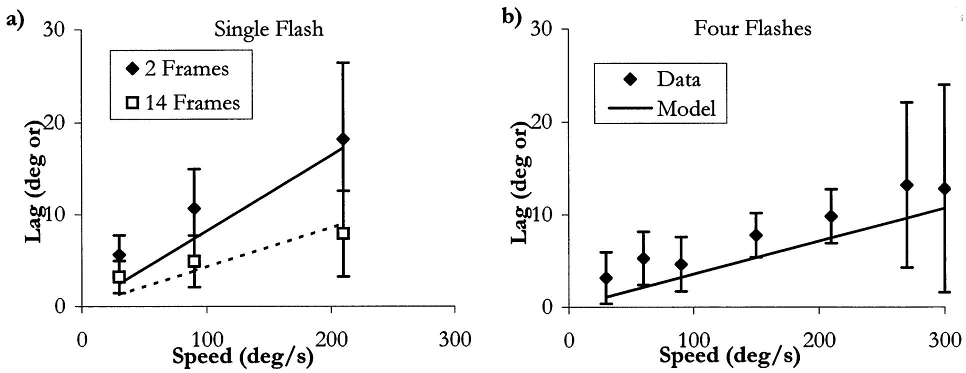

Fig. 9. A comparison of speed dependence in model and data. (a) Single flashes with a duration of two frames (28 ms, solid lines) or 14 frames (196 ms, dashed lines) are compared to continuous motion. In the model as in the data, there is an effect of duration (see Fig. 8) as well as a linear dependence on velocity. (b) The linear dependence on velocity is also found when the number of flashes is extended to four, even though the overall lag becomes smaller with an increase in the number of flashes. The model shows the same dependence.

the fact that the temporal impulse response function is slow (it takes $3\beta \simeq 36$ ms to reach the maximum), the position signal at the previous position will remain dominant for some time. Compared to this, the position signal of an object with a brief duration and a long IFI will immediately be dominant in the new position, because the position signal at the previous position will have decayed away. This competition predicts that a brief duration staircase stimulus should be seen to lead a long duration, zero IFI stimulus.

In Fig. 11a, we show two trajectories calculated by the complete spatio-temporal model for objects on a staircase motion path. Clearly, the staircase with the brief stand duration leads the staircase with a long stand duration and zero IFI. Fig. 11b shows the dependence of the lag on the stand duration. The lag is calculated with respect to the trajectory with a stand duration of 12 frames and an IFI of zero frames. Note that the lead effect for these staircases is an order of magnitude smaller than the lag effects shown for instance in Fig. 4. Also note that, as these predictions can be calculated only in the full spatio-temporal model, the absolute value of the lag will depend on the scale of the temporal impulse response function we use (see Section 2.2.2, in particular Fig. 5). The qualitative observation that a lead-effect should exist for brief staircases, however, is a generic feature, independent of the details of the temporal filters.

A second prediction can be derived from the staircase shape of the calculated positions. In the model the lag-effect is caused by the persistence of the position signal of the temporarily invisible object at the last seen position (see Fig. 6). If this is so, it should be possible to abolish the lag-effect by stopping the continuously visible object during the time when the other object is invisible. In that case, the position signals of the objects should be nearly identical, hence there should be no lag-effect. This inspires an experiment in which a stroboscopic trajectory is compared to a mixed continuous-staircase trajectory whose stop-time is under control of the subjects (see Fig. 2a and c).

4.2. Experimental methods

Fig. 12 shows the stimulus Baldo and Klein (1995) and we (Lappe & Krekelberg, 1998; Krekelberg & Lappe, 1999) have used to study the perception of distance for moving objects. In our setup all dots rotate around the central dot, which is also the fixation point of the observers. The inner dots are continuously visible, the outer dots only intermittently. The trajectories of the inner and outer dots vary between experiments and can be smooth, stroboscopic, staircase, or mixed (see Fig. 2). Note that the parameters are chosen such that whenever both objects are visible, their trajectories are identical. The retinal image is different only when either of the two objects is temporarily hidden.

The stimuli shown in Fig. 12 are rendered on a computer monitor. The screen refresh rate is 72 Hz, hence a single frame has a duration of 14 ms. Frames will be used as units of time in the description of the experiments and results. All stimuli move at 30 rpm and the experiments are done in darkness. Single dots subtend 0.4° of the visual field and their centres are separated by 1.5°. The whole stimulus of seven dots measures 9 degrees across. The outer dots have a luminance of 57.8 cd/m^2, and the background is at 0.05 cd/m^2.

In the first experiment, all dots are on a pure staircase trajectory (Fig. 2b). The inner dots stand duration is 12 frames and the IFI zero frames, while the outer dots stand duration and IFI are varied in tandem such that a period is always 12 frames long. In this experiment, the mouse buttons control an initially random offset angle between the two sets of dots. The subjects' task is to bring the outer and inner dots in alignment by pressing the mouse buttons. The offset-angle required for this is stored and interpreted as the angle by which the outer dots lag behind the inner dots (the 'lag').

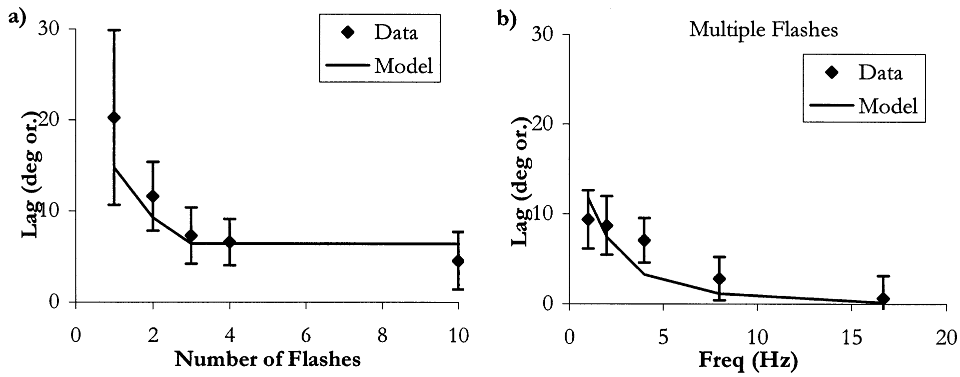

Fig. 10. A comparison of the dependence on the number of flashes and the interflash interval in model and data. (a) The outer dots are shown with a fixed interflash interval of 140 ms, but the number of flashes is varied. The decrease of the lag with the number of flashes is well captured by the model. (b) When a large number of flashes is shown, the lag-effect depends on the flash-frequency. Individual flashes have a duration of 28 ms.

In the second experiment, the outer dots are on a stroboscopic motion path with a variable duration. The inner dots are always visible, but move on a mixed continuous and staircase trajectory, see Fig. 2c. In this experiment pressing the mouse buttons changes the duration of the continuous part ('stop time'). This determines when, in each period, the inner dots will stop moving. Initially, the duration of the continuous part of the trajectory is set to a random value within five frames of the duration of the stroboscopic motion stations. The subjects' task is to bring the outer and inner dots in alignment by pressing the mouse buttons. Four subjects perform the experiments. Except for the two authors all are naive with respect to the hypothesis being tested.

4.3. Results

Fig. 13a and b show the individual results obtained from two subjects, Fig. 13c the pooled results of four subjects. For each subject, there is a significant effect of the stand duration. Post-hoc tests show that the lead effect was significantly different from zero for stand durations of one and two frames, but not for longer stand durations ($P < 0.01$).

Results of the experiments to test the second prediction of Section 4.1 are shown in Fig. 14. As the model predicts, the subjects adjusted the stop time such that the continuously visible objects stand still during the time that the flashed objects are hidden from view. The same results are found at other flash-frequencies of the trajectories (not shown).

4.4. Discussion

Some subjects' data in Fig. 14 show a slight offset: the subjects adjusted the trajectories of the inner dots such that they stopped moving one or two frames after the outer dots went off. The effect is small, especially considering that the smallest effect measurable in this setup is a single frame. Nevertheless, it may be a consequence of the competition effect studied in the first experiment. This competition would cause the stroboscopic dots to lead by a small amount the moment the dots appear at a new position. It seems possible that, to compensate for this lead-effect, subjects allowed the inner dots to move for a slightly longer time than expected.

Subjects performing the second experiment had performed several experiments in which they were able to adjust an offset angle between inner and outer dots directly (as in the first experiment). When instructed to do the second experiment, they were not told that the mouse clicks now affected the stop-time of the inner dots rather than the usual offset angle. When asked, none of the subjects reported any perceived changes in the adjustment procedures. To them, changing the duration of the smooth motion segment felt equivalent to direct adjustment of the offset angle. Although based on introspective reports, this gives further support to our hypothesis that position signals persist long after the object has disappeared.

5. General discussion and conclusion

The close fit of the model with previously obtained data as well as the corroboration of the models' predictions support our hypothesis that perceptual distance between objects is based on a long time scale (~ 600 ms) average of differences in position signals. The experiments confirm that the position signal of an object whose trajectory is temporarily occluded, persists at the last visible position. Moreover, the slow rise of the temporal impulse response function leads to a competition between position signals which, in the case of

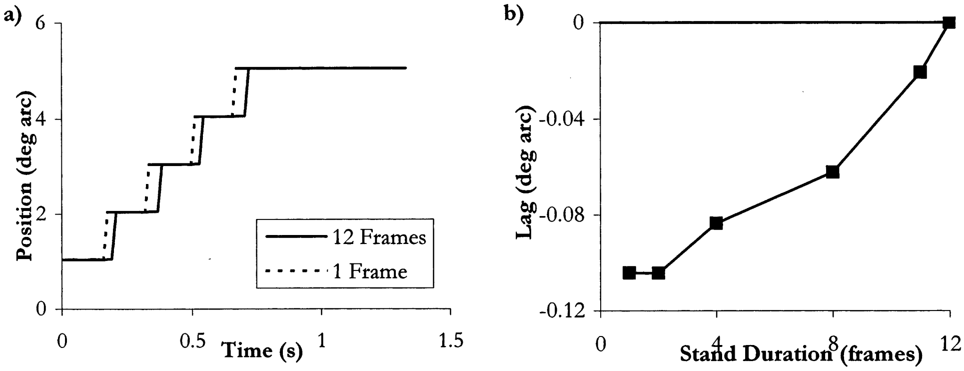

Fig. 11. Model predictions of lead effects for staircase motion. (a) The trajectories as calculated by the full spatio-temporal model. The dashed lines represent the trajectories of objects with a brief stand duration, the full lines objects with a long stand duration. (b) The lag calculated with respect to the stimulus with a stand duration of 12 frames. The brief stimuli lead the long stand-duration stimuli.

staircase trajectories, can cause a briefly presented object to be seen in front of an object with a long stand duration.

In the model we introduced the τ parameter to fit the time between the go-signal and the moment subjects decide whether they perceive a lag or a lead. One can interpret this as the time that goes by between the go-signal and the moment that some decision process 'reads out' the distance estimation module. The τ value we find, 250 ms, seems a reasonable estimate given the fact that reaction times (the time between go-signal and the moment an answer was given) were on the order of 800 ms.

Alternative interpretations of the lag-effect include a mechanism of motion extrapolation (Nijhawan, 1994) or attention shifting (Baldo & Klein, 1995). We discussed these alternatives in detail in (Krekelberg & Lappe, 1999). The experiments in Section 4 were not specifically designed to distinguish between these alternatives, but rather as a direct test of our own model. Nevertheless, the lead-effect shown in Fig. 13 seems hard to reconcile with either the motion extrapolation

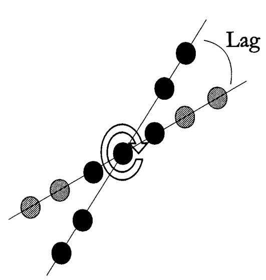

Fig. 12. Stimulus demonstrating a mis-perception of distance for objects on different motion trajectories. All dots rotate around the central fixation point, but the trajectories of the inner three and outer four dots differ. The black dots show the percept that is reported when the inner dots move smoothly while the outer dots are on a stroboscopic trajectory. The grey dots represent the positions where the outer dots are actually presented. The angle between inner and outer dots is called the lag-angle.

or the attention shifting view. Moreover, the linear velocity dependence of the lag-effect, which has been used as an argument in favour of a motion extrapolation mechanism, was shown to arise naturally in our distance perception model without the need for motion extrapolation.

One of our claims is that position signals of occluded trajectories persist at the last visible position. This is not the same as visible persistence. The objects are not perceived during the inter flash intervals, are therefore not 'visible', hence the persistence is not visible (Coltheart, 1980). What is available in these occlusion periods is information about the position of the objects. Rather than classifying this under echoic memory (Coltheart, 1980), we would like to use the term position persistence. This stresses the fact that various forms of persistence, with varying functions as well as durations, can be found in the visual system. Access to such persisting information can be restricted to special subsystems of the visual system. In our experiments, for instance, it is clear that the distance perception but not the object-detection system has access to the persisting position signal. Morgan (1977) proposed a similar dissociation between the perception of position and the perception of shape.

Visible persistence has been considered as an explanation of the lag-effect before. Nijhawan (1994) dismissed an explanation along these terms because subjects perceive the lag-effect even when the onset of inner and outer dots coincide ('flash initiated cycle paradigm'). If the lag-percept were formed at the time of onset, this would indeed be evidence against a role for any form of persistence. Surely though, the lag-percept takes some time to form, and during this time, persistence has ample time to play a role. Another proposal has been that the lag-effect between static, flashed objects and continuously visible, moving objects could be due to the fact that subjects align the offset (rather than the onset) of the flashed objects with the

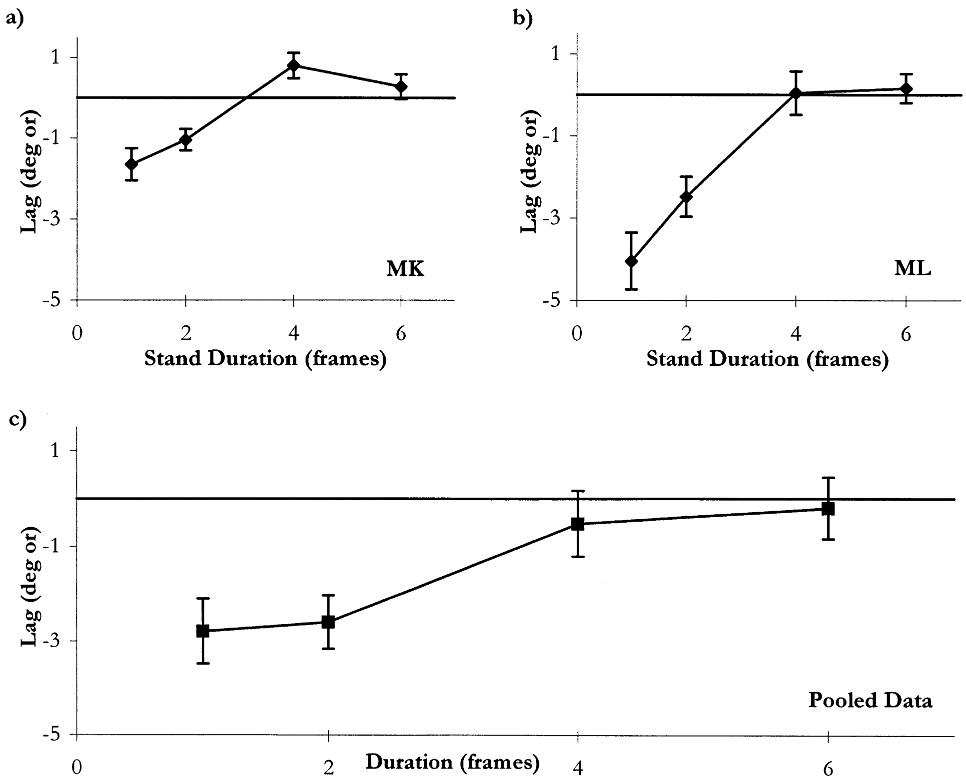

Fig. 13. A lead effect for staircase motion. For objects in staircase motion, a brief stand duration causes a lead when compared to objects with a long stand duration. Individual results are shown in the upper row, data pooled from four subjects in the lower figure.

continuously visible objects. Due to visible persistence this offset could be much later than the onset, even for briefly flashed stimuli. Namba, Kihara, Pires and Baldo (1998), however, showed that extending the duration of static stimuli had no influence on the lag-effect. This is just what we would expect from our model: the distance in either case results from an average difference in position signals. When the static stimulus is briefly flashed, its persisting position signal will be used in this comparison. If, on the other hand, the static object is shown for a longer period of time, its real position signal will be used. Hence, although the experiment of Namba et al. (1998) is an argument against a role for stimulus offset, it does not show that the persistence of the position signal is irrelevant.

There have been reports of lead-effects at stimulus offset. Baldo, Namba, Timo-Laria and Klein (1997) and Hill (1998) used a setup similar to that in Fig. 12, but in which the outer dots are static. The moving dots rotate clockwise until they reach the position of the outer dots (say, at ‘twelve o’clock’). Then, the outer dots are briefly flashed after which the stimulus is switched off completely. Subjects were asked whether, at the time of the flash, the moving dots were to the left or to the right of the flashed static dots. The motion extrapolation view would predict that for clockwise rotation the moving dots are seen to the right of the static dots. In both experiments, however, the opposite effect was found. This is in agreement with our averaging hypothesis: because the moving dots never move beyond the flashed dots, they are, on average, to the left of them. This average relative position is reported by subjects.

Recently, del Viva and Morrone (1998) published an extension of the local energy model and applied it to the perception of motion, not position as we did here. In their model the local energy filters receive direct retinal input while their output (the ‘perceived position’) is blurred. This is advantageous in the technical sense that localisation by the spatial filters will be more accurate. Much of the temporal integration in the visual system, however, already takes place at the retinal level, hence it seems unlikely that local energy operators in the visual system actually receive such a crisp signal. If the motion analysis model of del Viva and Morrone (1998) can still perform well with such early temporal blurring, it would be interesting to see whether a combined model could deal with those phenomena of position misperception where the motion-signal seems to play an important role (see Section 3.2 and Lappe & Krekelberg, 1998).

Concluding, we have presented a model of the perception of relative position that explains why and how trajectories influence perceived relative position. This not only explains the flash-lag phenomenon of Nijhawan (1994), but also the extensions to stroboscopi-

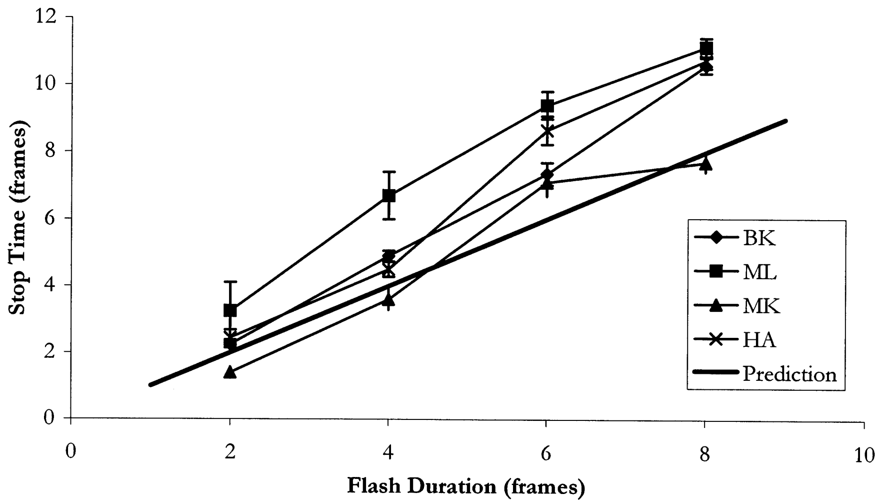

Fig. 14. A direct test of the persistence of position signals. As the model predicts, when asked to cancel the lag-effect subjects adjust the motion paths of the inner dots such that they stand still when the outer dots are invisible.

cally moving objects in Lappe and Krekelberg (1998), and flash-lead phenomena reported by Baldo et al. (1997) and Hill (1998). The dissociation between position and distance provides further evidence that the visual system can process information which we consider to be intricately entwined in parallel and, to a large degree, independently.

Appendix A. Mathematical description

This appendix formalises the description of the model. An object i moves along the one-dimensional retinal path $r_i(t)$ and its luminance signal is $l_i(x, t)$. Hence, $l_i(x, t)$ is non-zero only for $x = r_i(t)$. Stage I of the model in Fig. 1 calculates the temporally low-passed luminance distribution $s_i(x, t)$:

$$s_i(x, t) = \int_0^t h(t - t')l_i(x, t')\,\mathrm{d}t', \qquad (1)$$

where h represents the temporal impulse response function as measured by Roufs and Blommaert (1981):

$$h(t) = g(t/\beta)^3 \exp(-(t/\beta)), \qquad (2)$$

with g the gain of the filter and β the time constant. Note that this function reaches its maximum at $t = 3\beta$. Stage II convolves the signal $s_i(x, t)$ with odd and even spatial filters, the components are squared individually, then added to obtain a measure of the local energy $e_i(x, t)$ (Morrone & Burr, 1988):

$$e_i(x, t) = \left(\int f_o(x - x')s_i(x', t)\,\mathrm{d}x'\right)^2 + \left(\int f_e(x - x')s_i(x', t)\,\mathrm{d}x'\right)^2, \qquad (3)$$

with f_e, f_o even and odd spatial filters, respectively. We used Mexican hat shaped filters whose power spectrum reaches maximum at α cycles per degree. Unless otherwise mentioned, $\alpha = 1$ cpd. The position of the i-th object at time t, $p_i(t)$ is determined by finding the maximum in the local energy:

$$p_i(t) = x \ \text{for which} \ e_i(x,t) = \max_x \{e_i(x,t)\} \qquad (4)$$

This is the output signal of stage III of the model. Stage IV simply determines the instantaneous difference $d(t)$ between position of two objects, say i and j: $d(t) = p_j(t) - p_i(t)$. Stage V adds the temporal averaging hypothesis as a temporal low pass filter. In other words, we hypothesise that the perceived distance d^* between two objects is given by the average of the instantaneous distance over a period Δ:

$$d^*(t) = \frac{\int_0^\Delta d(t - t')\,dt'}{\Delta}. \qquad (5)$$

Hence, at time t, the perceived distance is given by the average difference between position signals in the last Δ seconds. In Section 2 we assume a fixed Δ which is large enough to encompass the whole of the simulated trajectory.

In the analytic model of Section 3 we exploit the fact that individual dots in our stimulus are small and far apart. This implies that the spatial interactions play a negligible role. Mathematically, this means that the even spatial filter can be approximated by $f_e(x) = \delta(x)$ and that the odd spatial filter is zero. To describe the stimulus we used in experiments, identify the spatial coordinate with the rotational angle of the dots. In that coordinate system, the dots move along $x = vt$, where v represents angular velocity, t time and x is the polar angle of the dots (see Fig. 12). For the continuously visible inner dots, the retinal luminance signal is given by:

$$l_c(x, t) = \delta\left(\frac{x}{v} - t\right). \tag{6}$$

The flashed outer dots generate the signal:

$$l_f(x, t) = \delta\left(\frac{x}{v} - t\right)\theta[D - t \bmod P], \tag{7}$$

where δ is a Dirac delta-function and θ a ramp non-linearity: $\theta[x] = 0$ for $x < 0$ and 1 otherwise. The parameters D and P represent the duration and the period of the stroboscopic motion trajectory, respectively. Substituting these spatio-temporal retinal activation patterns in the formulas above, it can be derived that for continuously visible objects:

$$p_i(t) = v(t - 3\beta).$$

This expression is incorrect when $t < 3\beta$, but we will ignore these onset effects. Hence, the final expression below will not be able to model the effects shown in Fig. 11. For objects on a stroboscopic trajectory we also ignore the onset effects and can derive that:

$$p_f(t) = \begin{cases} v(t - 3\beta) & \text{for } t \bmod P < D \\ v(\text{floor } [t/P]P + D - 3\beta) & \text{otherwise,} \end{cases}$$

where the floor-function determines the number of completed periods at time t. The perceived distance between two objects, defined as the averaged difference over the last Δ seconds can now be calculated as:

$$d^*(t) = \gamma \int_{t-\Delta}^{t} v(t' - \text{floor } [t'/P]P - D)\theta[t' \bmod P - D]\, dt'. \tag{8}$$

The parameter γ has been introduced to scale model units to measured lag-angles. Expression 8 is used in Section 3 to fit the parameters Δ and γ.

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