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The persistence of position

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Abstract

I describe a signal coined position persistence that stores information about the last seen position of an object. Position persistence is not the same as visible persistence, although some of its properties are similar. The duration of position persistence is such that objects visible briefly always generate a position signal for at least 180 ms. The signal is not affected by the intensity of the object, nor of the background. Position persistence decreases with increasing speed, but does not depend on retinal eccentricity. Finally, the persisting signal is not tightly bound to the object that causes it. The signal contains no information on the colour of the object, whereas shape information may become represented after approximately 100 ms. The existence of this signal is interpreted as a psychophysical signature of the parallel processing of visual information. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The human visual system is capable of detecting and processing exceedingly brief visual stimuli. To do this, the system needs to set-up an internal representation of the brief external stimulus. The existence of such an internal representation is demonstrated by visible persistence. This is the phenomenon that human observers still perceive objects whose physical exposure has been terminated (for a review, see Coltheart, 1980).

As observers report persistent perception of colour, shape as well as the position, one can deduce that many of the properties of a visual stimulus persist after physical exposure. The unity of the subjective experience suggests that all aspects are somehow represented 'together'. Physiological evidence on the specialisation of different areas in the visual cortex, however, suggests that it is unlikely that all visual properties are represented by a single neural mechanism. In line with that, one could expect separate mechanisms for each of the perceptual dimensions. Hence, 'colour persistence', 'shape persistence' and 'position persistence' could all be subserved by different mechanisms. These mechanisms of persistence of the different stimulus aspects must, at some point, be combined to reach a unified percept, but in principle, they could have different properties.

I believe that the flash-lag effect (Metzger, 1931; Nijhawan, 1994) demonstrates the existence of a persisting signal that represents the position of objects that are no longer exposed. Although this paper is not primarily about the flash-lag effect, I need to reiterate some of the arguments in (Lappe & Krekelberg, 1998; Krekelberg & Lappe, 1999, 2000) to clarify this point of view.

Metzger (1931) showed that when the position of a moving, continuously exposed object is compared with a flashed, briefly exposed object at the same position, the flashed object appears to lag behind the moving object. Nijhawan (1994) interpreted this phenomenon in terms of latency-correction. He argued that the visual system compensates for the latency of visual processing of a moving stimulus by predicting ahead spatially. This would cause a stationary flash, which is not predicted ahead, to appear to lag behind. Several authors have since pointed out that this interpretation is untenable. Mainly, the counter-argument is that changing the latency or velocity of a stimulus is not

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reflected appropriately in the flash-lag effect. In other words, the visual system does not display any accurate knowledge of the visual processing latency or of the trajectory of the moving stimulus and can, therefore, not be said to compensate for visual latencies in any useful way (Lappe & Krekelberg, 1998; Purushothaman, Patel, Bedell, & Ögmen, 1998; Brenner & Smeets, 2000).

An alternative hypothesis postulates that flashed objects have longer visual processing latencies than moving objects (Metzger, 1931; Purushothaman et al., 1998; Whitney, Murakami, & Cavanagh, 1998, 2000). While the flash is still being processed, the moving stimulus will move on, thus causing the flash-lag effect. Although the electro-physiological data of Berry, Brivanlou, Jordan, and Meister (1999) seem to support the main idea behind this hypothesis, they are unable to give a quantitative explanation of the many parameter dependencies of the flash-lag effect. Moreover, Eagleman and Sejnowski (2000), showed that giving the flashed stimulus a head-start by as much as 53 ms does not change the flash-lag effect. This shows that the latency of the flashed stimulus is not the only factor causing the lag.

I favour a different view of the flash-lag effect. It is important that the flash in the flash-lag experiments is not a neutral cue that allows one to determine the perceived position of the moving object. This is seen most clearly when the flash is shown multiple times: the perceived lag decreases with the number of flashes (Krekelberg & Lappe, 1999). This shows that the flash-lag experiments measure not the perceived absolute position of the moving stimulus, but rather the relative position of the moving stimulus with respect to the flash. The effect that multiple flashes, their duration and their frequency have, shows that the spatio-temporal history of both flash and moving object plays a role in this relative position percept (Lappe & Krekelberg, 1998; Eagleman & Sejnowski, 2000). Such a view of relative position perception of two objects leads naturally to the question, which position signals are compared when only one of the objects is exposed. The most straightforward comparison would be between the position signal of the exposed (moving) object and the visible persistence of the flashed object. Comparing the position signal of the moving object with the offset of the visible persistence would cause a lag-effect, because the offset could be up to 120 ms after the onset of the flash (Barlow, 1958). Several authors (Namba, Kihara, Pires, & Baldo, 1998; Whitney et al., 2000), however, have shown, either by extending the exposure of the flash or by terminating visible persistence with backward masking, that visible persistence does not cause the lag-effect. This led Krekelberg and Lappe (2000) to introduce the concept of position persistence — a signal that represents the last exposed position of an object that is no longer exposed. The model of relative position perception in (Krekelberg & Lappe, 2000) is based on this concept and quantitatively captures many of the parameter dependencies of the flash-lag effect.

Summarising, the concept of position persistence was introduced to explain the flash-lag effect. Using this new concept in a quantitative model explained successfully a range of flash-lag parameter dependencies, and generated two counterintuitive predictions, which were confirmed in experiments (Krekelberg & Lappe, 2000). In this paper, I wish to elucidate the properties of position persistence. In the first two experiments, position persistence is dissociated further from visible persistence. Experiments 3–5 show the influence of luminance, speed, eccentricity and exposure duration on the persistence of position. The last two experiments show that the persisting position signal does not contain much information on the colour or shape of the object that generates it.

2. General methods

2.1. Stimuli

Fig. 1 is a stimulus adapted from Baldo and Klein (1995). All dots rotate around the rightmost dot, which is fixated by the subjects. The two rightmost dots are exposed for a long period of time, they are called the long-exposure objects. Dots 3 and 4 are extinguished shortly after their onset; their total period of exposure is called the flash-duration. I refer to the brief presentation of these objects as a 'flash'. Note, however, that whenever the flash-duration is longer than a single frame, these dots also rotate around the fixation point.

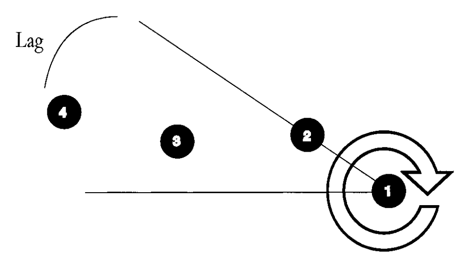

Fig. 1. A stimulus to investigate the perception of relative position of objects on a circular trajectory. Dots 1 and 2 are the long-exposure objects, while dots 3 and 4 have a brief exposure. All dots start to rotate around the rightmost (fixation) dot from the horizontal position. After a variable number of frames (the flash-duration) the brief-exposure dots are switched off, while the long-exposure dots rotate on. The figure shows the percept at stimulus onset (physically, all exposed dots are aligned at all times). The numbers are not shown during the experiment. Note that at stimulus onset, none of the dots are perceived at their starting positions, but shifted in the direction of motion. This is the Fröhlich effect (Fröhlich, 1923). The flash-lag is the difference in angle between the perceived position of the long and brief exposure objects.

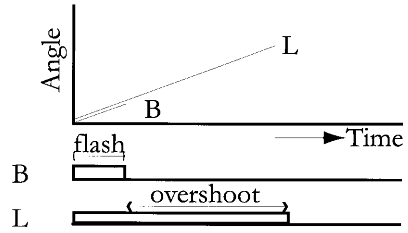

Fig. 2. Timing and parameter definitions. All dots start to rotate from the same angular position (lines are offset for visual clarity). The brief-exposure dots (B) are switched off after a flash duration. The long-exposure dots (L) are exposed for a further overshoot duration.

This is different from the setup in most other flash-lag studies, where the flash is stationary. These dots are referred to as the brief-exposure or flashed dots. I use 'exposure' and 'exposed' to refer to physical events. 'Visible' and 'seen' are their subjective, phenomenal equivalents.

A difference in exposure of the trajectory of two objects leads to the so-called flash-lag effect, continuously exposed, moving objects are perceived ahead of objects that are briefly exposed at the same position, at the same time (Metzger, 1931).

Unless stated otherwise, the dots rotate at 30 rpm around dot number 1 in Fig. 1. The experiments are done in darkness. Single dots subtend 0.4° of the visual field and their centres are separated by 1.5°. The dots have a luminance of 57.8 cd/m^2, and the background is at 0.05 cd/m^2. Fig. 2 shows the timing of the experiment and defines the important temporal parameters.

Stimuli are generated by a Silicon Graphics workstation on a monitor with a 72 Hz refresh rate, thus, limiting our timing to multiples of the duration of a single frame (14 ms). Note that this implies that a stimulus with a duration of 14 ms is stationary. As shown in (Lappe & Krekelberg, 1998) the use of a monitor, rather than continuous light, does not qualitatively change the flash-lag effect.

2.2. Participants

Ten colleagues and students of the department, including the author, participate in these experiments (two female, eight male, age group 25–35). Not every participant performs each experiment. Intersubject variability in position persistence is generally large. This is demonstrated most clearly in Fig. 6, where persistence ranges from 90 to 245 ms. The trends of the parameter dependencies, however, are similar for all subjects, hence I report mainly the group averages. To test for statistical significance, I use standard one and two-way repeated measures analyses of variance (ANOVAs), followed by Student–Newman–Keuls post-hoc tests where appropriate.

2.3. Model-assumptions

Krekelberg and Lappe (2000) developed a model of the flash-lag effect based on the spatio-temporal filtering properties of the early visual system, combined with the hypothesis that relative position is based on a slow averaging process. This model explains quantitatively many of the parameter dependencies of the flash-lag effect. Many aspects of the perception of relative position can be understood in an abstraction of this model that is based on merely two hypotheses (for details, see Krekelberg & Lappe, 2000, Section 3). The hypotheses are that first, the perceived relative position is based on a long ($\sim$ 600 ms) temporal average of the difference of position signals. Secondly, when an object is no longer exposed, the position signal used in this averaging procedure is the last exposed position — the persisting position signal.

Position persistence in the model in (Krekelberg & Lappe, 2000) was always of sufficient duration to allow the averaging process underlying relative position perception access to two position signals. It seems likely, however, that the period, over which a position signal persists, is limited. The model in Krekelberg and Lappe (2000) did not define what should happen to the perceived relative position when one of the position signals disappears. In this paper, I propose and test the hypothesis that when the position signal ceases to persist, the perceived relative position is no longer updated.

Fig. 3 illustrates the dependence of the flash-lag effect on the duration of position persistence. The model

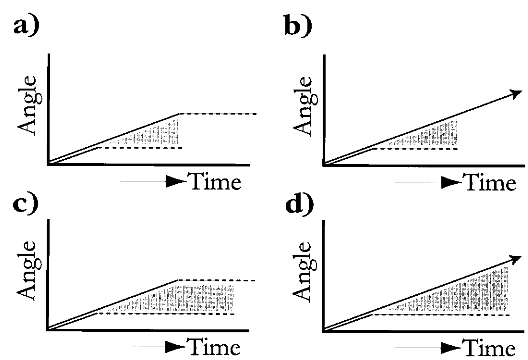

Fig. 3. Mislocalisation of long-exposure objects when compared with briefly exposed objects. The solid lines represent the exposed trajectories of the objects. The dashed lines represent the persisting position signal. After the disappearance of a briefly exposed object, the persisting signal stays at the last exposed position. (a) The long-exposure object overshoots the brief-exposure object by a small amount, and the position signal persists for a relatively brief period of time — the flash-lag is small. (b) Brief persistence but a large overshoot — the increased overshoot (compared with a) should not affect the perceived flash-lag. (c) The same retinal stimulus configuration as in a, but now the (internal) position persistence is assumed to be much longer. As this increases the shaded area for a fixed overshoot, this should increase the lag-effect. (d) With long position persistence, an increase in overshoot should increase the lag-effect.

hypothesises that the flash-lag is proportional to the average mismatch of a real and a persisting position signal. In Fig. 3, the total mismatch is indicated by the shaded triangles. The average mismatch is obtained from this by dividing the shaded area by the averaging period, which has been estimated at 600 ms (Krekelberg & Lappe, 2000).

If position persistence were of infinite duration, the mismatch triangles in Fig. 3 would grow without bound, theoretically causing infinite flash-lags. The growth of the mismatch triangles can be curtailed by assuming that perceived relative position is no longer updated when the position signal ceases to persist. For instance, if position persistence is brief (as in a), the flash-lag should be small. Moreover, the lag should not increase with longer overshoot durations (as in b). If, on the other hand, the persistence is long (as in c), the lag should be larger and it should increase when the overshoot is increased (d). This interaction between overshoot duration, position persistence and flash-lag provides a tool to estimate position-persistence in a flash-lag paradigm.

3. Results

3.1. Experiment 1: position persistence

The first experiment tests the prediction that the overshoot duration affects the flash-lag effect. By increasing the overshoot duration, subjects are asked to use the persisting position signal at ever later times after stimulus offset. The hypothesis illustrated in Fig. 3 predicts that the perceived lag increases with overshoot duration until the persisting position signal disappears.

3.1.1. Methods

The stimulus in Fig. 1 starts in a horizontal orientation and rotates at 30 rpm counter-clockwise. In this experiment the flash-duration (2, 8, 16, 32 frames) and the overshoot duration (2, 6, 14, 30, and 62 frames) are varied factorially and all conditions are pseudo-randomly interleaved. Five members of the department participate.

The perceived lag between flashed and long-exposure objects is determined with a two-alternative forced choice task. Subjects view a stimulus, then answer the question "At stimulus onset, did the outer two dots lag or lead the inner two dots?" This answer is used in a maximum-likelihood adaptive parameter estimation method to change the physical offset between the objects (for details, see Krekelberg & Lappe, 1999). The point of subjective equivalence is defined as the physical offset angle that leads to 50% 'lag' answers and 50% 'lead' answers. This angle is interpreted as the perceived relative position of the two objects — the flash-lag.

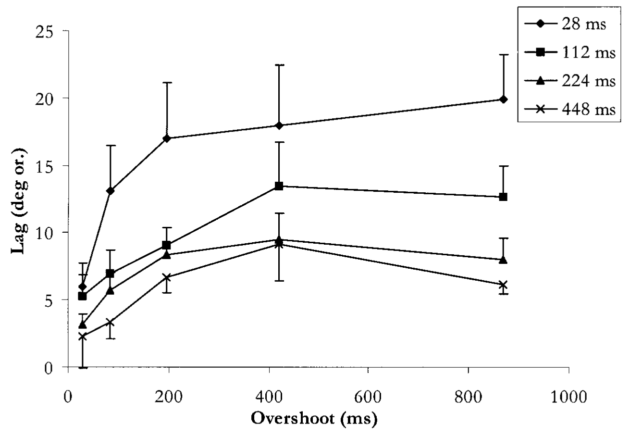

Fig. 4. The perceived distance increases with overshoot duration. Curves represent average data from five subjects. Each curve represents the results for a stimulus with the flash-duration as indicated in the legend. Errorbars show one standard error.

3.1.2. Results

Fig. 4 shows two clear effects. First, the flash-lag for each flash duration increases with overshoot-duration, and reaches an asymptote for long overshoot durations. Secondly, the lag-effect decreases with increasing flash-duration. The latter has been reported before by Bachmann and Kalev (1997) and Lappe and Krekelberg (1998). Both, the effect of the overshoot, and that of the flash-duration, are highly significant ($P < 0.001$), but their interaction is not.

3.1.3. Discussion

The experiment shows that the perceived distance between a flashed object and a long-exposure object increases when the long-exposure object overshoots the position of the flashed object. This is expected if the visual system determines an average of the difference in position signals (Lappe & Krekelberg, 1998; Eagleman & Sejnowski, 2000). However, if the position signal of the flashed object were to persist indefinitely at its last visible position, one would expect an indefinite increase of the perceived distance with the overshoot duration. Clearly, this is not the case. In terms of the model, the saturation of the flash-lag with increasing overshoot can be interpreted as follows. The short overshoots correspond to the situation depicted in Fig. 3c — the persistence signal outlasts the overshoot. By increasing the overshoot, the situation in Fig. 3d occurs, the mismatch triangle increases and hence the perceived flash-lag increases. By increasing the overshoot even more, the overshoot duration will, at some point, be equal to the position persistence (as in Fig. 3a) and the flash-lag will be maximal. Further increases in overshoot (Fig. 3b) will, then, no longer affect the flash-lag. Hence, the saturating dependence of flash-lag on the overshoot duration can be understood if perceived relative position is given by the average difference in position signals, but once either of the (persisting) position signals is no longer available, the relative position is no longer updated.

I define the duration of position persistence as the overshoot duration for which the relative position saturates. The saturation level is chosen as 85% of the maximum level. Clearly, choosing a higher level would increase the estimate of the persistence of position. The 85% level should be interpreted as a lower bound to the persistence of position. The data in Fig. 4 allow a rough estimate of the duration of persistence. For instance, for a 28-ms stimulus, the 85% level is reached after approximately 150 ms. Hence position persistence for a 28-ms stimulus is of the order of 150 ms. A more accurate method to measure the persistence duration is described in the next section.

3.2. Experiment 2: position persistence versus visible persistence

To dissociate position persistence from other forms of persistence, stimulus contrast is reversed. In the first experiment, white dots move on a dark background. This configuration leads to both phosphor persistence and considerable visible persistence. Reversing contrast, however, abolishes phosphor persistence and significantly reduces the visible persistence (Barlow, 1958; Hogben & Di Lollo, 1985). If position persistence were in fact phosphor or visible persistence in disguise, one would expect a smaller position persistence for black dots on a white background.

3.2.1. Methods

To ensure that visible persistence is indeed different for the two stimulus configurations I use, I measure the visible persistence of a single dot. This dot moves on the trajectory of dot number 3 in Fig. 1, and at variable times after its extinction a probe dot appears at the fixation point. The six subjects report whether they perceive a single dot at a time or two simultaneously. A psychometric curve is fitted to their mean responses and the duration of visible persistence is identified with the 50% point. This experiment was done for a white dot (57.8 cd/m^2) on a black background (0.05 cd/m^2) as well as for a black dot on a white background (luminances reversed). The duration of the trajectory was eight frames. Six participants performed this experiment.

In a pilot experiment to determine the effect of polarity reversal on position persistence, I use the 2AFC method described in Section 3.1.1. The 'white' stimulus is as described in Section 2.1, the 'black' stimulus is identical in all respects, except that the background now has a luminance of 57.8 cd/m^2 while the dots have a luminance of 0.05 cd/m^2. The overshoot duration was varied (2, 6, 14, 30, and 62 frames), for a flash duration of two and eight frames, respectively.

After the pilot experiment, I measure position persistence more accurately, with a nulling method. I first use the above 2AFC method to determine the lag-effect for a long (many seconds) overshoot duration. This gives an estimate of the asymptote of the lag-effect for a particular stimulus configuration and subject. Then, a stimulus is shown with the same parameters as in the first stage, but a physical offset is introduced between the inner and the outer dots that is opposite to the expected lag-effect. The amount of offset is 85% of the asymptotic lag-effect. The initial overshoot duration is set to zero, and the participant is given the control of the overshoot duration. By pressing two buttons, the participant can increase or decrease the overshoot. The participants are instructed to 'rotate the inner dots until they line up with the outer dots'. Note that participants are not aware that they in fact manipulate the overshoot duration; their reported perceptual experience is one of 'rotating'. The subjects adjust the overshoot duration until the inner and outer dots align, then press a third button, which stores the selected overshoot and starts the next trial. Each stimulus configuration in this nulling method is repeated at least 20 times. Five participants perform this experiment. The experiments with different background intensities are blocked. Stimulus parameters are the same as in the pilot experiment of this section.

3.2.2. Results

The first experiment shows that, as expected, the visible persistence of a white dot on a black background is significantly larger (49 ms on average) than that of an otherwise identical black dot on a white background ($P < 0.05$). Because this dot is on the same trajectory and has the same size as the flashed-dots in the experiments below, it is safe to assume that the visible persistence of the white flashed dots on a black background is considerably larger than that of the black dots on a white background.

In the pilot experiment, I find that reversing contrast has no significant influence on the perception of the relative position. Fig. 5 depicts the overshoot dependence for white-on-black versus black dots on a white background. Clearly, and in contrast with visible persistence, the overshoot dependence does not depend on contrast polarity.

Fig. 6 shows the results of the nulling method to determine the (duration of) position persistence. None of the subjects shows a significant ($P > 0.05$, Mann–Whitney Rank Sum test) effect of contrast polarity. The mean effect is less than 1 ms.

The three experiments in this section show that a manipulation that significantly changes the visible per-

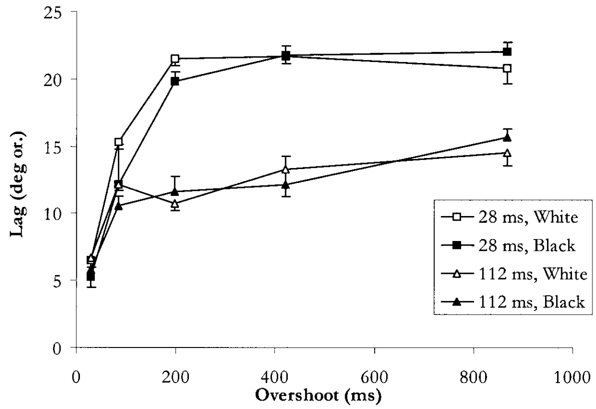

Fig. 5. The amount of visible persistence of the flashed objects does not influence the perceived distance. The two curves show results for a single subject (BK). The curves represent different flash-durations and different contrast polarities, as indicated in the legend. Errorbars show the 95% confidence levels, for clarity in one direction only.

sistence of the dots, does not affect the position persistence of the same dots. This indicates that different mechanisms must underlie these two forms of persistence. Namba, Kihara, Pires, & Baldo (1998) and Whitney et al. (2000) demonstrated already that the flash-lag effect is not due to visible persistence. This is confirmed here in a slightly different paradigm, with the extension that the way, in which the flash-lag depends on the overshoot duration, is not due to visible persistence either.

3.3. Experiment 3: intensity

For relatively low stimulus luminances, the duration of visible persistence of a stationary object increases with decreasing luminance, whereas for higher luminances this relation reverses or the luminance ceases to affect visible persistence (Coltheart, 1980; Farrell, Pavel, & Sperling, 1990; Castet, Lorenceau, & Bonnet,

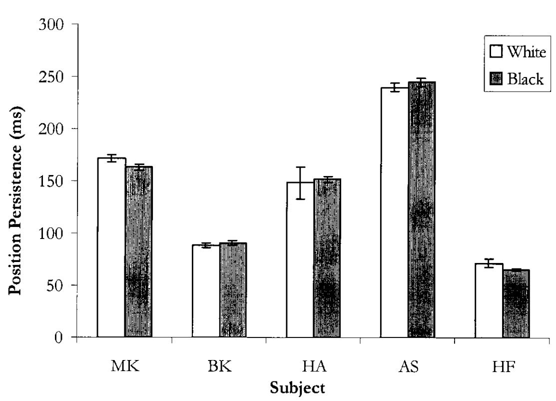

Fig. 6. Position persistence is not visible persistence. The persistence of position is shown for ‘white’ stimuli (long visible persistence) and ‘black’ stimuli (brief visible persistence). Errorbars show ± 1 standard error.

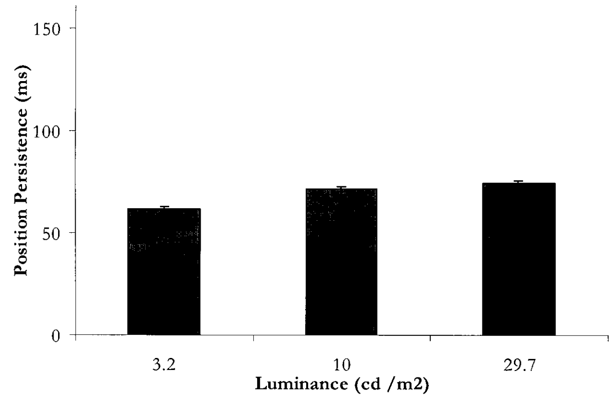

Fig. 7. Luminance does not affect position persistence. Data pooled over four subjects, errorbars are standard errors.

1993). To find the analogous role of luminance in position persistence the luminance of the flashed objects is varied.

3.3.1. Methods

Four participants are tested with the nulling method described in Section 3.2.1. The luminance of the white dots on a black background (0.05 cd/m^2) is varied (3.2, 10 and 29.7 cd/m^2). Before commencing the experiment, participants are darkadapted for at least 10 min. The flashed dots are on for two frames. The stimulus rotates at 30 rpm.

3.3.2. Results

No significant effect of luminance on position persistence and luminance can be found (Fig. 7). This may be due to the relatively high luminances of the stimuli, although Castet, Lorenceau, & Bonnet (1993) showed an inverse relationship of visible persistence for luminances as high as 12 cd/m^2. As lower luminances make the alignment task increasingly difficult for the participants, I could not test an increased range of luminances. The absence of a luminance-dependence further dissociates position persistence from visible persistence.

3.4. Experiment 4: duration

An intriguing aspect of visible persistence is that, for briefly presented objects, its duration is such that the overall visibility (physical exposure plus persistence) is constant. To determine whether position persistence similarly complements the signal for briefly presented objects, the duration of the flashed objects is varied. Four participants perform this experiment. The flash-duration is 2, 4, 8, 16, 32 and 64 frames. Note that the longest of these ‘flashes’ are visible for 890 ms and are clearly perceived to be in motion. Subjects, however, are instructed to always report the perceived lag at stimulus onset.

3.4.1. Results

Fig. 8 shows that, similar to visible persistence, position persistence is largest when an object is only briefly presented. This effect of stimulus duration is highly significant ($P < 0.001$). A post-hoc test shows that position persistence for flash-durations above 16 frames are not significantly different from zero.

The best-fitting line to the first half of the data-points has a slope of -1.01 ± 0.08 and an intercept of 184 ± 10 ms, which means that the position signal of objects with such brief exposure is present for 184 ms regardless their physical exposure. Objects with a longer physical exposure have zero position persistence.

3.5. Experiment 5: speed and eccentricity

If visible persistence for moving stimuli were the same as for stationary stimuli, one would expect the world to appear very blurred. In fact, it is well known that visible persistence of moving stimuli is suppressed (Burr, 1980; Hogben & Di Lollo, 1985). Moreover, this suppression depends on the eccentricity of the stimuli in that suppression increases for parafoveal stimuli (Di Lollo & Hogben, 1985).

To determine the analogous properties of the position signal, we test four participants with stimuli whose angular velocity is varied, and in which the flashed dots are at an increased eccentricity.

Four subjects perform this experiment in six conditions (speed × eccentricity, (10, 20, 30 rpm) × (4, 8° of arc)). The eccentricity is expressed as the position of the most foveal, flashed dot. One participant was not able to bring the stimulus with increased eccentricity into alignment and her data are discarded from further analysis.

3.5.1. Results

Averaged over participants, position persistence decreases significantly with the increasing speed ($P < 0.01$)

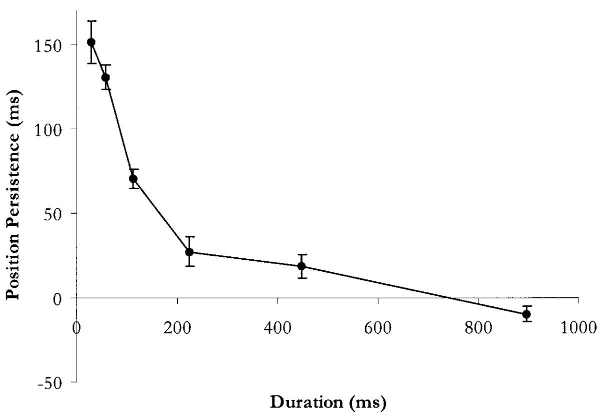

Fig. 8. Position persistence decreases with increasing duration of an object. Data averaged over four subjects, errorbars show standard errors.

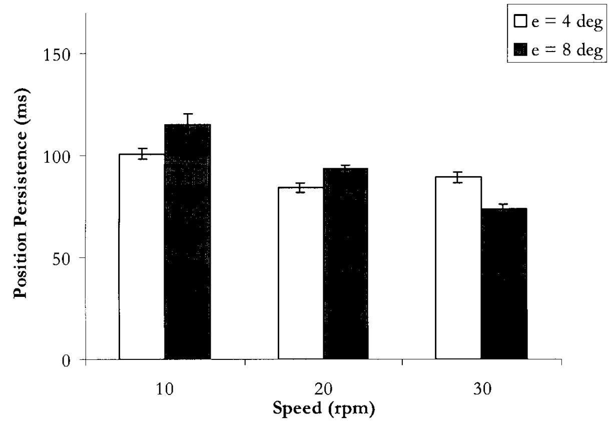

Fig. 9. Position persistence decreases with increased speed, but eccentricity does not affect it significantly. Data are averaged over three subjects, errorbars, are standard errors. White bars show results for the stimulus shown in Fig. 1, black bars for a stimulus where the flashed dots are at an increased eccentricity.

and this decrease is affected by the eccentricity ($P < 0.01$), but the eccentricity itself does not affect the persistence ($P > 0.05$) Fig. 9.

Hence, the suppression that occurs for visible persistence is found for position persistence as well. Note, however, that the suppression of visible persistence is much more complete than that of position persistence. Whereas visible persistence is commonly reduced to durations of the order of 30 ms for moving stimuli (Burr, 1980), position persistence is still of the order of 80 ms, even at high speeds. Functionally, this may be related to the fact that the position signal has no direct effect on the percept of moving objects. The persisting position signal itself does not lead to a blurred percept. It does, however, affect the perceived distance between moving objects.

3.6. Experiment 6: object dependence

The previous experiments have described the basic, low-level properties of position persistence. The next question that arises is about the specificity of this signal. How much information about the nature of the object is coded implicitly in this signal? In other words, does the signal stand for 'there was an object at this position' or 'a white circle was here'?

To test this, I present the same stimulus as before (Fig. 1), but change the nature of the long-exposure object during the overshoot. If the position signal is purely spatial ('Something was at position x'), such a change is not expected to affect the perceived relative position. If, on the other hand, the position signal is bound to a particular object ('A white square was at position x'), changing the object should reset the position signal, and, thus, influence the perceived relative position.

3.6.1. Methods

Five conditions are interleaved pseudo-randomly. In the first three, called overshoot-conditions, the overshoot duration is varied from 2, 6 to 14 frames. The two other conditions are called switch-conditions. In these trials, the overshoot duration is also 14 frames, but the nature of the long-exposure objects changes after two or six frames (called the 'switch time'). If the perceived relative position were sensitive to the nature of the objects, the effective overshoot in the switch conditions would be two and six frames, respectively. Hence, one would expect the same flash-lag effect in both the 2-overshoot and 2-switch condition, and similarly, the same flash-lag for the 6-overshoot and 6-switch condition. The flash-duration is two frames.

I look at two ways in which the nature of the object can be changed. One is shape, the other colour. In the shape experiment, all objects start as round filled circles, but change to squares at the switch-time. The sides of the squares are twice the radius of the circles. In the colour experiment, all objects start as green dots and change to red at the switch-time.

Four subjects perform this experiment. They are instructed specifically to report the perceived onset flash-lag between the dots and ignore the squares (shape experiment) or the green dots and ignore the reds (colour experiments).

3.6.2. Results

Figs. 10 and 11 show that the overshoot dependence is of the same saturating type as in Fig. 4. Hence, relative position perception is not affected strongly by a change in colour or shape. To be more precise, there is a significant effect of overshoot duration ($P < 0.01$) in both experiments. For the colour change experiment, a post-hoc SNK test reveals that the 2-overshoot condition leads to a flash-lag that is significantly different from that in the 2-switch condition. Similarly, the 6-overshoot is different significantly from the 6-switch ($P < 0.01$). The difference between the three data points with an overshoot duration of 14 frames (14-overshoot, 2-switch, 6-switch) is not significant ($P > 0.05$). Taken together, these data show that the colour change does not affect the perceived relative position, only the amount of overshoot is relevant. Hence, the position signal does not know the colour of the object it represents.

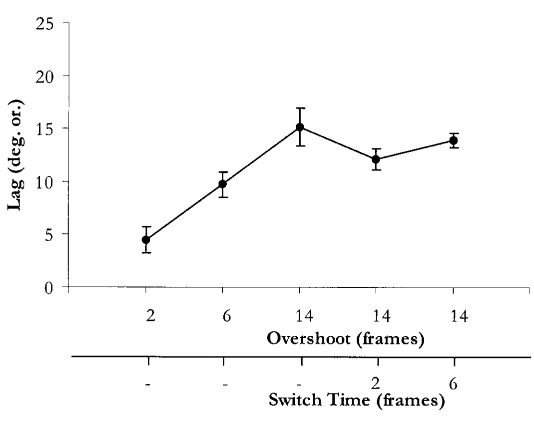

Fig. 10. The position signal is colour blind. The perceived relative position between two objects is not affected by a change in the colour of one of the objects. Data averaged over four subjects, errorbars show ± 1 standard error.

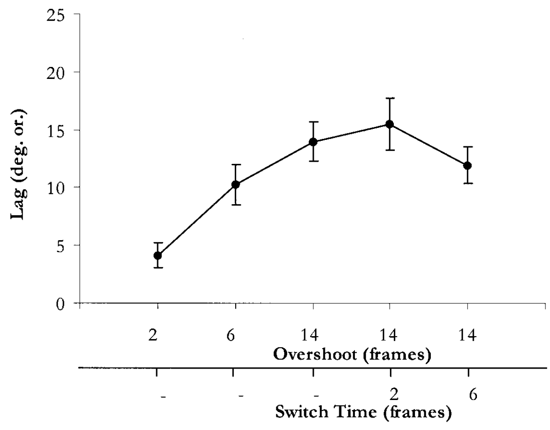

Fig. 11. The influence of a shape change on the perceived relative position of two objects. Data averaged over four subjects, errorbars show ± 1 standard error.

The statistics of the shape change experiment are not as conclusive (Fig. 11). The three datapoints with a 14 frame overshoot duration are not ($P > 0.05$) different significantly, indicating that the total overshoot is the main factor. Moreover, the 2-overshoot and 2-switch conditions are different significantly ($P < 0.01$). This shows that the position signal of very briefly presented objects ($\simeq 4$ frames) does not carry shape information. However, it is possible that the difference between the flash-lag in the 6-overshoot and the 6-switch condition is due to random variations. This opens the possibility that the position signal of objects that have been visible for more than four frames implicitly carries shape-information.

3.6.3. Discussion

This experiment addresses the implicit coding of information on colour and shape in the persisting position signal. Although subjects perceive a change in colour, the flash-lag effect is as large as it would have been without a colour change. This allows us to conclude that the relative position perception mechanism does not notice these colour changes. Hence, the persisting position signal carries no colour information.

The colour experiment does not exclude the possibility that larger changes in the nature of the object affect the position signal more significantly. Such seems indeed to be the case for the change from circle to rectangle. This change, which affects the shape and, to a small extent, the area of the object, does affect the perceived position. This implies that the position signal implicitly codes the information about the shape of the objects whose position it represents. The fact that this could only be demonstrated for objects that have been visible for a relatively long period of time (eight frames = 112 ms), could be taken as an indication that the processing of shape information and its integration into the position signal is relatively slow.

4. General discussion

Krekelberg and Lappe (2000) proposed a model of the flash-lag effect that is based on the spatio-temporal filters of low-level vision. The main features of this model can be understood in an abstraction of the model that postulates the existence of a signal that represents the last-exposed position of an object that is no longer exposed. Here, I investigated this signal, coined position persistence, in more detail. I showed that contrast polarity, while changing visible persistence, does not affect position persistence. Taken together with the findings of Namba et al. (1998) and Whitney et al. (2000), who showed that the flash-lag effect is not due to visible persistence, this demonstrates that position persistence is not the same as visible persistence. Secondly, luminance and eccentricity have no effect on position persistence, while increases in speed and duration reduce position persistence. Although some of the dependencies are similar to visible persistence, the details suggest that different mechanisms underlie these phenomena. Finally, I showed that the persisting signal represents the position without reference to the colour or shape of the object that caused it.

The argument in favour of the existence of position persistence depends on the claim that a slow average of relative position signals explains the flash-lag effect. This implies that if a better explanation of the flash-lag effect is found, there may not be a need to introduce the concept of position persistence. Such an explanation of the flash-lag effect, however, would have to be able to explain not only the basic lag-effect (Metzger, 1931), but also the later additions, including the dependence on frequency, duration and number of the flashes (Bachmann & Kalev, 1997; Lappe & Krekelberg, 1998), the peculiar role of the trajectory of the moving object (Krekelberg & Lappe, 2000, Figure14) and (Whitney et al., 2000, Fig. 5), as well as the overshoot dependence shown in Section 3.1.

The main alternative model for the flash-lag effect is that flashed objects have longer latencies than moving objects (Purushothaman et al., 1998; Whitney et al., 1998). Such a difference in latencies could be caused by a mechanism of visual focal attention and meta-contrast masking (Kirschfeld & Kammer, 1999). The effects of overshoot and flash-duration (Figs. 4 and 8) could, in this view, be interpreted as an incremental reduction of the visual latency with increasing trajectory length. Or, in the model of Kirschfeld and Kammer, the build-up of visual focal attention with time. With the existing experimental data choosing between the model of (Kirschfeld & Kammer, 1999) and ours (Krekelberg & Lappe, 2000) is difficult. This presumably reflects the fact that the underlying form, if not the interpretation, of the spatio-temporal interactions among flashed and moving stimuli is quite similar in these models. Further research of the neural correlates of these psychophysical effects along the lines of (Berry, Brivanlou, Jordan, & Meister, 1999; Jancke et al., 1999) may resolve these issues.

The persisting position represents the last exposed position of an object. This stands in stark contrast to the concept of an interpolated position signal as proposed by Morgan and Watt (1982, 1983). Morgan and Watt showed that the position, at which an object in stroboscopic motion is perceived is the position, at which it would have been if it were in continuous motion. This interpolation, however, is found only for small displacements of the stimulus (4-min arc for a temporal interval of 30 ms, although spatial blurring can increase the temporal limits of integration (Burr, 1981; Fahle & Poggio, 1981)). Hence, phenomenological interpolation is found only for small distances between successive views of an object. This does not mean, however, that an observer cannot interpolate between two successive positions separated by a larger distance. Humans can predict the reappearance of an object that moves temporarily behind an occluder, which shows that they have access to information about the interpolated position. In fact, information about such inferred positions is known to be carried by neurons in the posterior parietal cortex of rhesus monkeys (Assad & Maunsell, 1995). Perceptually, however, this information is not accessible; the object is not perceived at intermediate positions. The signal I discuss in this paper can represent a different aspect of the same stimulus. There is no contradiction in the fact that both aspects of the stimulus are represented. Depending on the task, the visual system reads-out the appropriate signal. In the task we put to the subjects, for instance, they are asked explicitly to compare the positions of two objects. Because one object is exposed only briefly, the system is forced to use the persisting signal and this causes the flash-lag effect. In a different setting, for instance when asked to report the position of a moving object behind an occluder, an interpolating position signal could be used.

A question not addressed in this paper is whether the persisting position signal codes for retinal location or for the position of the object in allocentric coordinates.

It has been reported, however, that a flashed stationary target is perceived to lag behind a target that is pursued with smooth eye movements. In other words, retinal motion is not necessary for the flash-lag effect, motion in allocentric coordinates suffices (van Beers, Haggard & Wolpert, 1999; Schlag, Cai, Dorfman, Mohempour, & Schlag-Rey, 2000). In terms of our model of position perception, this implies that the persisting position signal codes for the position of an object in the world, not on the retina. Visible persistence, on the other hand, is tied closely to retinal coordinates (Irwin, 1992) and may, at least in part, be explained from retinal physiology (Coltheart, 1980). Position persistence makes position information available for a longer time. This may be a strategy of the visual system to process successfully the spatial relationships in a rapidly changing environment. Coding the allocentric position of objects opens up the intriguing possibility that this signal could be used to realign the internal representation of the world after an eye-movement (Lappe, Awater, & Krekelberg, 2000).

Position persistence briefly (− 180 ms) holds on to one aspect (the last exposed position) of a briefly exposed object. As such, a short-term memory for position is not surprising. The iconic memory experiments of Sperling (1960), for instance, have conclusively demonstrated this. Position persistence as I propose here, however, is an intermediate form of memory between the phenomenologically available (visible persistence) and the phenomenologically unavailable (iconic memory). Position persistence does not lead one to perceive an object at its last exposed position, but it affects the perception of the (relative) position of other objects. Viewed from the introspective unity of visual experience, a signal representing only the position of an object without any other properties may seem peculiar. Given our knowledge of parallel processing in the visual system, however, parallel representations of different feature dimensions do not seem to be far-fetched. Section 3.6 shows that the persisting position signal does not encode much information about the shape or colour of the object. One could speculate that those and possibly other aspects of a brief stimulus could be represented in similar persisting signals, which are waiting to be read out when the task requires it. Recent work by (Sheth, Nijhawan, & Shimojo, 2000) seems to support this. Sheth et al. (2000) showed, among other things, that a coloured object that is flashed next to a stationary object with continuously changing colour, appears to lag in colour space. Part of the appeal of an abstract model of the flash-lag effect such as I used here is that it may reflect a general principle of neural computation and is, therefore, easily amenable to different perceptual domains. Analogous to the spatial flash-lag effect, the lag in colour space could in this view result from a comparison of the changing colour signal with a persisting colour signal.

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