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Influence of viewing distance on aftereffects of moving random pixel arrays

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Abstract

Viewing-distance invariance of visual perception has evolutionary advantages, but it is of necessity limited by spatial and temporal resolution. Even within these resolution limits viewing-distance invariance might not be perfect or even good, but there are remarkably few studies of its precise limits. Here we ask to what extent viewing-distance invariance holds for motion aftereffects (MAEs). There are (at least) two different MAEs: one can be seen on a static test pattern (sMAE) and is tuned to low speeds, the other only becomes manifest on a dynamic noise test stimulus (dMAE) and is sensitive to higher adaptation speeds. We show that each of these MAEs has a limited viewing-distance invariance, the dMAE only for higher screen-speeds and the sMAE only for lower screen-speeds. In both cases upper angular-speed limits shift to higher values for smaller viewing-distances (lower spatial frequencies, larger fields). This upper limit is constant, independent of viewing distance, if expressed in terms of screen-speed. On the other hand the lower speed limit is fixed in angular-speed and variable in screen-speed terms. Explanations for these findings are provided. We show that there is no fixed optimum viewing-distance or optimum angular stimulus-size for either of the two MAEs. © 2003 Elsevier Ltd. All rights reserved.

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1. Introduction

If we walk backwards away from a screen displaying motion of constant spatio-temporal properties, we do not usually have the impression that the motion changes in speed, contrast, or detectability, despite the fact that retinal speed and the retinal spatial frequencies change with viewing distance. Casual observations such as these cannot be taken at face value, and in fact it is a priori clear that there must be limits to viewing-distance invariance, such as those set by spatio-temporal resolution. Even within these resolution limits viewing-distance invariance might be less than perfect. For example, the nearer we are to a screen displaying motion, the larger the retinal area covered by the moving images. Therefore one might expect retinal inhomogeneity to play a role. In previous studies it was found that

motion detectors of any given speed-tuning are not distributed evenly across the visual field. The lower their tuning-speed the more they are concentrated in and around the fovea, and the higher their tuning speed the more they are concentrated around higher eccentricities and absent from central regions (van de Grind, Koenickerink, & van Doorn, 1986, 1992). Despite this inhomogeneity, van de Grind et al. (1992) found a wide range of viewing-distance invariance for coherent motion detection in moving random pixel arrays (RPAs, moving Julesz-patterns), and they quantified the limits of this invariance.

Here we ask if movement aftereffect durations show a similar viewing-distance invariance, possibly with similar limits. There are (at least) two independent classes of motion aftereffects (MAEs). If, after adaptation to a moving random dot pattern or to a moving random pixel array (RPA), a drift-free dynamic noise test-stimulus is presented, a MAE is elicited that is phenomenally different (Hiris & Blake, 1992) from the (classical) or 'static' MAE, found with a static test stimulus. It was

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subsequently shown that this ‘dynamic MAE’ or dMAE can be elicited for medium to high speeds, whereas the static MAE (sMAE) stops somewhere around 20°/s, and is thus a low-speed effect (Verstraten, van der Smagt, Fredericksen, & van de Grind, 1999; Verstraten, van der Smagt, & van de Grind, 1998). This finding inspired further research showing that these effects and their underlying systems are mutually independent. If one adapts to two transparently moving RPAs, one of high speed and one of low speed, a static test gives an sMAE opposite the slow adaptation motion, a dynamic test gives a dMAE opposite the fast adaptation motion. If tested with the sum of a static and a dynamic pattern, a transparent MAE results with both components fully present, without apparent interactions (van der Smagt, Verstraten, & van de Grind, 1999). Finally it was shown that the slow and fast motion channels, which we now hold responsible for the sMAE and dMAE respectively, have independent binocular rivalry stages (van de Grind, van Hof, van der Smagt, & Verstraten, 2001). To the extent that these two MAEs indeed probe two independent motion analysis systems it is interesting to quantify their individual viewing-distance dependencies. That is the purpose of this paper, and we will use MAE-duration as a measure of MAE strength.

Early studies by the later Nobel-Laureate Ragnar Granit (1927, 1928) appear to show that there is an optimum distance for eliciting an sMAE in terms of the duration of the effect. Granit quantified the influence of stimulus size on sMAE-duration by changing the viewing distance and reached the conclusion that stimuli larger than 2–4° gave a weaker (shorter) sMAE. Granit’s work was inspired by still earlier findings regarding the MAE, that have survived to the present time, viz.

- (1) if you start at very low speeds the sMAE-duration increases (up to a limit) with speed (Basler, 1909; Kinoshita, 1909; Wohlgenuth, 1911). Comment: We now know that the sMAE-duration decreases again above about 8–12°/s and that there is no sMAE in the fovea above about 20°/s (van de Grind et al., 2001; Verstraten et al., 1998);
- (2) if you start with a small stimulus size the sMAE-duration increases up to a limit with stimulus size (Basler, 1909). With further increase in size the sMAE-duration must decrease again, because for a full field stimulus there is a weak (Thalman, 1921) to very weak sMAE or none at all (Aitken, 1878; Wohlgenuth, 1911).

Granit reasoned from these older findings, that if a stimulus of constant low speed and modest size is brought closer to the eye there is a double reason to expect an increase of sMAE-duration: an increasing angular stimulus size and an increasing angular speed. It was therefore highly surprising that the sMAE-duration

reached its maximum already for viewing distances that made the stimulus a mere 2–4° of visual angle. This optimal stimulus only covered the fovea and a small parafoveal region. Granit’s explanation (in terms of inhibition of central cones by peripheral rods) can nowadays easily be dismissed, but his findings still stand. It appears that nobody has clarified this problem of the influence of viewing-distance on sMAE-duration up to now. Is there an optimal stimulus size or viewing-distance for the sMAE as Granit surmised, and if so why? How is this for the dMAE? We also think it is important for our understanding of the relation between MAEs and motion detection to know whether or not MAEs show viewing-distance invariances commensurate with those found for motion detection (van de Grind et al., 1992).

What kind of influences of viewing distance on MAE-durations do we expect from a more modern perspective? It seems a priori reasonable to expect that low spatial frequencies (close distances) favour high speeds and high spatial frequencies (far distances) favour low speeds. This expectation is based on the idea that a fast and small stimulus will be beyond the temporal resolution of small receptive fields, which will be stimulated too briefly, whereas it can still stimulate larger receptive fields with the same temporal resolution. Moreover, larger receptive fields (bigger cells) are usually faster. This a priori reasoning has been supported by a host of psychophysical studies, including studies on the sMAE. For example, Pantle (1970) found that the higher harmonic components of a low spatial frequency square-wave grating contribute to its detection when it is moved at low speeds, but not at high speeds. This can be explained if low speed units have a higher spatial resolution. Watanabe, Mori, Nagata, and Hiwatashi (1968) had shown that there is an approximate inverse relationship between the spatial frequency of a grating and its optimal speed. This inspired Pantle (1974) to look at consequences for the sMAE of varying the number of sectors of a rotating sector disc. He found that the sMAE had a lower cut-off speed the more sectors he used on the disc (the higher the spatial frequency). He reported that the optimal temporal frequency, in terms of sMAE-duration, was always around 5 Hz and independent of spatial frequency. Wright and Johnston (1985) also found that the MAE is broadly tuned to temporal frequency and that temporal tuning was independent of spatial frequency. In addition they found that the MAE did not change with eccentricity, provided the stimuli were acuity-scaled (M-scaled).

Given the above findings we expect that for any given moving pattern of constant spatial properties and speed on a display screen, the dMAE will have a tendency to increase (or stay constant) for decreasing viewing distance, whereas the sMAE will have a tendency to decrease (or stay constant). This follows from our

assumption that the dMAE reflects adaptation of medium to fast motion sensors and that the sMAE reflects adaptation of slow to medium speed sensors. Viewing-distance invariance will then hold for either MAE as long as an approximately constant number of sensors contribute, regardless of the distance in the invariance-range. This is only expected if either system can ‘recruit’ sufficient sensors of different spatial tunings for different distances. Such a recruitment process can also include an extension to higher eccentricities while an approaching stimulus grows in retinal size. Variation of viewing-distance causes a covariation of overall stimulus size, angular spatial frequency and angular speed, which might complicate its interpretation. Yet, it has the obvious advantage that it is a *natural transformation*, one to which our visual system might have been tuned during evolution. We primarily want to quantify the robustness of this tuning before attempting an explanation. Because we want to compare distance variations (or invariances) of the sMAE and dMAE, it is necessary to use a stimulus that allows such a direct comparison. In our previous studies of MAEs (cited above) moving RPAs were found to be very convenient in this respect, and will therefore be used again. Castet, Keeble, and Verstraten (2002) have argued that sparse random-dot patterns underestimate MAE strength, making RPAs a better choice.

Test and adaptation stimuli in the present study always have the same spatial (broad-band) properties. For narrow-band stimuli (e.g. gratings) this equality of adaptation and test spatial properties was found to be the optimal choice by Ashida and Osaka (1994), Cameron, Baker, and Boulton (1992), and Over, Broerse, Crassini, and Lovegrove (1973). We used RPAs rather than narrow-band stimuli, because they can just as easily evoke a dMAE as an sMAE, and, most importantly, they appear to isolate a high-speed and low-speed motion system quite well. This does not appear to be possible with narrow-band stimuli, such as gratings. To illustrate this we briefly mention work on a MAE caused by adaptation to sinewave gratings, if the test is a counterphase flickering sinewave. We will call this the cMAE (c from ‘counterphase’) and it is presumed to be the closest narrow-band analog of the broad-band dMAE. Ashida and Osaka (1994, 1995) showed that the cMAE is not spatial-frequency selective, and that it is speed-tuned, rather than temporal frequency tuned. These findings suggest a certain similarity between the dMAE and cMAE, but there are also important differences. Whereas it does not seem possible to generate a dMAE with moving sinewave gratings, it is easily possible to evoke a cMAE with moving RPAs. The test then consists of a spatially static RPA of which the light and dark dots change luminance in counterphase. With such a test it was found that the cMAE-duration for RPAs is in between those for the sMAE and dMAE, as if it were

a mixed response of the low speed and high-speed system (van der Smagt, 1999, Chapter 5; van der Smagt, Verstraten, & van de Grind, 2000). This is one reason why we prefer RPAs. They enable us to study the low speed and high-speed system in isolation, using one and the same moving RPA adaptation stimulus and either a static RPA test (unlimited lifetime of the static test pixels) or a dynamic noise test, an RPA with limited lifetime of the static pixels, after which they are randomly refreshed.

In summary: The goal of this paper is to quantify the influence of viewing-distance on both the sMAE and the dMAE, using moving RPAs as adaptation stimuli. The expectation being that we can draw conclusions regarding distance-invariance (or its absence) for the low-speed and high-speed systems separately.

2. Methods

2.1. The psychophysical experiments

Experienced subjects adapted for 30 s to a moving RPA (Julesz-pattern) of 256×256 contiguous square pixels, which were randomly either lighter or darker than the average luminance of 50 cd/m^2 . The size of these ‘screen-pixels’ was fixed by the hardware. Root-mean-square (rms-) contrast of the RPAs was kept constant at 0.7 (70%). Full-screen RPAs were square with sides of 140 mm on the screen, so that the pixel size (height or width) is 0.547 mm. Stimuli were generated by a custom-built hardware device (NIM, noise image machine) on an ElectroHome EVM-1200 monitor with a P4 phosphor. At a speed of 1 ppf (pixel per frame step) and with 256^2 pixels in each frame the maximum-length shift registers of the NIM first start to repeat their sequence after about 24 min. Thus, there is no wrap-around of any kind. Screen speed was usually varied from 6.2 mm/s, which at a frame rate of 90 Hz corresponds to 1 pixel step every 8th frames, to 1188 mm/s, which corresponds to a step-size of 24 pixels every frame. Of course ‘velocity’ is a vector and speed V is the modulus of this vector, but in this paper we are only interested in the influence of *speed*, the direction of motion will not be used as a parameter. Viewing distance was varied in steps of 300 mm between 300 and 3600 mm in some experiments and by distance-doubling between 450 and 3600 mm or between 500 and 2000 mm in other experiments. The authors served as observers in all experiments. They had normal or corrected-to-normal vision. WG (presbyopic) used separately optimised corrections for each of the distances below 1000 mm. The head was stabilised in space with a chin and forehead rest. A mark at the center of the stimulus was fixated both during adaptation and during subsequent testing of MAEs. The test stimulus was a static RPA to

induce the sMAE and an RPA of which all pixels were randomly refreshed every other frame (45 Hz dynamic noise) to elicit a dMAE. Observers pressed a computer key to indicate the end of an aftereffect and the computer then registered MAE-duration. There was a special key to indicate that no MAE had occurred. This is necessary, because it usually takes some time for the observer to be certain that no MAE is seen. Without a special key for this decision one would never measure a duration of 0 s. All measurements were repeated at least 3 times and in a few cases up to 10 times. The various conditions were randomly distributed across sessions of about 1 h each, and ordered quasi-randomly within each session. After every determination of an MAE-duration a pause of 1 min was given to the subjects, who were then warned with a beep that the next adaptation was about to start. The width W or height H of the RPA patterns could be varied independently and could have any integer value between 2 and 256, but we kept $W = H$ and only used the values $H = W = 256$ or 64 pixels in this study. Therefore, only W will be used to specify stimulus size.

2.2. The parameters of interest and their symbolic designation

In this study it is important to keep the various parameter values in terms of pixels on the screen, mm on the screen or degrees of visual angle at the eye clearly apart and to prevent any confusion of symbols. Therefore we will adhere to the following strict conventions. Viewing distance D is always given in mm. However, to specify stimulus width W or speed V we can use pixels (index p), mm on the monitor screen (index m for ‘monitor’ or ‘metric’) or degrees of visual angle (index r from ‘retinal’-measure). Therefore we have three different *speed* symbols V_p in pixels per frame (ppf); V_m in mm/s on the screen; V_r in degrees of visual angle per s ($^{\circ}/s$). Similarly W_p is the stimulus dimension in pixels, W_m in mm, and W_r in degrees of visual angle at the eye. To

denote duration of the static and dynamic MAE, we will use the abbreviations T_s and T_d , respectively. Finally, the size of a pixel on the screen in mm or degrees will be denoted by α . Thus $\alpha_m = 0.547$ mm and α_r is the size of a pixel in deg of visual angle. Table 1 summarises these conventions for ease of reference.

Because $\alpha_m = 0.547$ mm and the framerate of our monitor is 90 Hz, a speed of $V_p = 1$ ppf corresponds to $V_m = 49.5$ mm/s. Neglecting the slight errors for very short viewing distances (in our case max 3.6% at $D = 225$ mm) we have $V_r = 5156.6V_p \arctan[\alpha_m/D]$, with D in mm. The numeric constant in this equation equals 90 (frame rate) times $180/\pi$ since the arctan is in radian and we want V_r in $^{\circ}/s$.

Given a fixed pixel-size on the screen, the retinal pixel-size α_r is completely determined by viewing-distance D , so that viewing-distance invariance could just as well be called retinal-pixel-size invariance. However, we think it is sensible to use the manipulated parameter ‘distance’ in (phenomenological) descriptions of the results, and the equivalent parameter retinal-pixel-size in reasoning about possible underlying physiological mechanisms.

2.3. Data analysis

It is well-known that MAE-duration data are rather ‘noisy’, especially with inexperienced subjects. All classical papers mention this problem and Dureman (1962) showed explicitly that it is not a good idea to use large groups of inexperienced observers in MAE-studies. To reduce the noise one needs subjects who can stick to a chosen criterion. Therefore we used highly trained subjects, the three authors. They had no specific a priori expectations about the outcome of the experiments and could not know or guess which conditions were presented from trial to trial. The data were first analysed after completion of all experiments on all subjects. For our subjects the standard deviations were between 0.1 and 0.25 times the mean for relatively long MAE-durations ($>2-3$ s). However, the relative standard

Table 1

D	Viewing-distance, always in mm. Maximum value 3600 mm
RPA	Random pixel array (Julesz-pattern)
W_p	Width of square stimulus in pixels, maximum $W_p = 256$ pixels
W_m	Stimulus-width in mm; maximum 140 mm for full field of 256×256 pixels
W_r	Angular stimulus-width at the eye-retina in degrees
V_p	Speed on the screen in pixel-steps per frame (ppf)
V_m	Speed on the screen in mm/s; $V_m = 49.5V_p$ mm/s
V_r	Angular speed at the eye-retina in $^{\circ}/s$; $V_r = 5156.6V_p \arctan[\alpha_m/D]$
α_m	Size of a single pixel on the screen in mm: $\alpha_m = 0.547$ mm
α_r	Angular pixel-size at the eye-retina in min arc
T_s	Duration in s of the MAE seen on a static test RPA (sMAE)
T_d	Duration in s of the MAE seen on a dynamic noise test (dMAE)

deviation (ratio of standard deviation to the mean) increased strongly for shorter MAE-durations, and reached values of 1 or more for MAE-durations below about 2 s. A well-known and simple method to further reduce the noise in such data is to use a three-point running average, where each point (except the endpoints) of a graph is averaged with its two neighbours. Fig. 1 illustrates the idea with typical results for one screen speed $V_p = 2$ ppf and one observer (WG). Results

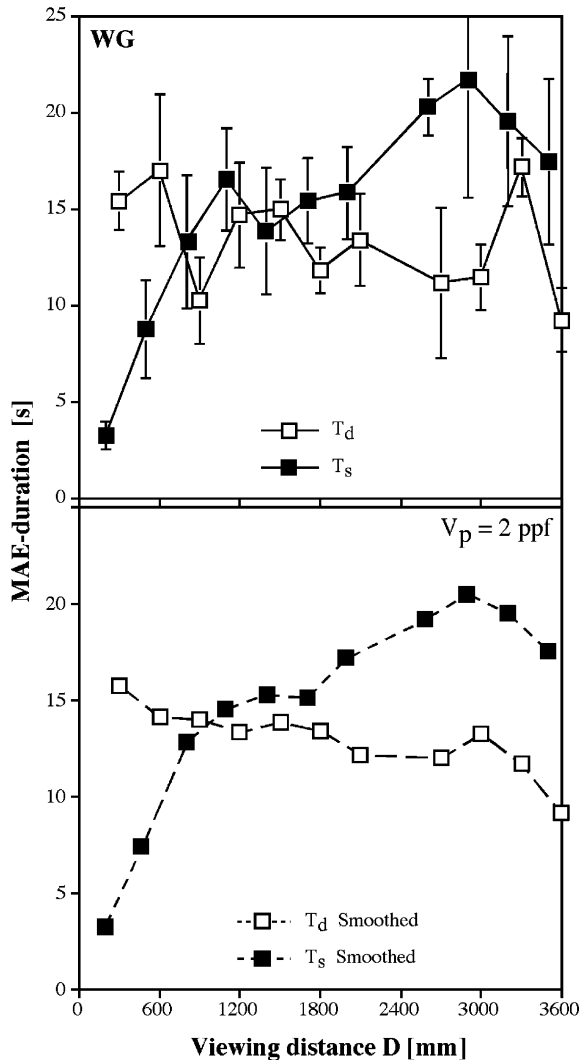


Fig. 1. The upper panel presents sMAE-durations (T_s , filled squares) and dMAE-durations (T_d , open squares) with standard deviations, as a function of viewing-distance D , for a screen-speed of 2 ppf (99 mm/s). The lower panel presents smoothed results. We used a standard three-point running-average smoothing operation, where each data-point except the leftmost and rightmost is averaged with its neighbouring point to the left and the one to the right in the graph. The endpoints are unchanged. It can be seen that this smoothing operation preserves the overall form of the graphs, while making outliers and noise less pronounced. Closed symbols are used in all figures for sMAE-durations, open symbols represent dMAE-durations. The sMAE-curves have been shifted slightly to the left in both panels to prevent cluttering of the standard-deviation bars in the upper panel.

for the sMAE-duration in Fig. 1 have been shifted a scale-equivalent distance of 100 mm to the left, parallel to the abscissa, in order to prevent mutual masking of the standard-deviation bars for the two types of MAE. The bottom panel in Fig. 1 presents results of the smoothing operation. In both panels open squares give results for the dMAE, closed squares for the sMAE.

Fig. 1 illustrates that smoothing by the running average method indeed captures the whole pattern of results very well and minimizes the problem of outliers. In the following we will usually only present the smoothed data and leave out error bars in order to emphasize the general pattern of results. There is one more problem in studying MAE-duration, namely its clear subject-dependence. Some subjects consistently show relatively long durations, others just as consistently show relatively short durations for all conditions, including their optimal conditions for evoking strong MAEs. To deal with this problem we will present both the individual data and the data of a kind of hypothetical observer, constructed by normalising and averaging across subjects, as described in the results section.

3. Results

3.1. Experiment 1: Distance-dependance of MAE-durations

Fig. 2 presents the sMAE-duration (closed symbols) and dMAE-duration (open symbols) for the three subjects WG (top panels), MS (center panels) and FV (bottom panels), as a function of viewing-distance, with screen-speed V_p as a parameter. The data are smoothed as explained in the methods section. The left column gives data for the lower speeds of 0.125 ppf (6.2 mm/s) and 0.5 ppf (24.75 mm/s), the right hand column for the higher speeds of 2 (99 mm/s) and 8 ppf (396 mm/s).

It is clear that there is no *universal* viewing-distance invariance of either of the two types of MAE for the whole screen-speed range. Yet, static MAEs show a reasonable viewing-distance invariance for the lower two screen speeds (left hand column, closed symbols), at least for subjects MS and FV. At $V_p = 2$ ppf (right-hand column, closed triangles) there appears to be an optimal distance for these subjects and at $V_p = 8$ ppf (closed diamonds) all three subjects show an increasing sMAE-duration with increasing distance. This is most probably due to known speed-limits of the sMAE (Verstraten et al., 1998), since the angular speed that corresponds to $V_p = 8$ ppf at a short viewing distance like $D = 300$ mm ($V_r = 75^\circ/s$) is too high for the sMAE, but retinal speed is much lower ($V_r = 6.3^\circ/s$) at $D = 3600$ mm. For subject WG the data for screen-speed $V_p = 2$ ppf show a decrease for short viewing-distances that is similar to the one for $V_p = 8$ ppf. This might indicate a slightly lower

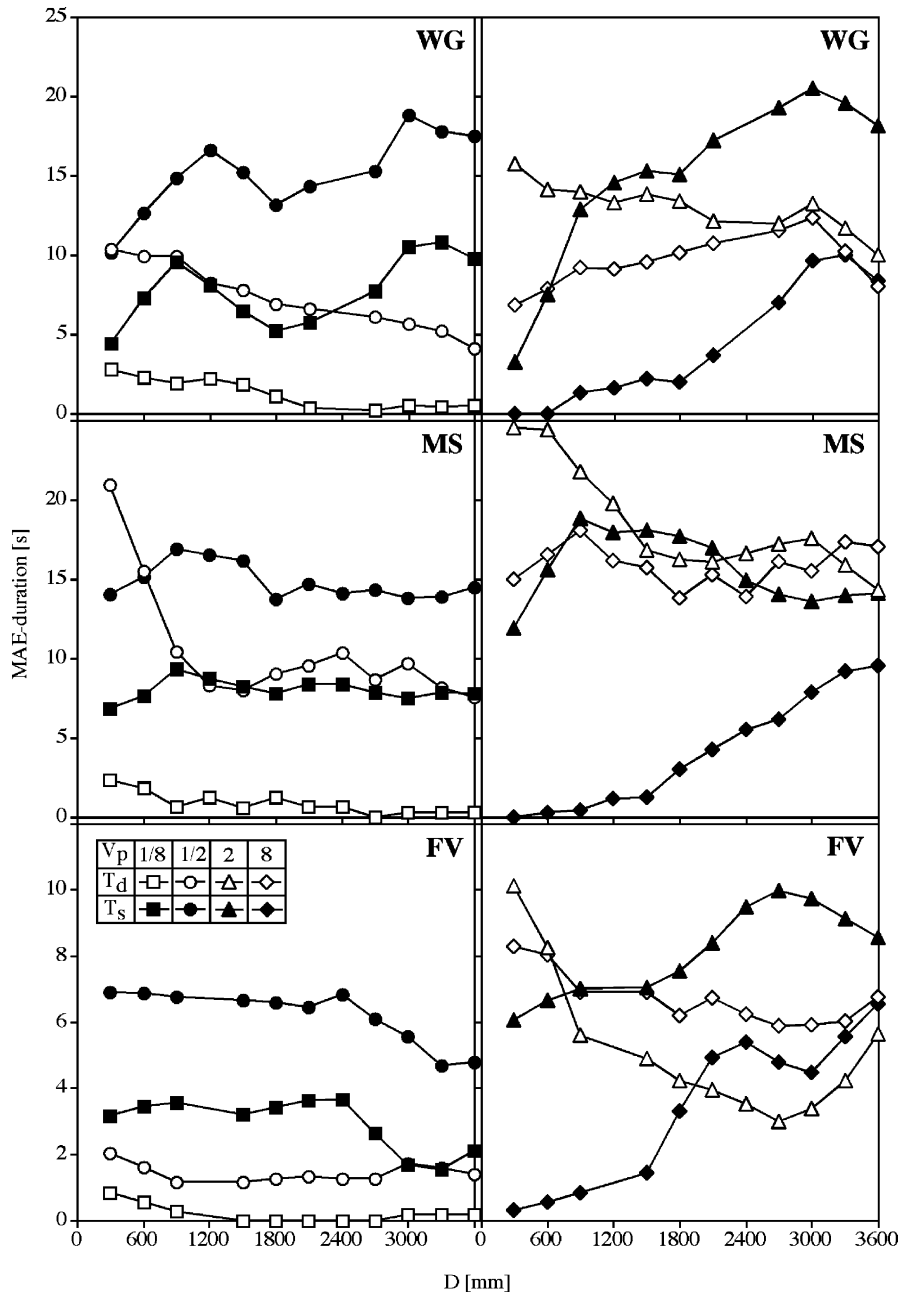


Fig. 2. Durations of the sMAE (T_s , closed symbols) and dMAE (T_d , open symbols) as a function of viewing-distance D for four different screen speeds, and from top to bottom for the observers WG, MS and FV. Left-hand column gives results for the lower speeds of 0.125 and 0.5 ppf, whereas the right hand column presents results for the higher speeds 2 and 8 ppf. All data are smoothed in the way illustrated in Fig. 1. Circles, triangles, squares and diamonds represent screen-speeds V_p of 0.125, 0.5, 2 and 8 ppf, respectively (see inset in the bottom left panel), a convention that is also used in the Figs. 1, 3 and 6 (and not applicable in the Figs. 4 and 5).

cut-off speed for his sMAE than for the other two subjects. For the dMAE Fig. 2 shows that there was no dMAE to speak of at the lowest screen speed of $V_p = 0.125$ ppf (open squares), regardless of viewing-distance. For the next higher speed (0.5 ppf, open circles) there is a decrease of dMAE-duration T_d with distance, except perhaps for FV. At 2 ppf (open triangles, right hand column) there is a range of viewing-distance invariance for the dMAE beyond about 1.5 m

viewing-distance and an increase for shorter distances (and thus higher angular speeds). At the highest speed $V_p = 8$ ppf (open diamonds) there is viewing-distance invariance for subjects MS and FV and a slight increase of dMAE-duration with distance for WG. Taken together, this is not a very simple pattern of results.

To remove some of the complexities resulting from individual differences and thus simplify the presentation, one could average across subjects. However, the

absolute values of MAE-durations tend to be strongly subject dependent and are often widely different for different observers. For example, MS usually has about double the MAE-durations of FV. To take this general difference into account we correlated the data of our subjects pairwise, taking MS as the norm, by determining regression lines. Thus we found:

$$T_d(\text{WG}) = 0.584T_d(\text{MS}) + 1.09 \quad r^2 = 0.884$$

$$T_d(\text{FV}) = 0.33T_d(\text{MS}) - 0.392 \quad r^2 = 0.682$$

$$T_s(\text{WG}) = 0.918T_s(\text{MS}) + 0.722 \quad r^2 = 0.705$$

$$T_s(\text{FV}) = 0.403T_s(\text{MS}) + 0.921 \quad r^2 = 0.662$$

Neglecting the small biases, these formulae were then used to scale MAE-durations of FV and WG up to the level of those of MS, a step we call ‘normalisation’ (results for MS being the norm). After that we averaged these normalised data for the three subjects. The results of Fig. 2 can then be summarised as in Fig. 3. A visual comparison of Figs. 3 and 2 will convince the reader that

Fig. 3 captures the general pattern of results of Fig. 2 quite well, but simplifies them by averaging out the idiosyncracies of individual subjects. The resulting curves can be thought of as representing data for a hypothetical average subject.

For the lower two screen speeds (upper panels) the sMAE (filled symbols) shows viewing-distance invariance, but at the higher two speeds (lower panels) the sMAE-duration shortens for shorter viewing-distances. This is no doubt a reflection of the upper speed limit of the sMAE, since retinal (angular) speed increases up to 18.8°/s in the lower-left panel for the shortest distance, and up to 75.2°/s in the lower-right panel. The static MAE is known to break down around 20°/s (Verstraten et al., 1998), so the results in Fig. 3 are in line with expectations based on previous results. Apparently the sMAE shows viewing-distance invariance as long as retinal speed stays below some upper limit of, say, 10°/s. The precise value of this limiting speed is subject-dependent and not of present concern.

The dMAE only shows viewing-distance invariance for the highest screen-speed used in this experiment

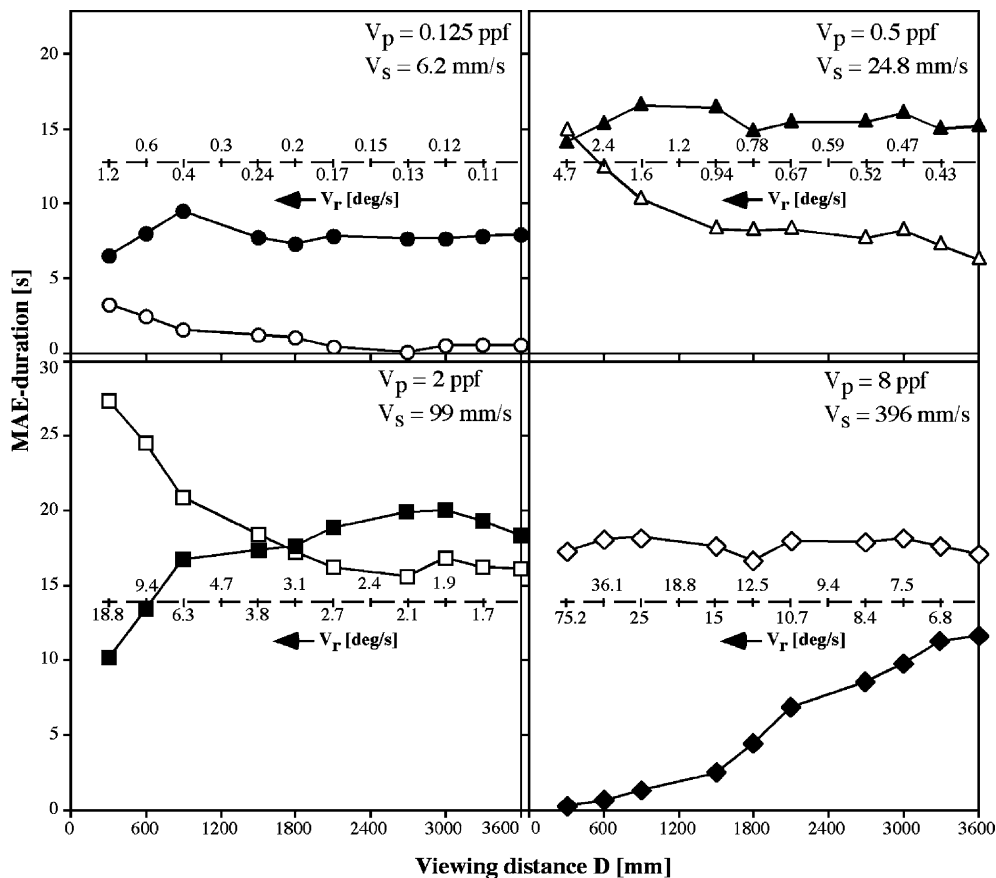


Fig. 3. Normalised MAE-durations averaged across observers, as a function of viewing-distance for the same screen-speeds as in Fig. 2. The normalisation operation, taking the data of observer MS as ‘norm’, is explained more fully in the text. Briefly, pairwise regressions were used to scale the data of FV and WG and make them overall as compatible with the data for MS as possible. After that we averaged across observers. Viewing-distance invariance is signified by horizontal regions of the graphs, as summarised in the text. A retinal-speed (V_r) scale is included in each of the panels to facilitate the interpretation of limitations to viewing-distance invariance, as discussed in the text.

(open diamonds, lower-right panel in Fig. 3). At lower speeds, such as 2 and 0.5 ppf, dMAE-duration increases for decreasing viewing-distance, which might simply reflect speed-tuning of the dMAE. At short viewing-distances and $V_p = 2$ ppf we see the longest of all MAE-durations measured in our experiments. This can be traced to the results for the subjects FV and MS in Fig. 2, and it shows that a dMAE can be just as long-lasting as a sMAE if the conditions are right. One of the conditions that appears to be favourable for long-lasting dMAEs is a retinal speed of 20–30°/s combined with large pixels (close viewing-distance). This follows from a comparison of dMAE data in the lower-right and lower-left panels of Fig. 3. In the lower-right panel retinal speeds range from 6.3°/s at 3600 mm viewing distance to 75°/s at 300 mm viewing distance. Therefore, it also covers the retinal speed of 18.8°/s that gives a considerably longer dMAE-duration in the bottom-left panel (the leftmost open square symbol). If one and the same retinal speed gives such different MAE-durations in the two cases and the only difference is viewing distance, it seems reasonable to conclude that either the pixel-size or the total stimulus-size or both are responsible for this. We think pixel-size is likely to be the physiologically most important factor here, because the total motion information (number of pixels) is constant, but spread out over a larger retinal area for shorter viewing-distances. This should hinder rather than promote (distance-limited) spatial summation of motion signals, so if the duration increases despite this overall size-increase we think it is likely due to stronger stimulation of individual local high-speed motion sensors by larger pixels.

The sMAE of our average observer in Fig. 3 appears to have an optimum viewing-distance of around 900 mm for the lowest speed, corresponding to a stimulus-diameter of about 9°, but this is a rather shallow optimum. Furthermore the results indicate that the two MAEs do not show a general viewing-distance invariance commensurate with that reported for motion detection by van de Grind et al. (1992). This might be due to the fact that detection uses both the low-speed and high-speed system, whereas the two MAEs appear to isolate these systems and represent them separately (see Section 4).

3.2. Experiment 2: Influence of speed on MAE-durations

In the first experiment we took 4 fixed screen-speeds and varied the viewing-distance. Therefore retinal (angular) speeds changed automatically with viewing-distance and were not varied independently. This limits the conclusions we can draw concerning the influence of angular speed as distinct from that of the other co-varying parameters, retinal stimulus-size and pixel-size. However, it is much too time-consuming to measure complete MAE-duration speed-tuning curves for three

subjects and two types of test stimulus at the ten distances used above. We therefore decided to measure the duration of both MAEs for one observer (WG) as a function of retinal speed for a coarser sampling of the viewing-range of 3600 mm. We chose the viewing-distances 3600, 1800, 900 and 450 mm. This should suffice, since the experiment mainly aims to provide a clarification of some aspects of the above data set. The other two subjects did the third experiment, which is designed to partly disentangle the parameters angular stimulus-size and pixel-size, as described later.

Fig. 4 summarises results of the speed-tuning experiment in two different forms. The left column gives MAE-duration as a function of screen-speed V_p , with sMAE-data (closed symbols) in the upper and dMAE-data (open symbols) in the lower panel. The right-hand column of Fig. 4 presents the same duration-data as a function of retinal (angular) speed V_r , also with sMAE-results in the upper and dMAE results in the lower panel. Downward arrows indicate that the MAE-duration for the next higher speed was 0 s, no MAE at all.

The left-hand column in Fig. 4 shows that there appears to be a rather fixed upper screen speed for MAE-generation, regardless of viewing distance, except perhaps for the smallest distance of 450 mm. Such a fixed upper screen speed is remarkable, since screen speed is not an internal, physiological, parameter. If we plot the data against retinal speed, as in the right hand column, we see that the upper angular cut-off speed for both MAEs depends on the viewing-distance (that is, on the spatial dimensions on the retina). It increases for shorter viewing-distances, that is for larger retinal sizes of the pixels and stimulus width. Thus, the left-hand column of Fig. 4 shows that there is a kind of viewing-distance invariance for the high-speed limits of MAEs. The right-hand column suggests that this must be due to the recruitment of motion sensors with larger receptive fields, tuned to higher speeds, for smaller viewing-distances: larger pixels give higher cut-off angular speeds. The basis for understanding this phenomenon is likely to be that motion sensors with receptive field sizes on the order of the pixel-size dominate in the stimulated population (van de Grind et al., 1992).

The low-speed results for the various viewing-distances come together in a common envelope in both right-hand panels of Fig. 4. These common low-speed envelopes are different for the two types of MAE: compare upper and lower panel of the right-hand column in Fig. 4. The sMAE shows low-pass and the dMAE shows bandpass properties in the angular-speed domain. Of course, eventually also sMAE-duration must drop to zero before a speed zero is reached, so on a coarser scale it must also have bandpass-properties in the angular-speed domain. However, with a lowest speed of 0.1°/s, as used in these experiments, the sMAE curves (closed symbols) do not yet fall off appreciably.

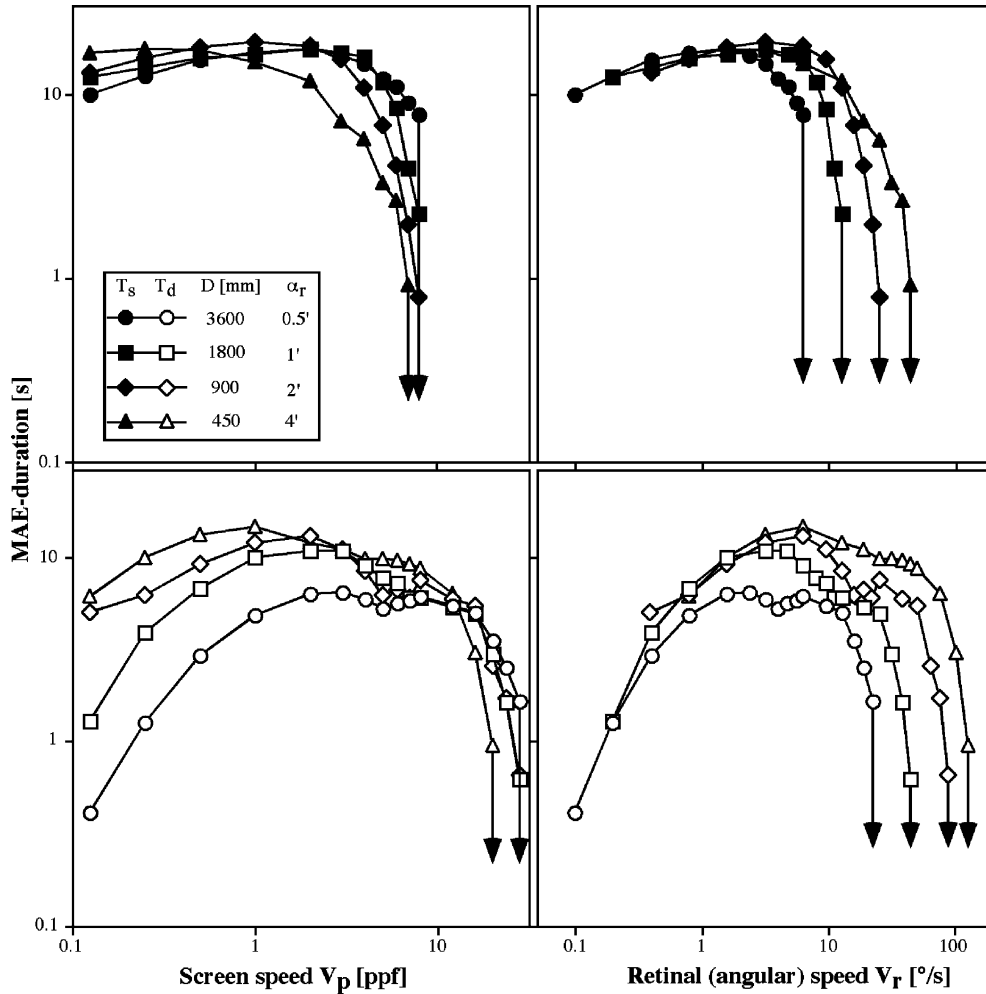


Fig. 4. For one observer (WG) we measured duration-versus-speed curves for 10 or more speeds at 4 distances to complement the data in the previous figures. The upper graphs are for the sMAE (closed symbols), the lower panels for the dMAE (open symbols). The left hand column presents MAE-durations as a function of screen-speed V_p in ppf, the graphs on the right present durations as a function of angular (retinal) speed V_r in $^\circ/s$. The high-speed fall-offs in the left column are almost viewing-distance invariant, except for the smallest viewing-distance. On the right we see that this is caused by an increasing cut-off angular speed for shorter distances, larger stimuli. As seen in the right-hand curves, the low-angular-speed cut-off is almost independent of viewing-distance, which means that viewing-distance matters in terms of screen-speed, as discussed in the text.

In contradistinction, the dMAE-curves (open symbols) clearly do. The left-hand column of Fig. 4 shows that low screen-speed MAE-durations depend on viewing-distance, whereas the right hand column shows that the low retinal-speed MAE-durations do not. This might reflect the fact that any given low screen speed gives higher retinal speeds for closer viewing-distances and we are at the left side of the speed-tuning curves where higher retinal speeds give longer-lasting MAEs.

The main conclusions derived from Fig. 4 are:

1. High screen-speed viewing-distance invariance for both MAEs is probably due to recruitment by the coarser texture and/or the larger retinal stimulus-size (approaching screen) of coarser motion sensors, which are tuned to higher speeds. The sMAE has a much more limited recruitment range so that its

high-speed invariance is lost sooner than for the dMAE. In both cases the process breaks down for very close viewing-distances, where angular-speeds are too high and/or pixels too large to stimulate sufficient numbers of motion sensors.

2. The MAE-duration for low speeds is completely determined by retinal speed and there are no possibilities for recruiting additional low-speed motion sensors for decreasing retinal pixel-size and stimulus-size. The relatively flat retinal-speed tuning curve for sMAE-duration (low-pass) ensures that the sMAE is reasonably viewing-distance invariant in the low-speed range. The steep fall-off for the dMAE severely limits its viewing-distance invariance for low speeds. Observe how the fused low-speed roll-offs in the right-hand column translate into a spread in the low-speed regions of curves in the left column in Fig. 4.

3.3. Experiment 3: Influence of stimulus-size and grain-size on MAE-durations

To partly disentangle the influence of stimulus-size and pixel-size at short viewing-distances we did a third experiment, involving the other two subjects (MS and FV). A stimulus of 64×64 pixels spans (about) the same visual angle at distance D as a stimulus of 256×256 pixels at a distance of $4D$. If we compare the speed-tuning curves of both MAEs for these two cases of equal angular stimulus-size, any differences in the results are likely due to the differences in angular pixel-size. There is again a confounding variable in such an experiment, however, viz. the number of pixels in the stimulus. If we also measure the tuning-curves for 256×256 pixels at the closer viewing distance we might be able to estimate the influence of this parameter as well.

We chose the distances 500 and 2000 to compare stimuli of equal angular-size, of 64^2 and 256^2 pixels, respectively. Results, consisting of sMAE-durations (left column, closed symbols) and dMAE-durations (right-hand column, open symbols), are presented in Fig. 5 for the subjects MS (upper row) and FV (lower row). Despite differences in detail between the two subjects, especially concerning absolute duration values, the overall pattern of results is similar and consistent. Comparing the dotted curves ($D = 2000$ mm, 256^2 pixels, triangles) to the results for an equal angular stimulus-size but 4 times shorter viewing-distance (circles), shows that the larger pixels in the latter case promote MAEs at higher speeds but lead to weaker MAEs at lower speeds. The high-speed improvement is amplified if the closer stimulus is enlarged to 256^2 pixels (square symbols in Fig. 5), but the weakening at the low-speed end is not com-

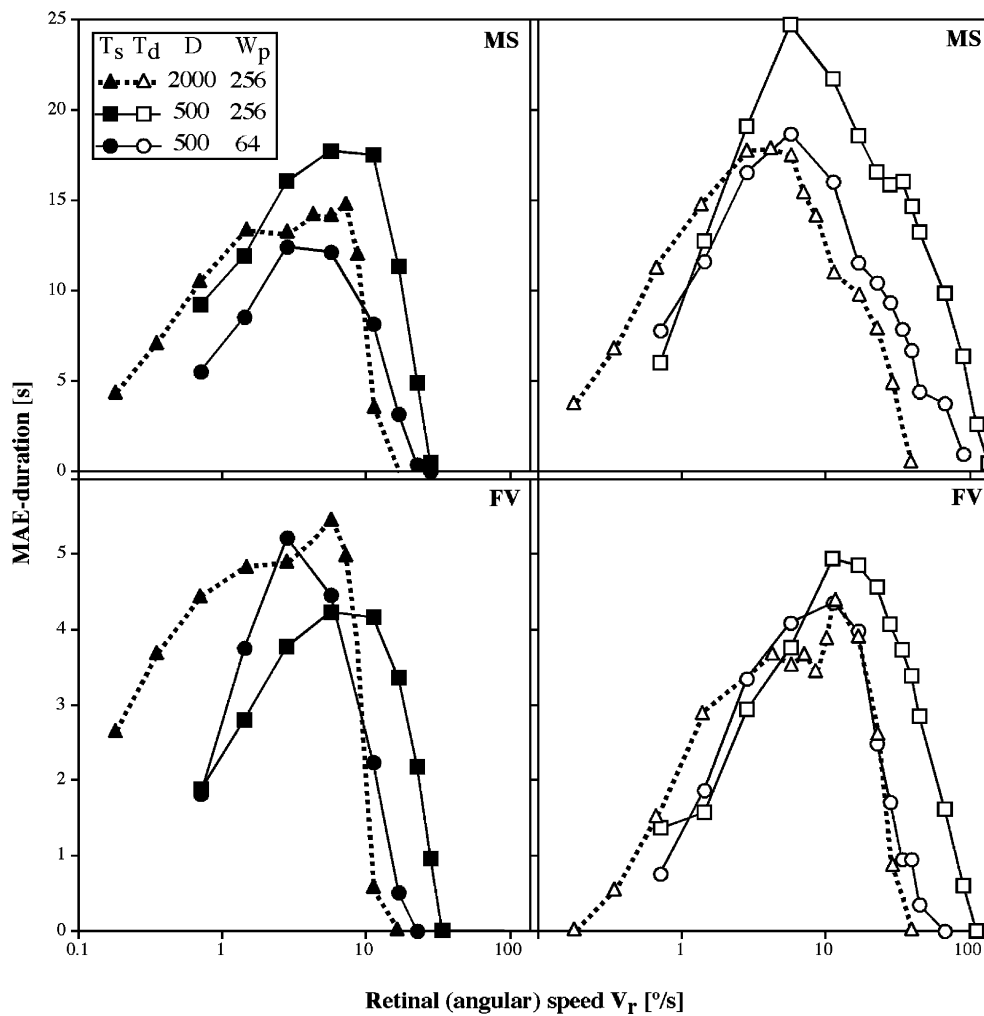


Fig. 5. MAE-durations as a function of angular speed for equal angular-size stimuli at 2000 mm (triangles, $W_p = 256$) and 500 mm (circles, $W_p = 64$) and for a stimulus with a size ($W_p = 256$) equal to the former, but viewing-distance (500 mm) equal to the latter (squares). Results for two observers: MS in the upper panels and FV in the lower panels. On the high-speed end larger pixels give longer MAE-durations for both stimulus-width values W_p , so larger pixels promote longer durations at higher speeds. On the low-speed end durations are always longer for the farther stimulus, indicating that low-speed motion sensors prefer smaller pixels. These rules appear to hold both for the dMAE (right-hand column) and sMAE (left-hand graphs).

compensated by this enlargement. At low-speeds MAE-durations increase for smaller pixel-sizes (larger viewing-distances), almost regardless of the overall stimulus-size on the screen (64^2 or 256^2 pixels). This can be understood if we assume that low-speed motion sensors have small receptive fields, so that a stimulus of small pixels is more effective at low speeds than if the pixels are larger, even if equally numerous.

4. Discussion

For a range of tested distances (300–3600 mm) we found in the first experiment (Figs. 2 and 3) that:

- 1a. the sMAE showed a reasonably good viewing-distance invariance for low screen-speeds of around 6 mm/s;
- 1b. there was no dMAE at these low speeds for larger viewing-distances and hardly any for shorter viewing-distances in the tested range;
- 2a. the dMAE showed a reasonably good viewing-distance invariance for high screen-speeds of around 400 mm/s;
- 2b. the sMAE was non-existent for these high screen speeds at viewing distances below about 1.5 m, but increased gradually for larger viewing distances;
3. both MAEs showed viewing-distance invariance only for distances beyond about 1.5 m for medium speeds of around 25–100 mm/s. At these medium speeds the dMAE increased and the sMAE decreased for shorter viewing distances.

These results are compatible with our proposal (van de Grind et al., 2001; van der Smagt et al., 1999) that the sMAE and dMAE reflect actions of automatic gain-control processes in a low-speed (form-from-motion) and a high-speed (navigational) motion vision system, respectively. They also fit nicely with earlier findings summarised in Section 1, suggesting that motion sensors tuned to high speeds have large and those tuned to lower speeds have smaller receptive fields (Pantle, 1970, 1974; Watanabe et al., 1968). It was also found from motion detection thresholds for moving sinewaves (Anderson & Burr, 1985) and moving RPAs (van de Grind et al., 1992), that lower spatial frequencies increase high-speed sensitivity and decrease low-speed sensitivity, and vice versa for high spatial frequencies. The medium speed-range results in Fig. 3 suggest that the sum or average of the durations of the two types of MAE shows a better viewing-distance invariance than either of the MAEs in isolation. This ties in with the better viewing-distance invariance of motion detection (van de Grind et al., 1992), if it is assumed that the two separate motion systems, isolated in sMAE and dMAE phenomena, cooperate in motion detection tasks.

In the second experiment (Fig. 4) we found that the upper dMAE and sMAE cut-off *screen*-speeds do not depend on viewing distance, except perhaps for very short viewing-distances (below 450 mm). Fig. 4 also clarifies how this viewing-distance invariance is obtained or approximated. An approaching screen with translational fronto-parallel motion recruits more and more motion-sensors with larger receptive fields, which are tuned to higher speeds. Therefore the high *angular*-speed end of the curves in Fig. 4 (right hand column) shifts with changing viewing-distance. This happens in such a way, that viewing-distance invariance is obtained, as seen from the common high screen-speed envelopes in the left column of Fig. 4. Retinal inhomogeneity (larger receptive fields at higher retinal eccentricities) probably contributes significantly to this intriguing viewing-distance invariance.

For low screen-speeds dMAE-durations are far from viewing-distance invariant, but sMAE-durations approximate it (left column Fig. 4). The right-hand column of Fig. 4 shows that the low-speed limitation is defined by a common envelope for all distances, but this envelope is different for the sMAE and dMAE. Clearly, retinal (not screen) speed completely determines MAE-durations in this low-speed range, both for the sMAE and the dMAE. Because the common low speed envelope for the sMAE, as seen in the upper-right panel of Fig. 4, is rather flat this does not limit distance-invariance too severely, as confirmed in the upper-left panel of Fig. 4. On the other hand, the common low-speed envelope for the dMAE (lower-right panel in Fig. 4) is rather steep. Since larger viewing-distances lead to lower retinal speeds, this steep low retinal-speed curve explains why the dMAE-duration is lower for larger viewing-distances at a fixed low screen-speed. The bottom-left panel in Fig. 4 confirms this and shows how a common steep low-speed envelope in a $T - V_r$ graph translates into a divergence of $T - V_p$ curves for the different distances. Fig. 5 shows that both the sMAE and dMAE-durations at low angular speeds increase for smaller pixels, regardless of angular window-size. These findings are compatible with the idea that low-speed motion detectors have small receptive fields, that are most effectively stimulated by small pixels (e.g. van de Grind et al., 1992), and that do not appear to contribute significantly to the fast motion system (the dMAE).

Taken together the results support model-assumptions developed in previous work from our laboratory, both on motion detection and on MAEs (van de Grind et al., 1986, 1992, 2001; van der Smagt et al., 1999; Verstraten et al., 1998). In addition, the presented results clarify a long-standing problem, first posed explicitly by Granit (1927, 1928): how to explain changes of the MAE with viewing distance. The present results show that the optimal angular stimulus size depends on various parameters, such as speed and grain-size (spatial

frequency content) of the adaptation stimulus, and is therefore not tied to a fixed retinal map of receptor types, as Granit assumed. To make this explicit we replot the results from Fig. 4 in a different format in Fig. 6. In the upper panel we see T_s as a function of angular stimulus-diameter W_r , in the lower panel T_d is also plotted against W_r . A few additional data points had to be measured at $D = 225$ mm to be able to illustrate how the trends continue for larger stimulus diameters.

In Fig. 6 we see in the upper panel that there is usually some optimal stimulus diameter for the sMAE, but that this optimum changes with screen speed V_p . At low screen speeds the optimum is found around 20° , after which it moves to smaller angular sizes for successively higher speeds. The dMAE-results in the lower panel in Fig. 6 show an increasing duration with increasing angular stimulus-size W_r and pronounced optima are only found for speeds above 4 ppf. This is due to the upper speed limit of the dMAE, because 4 ppf at

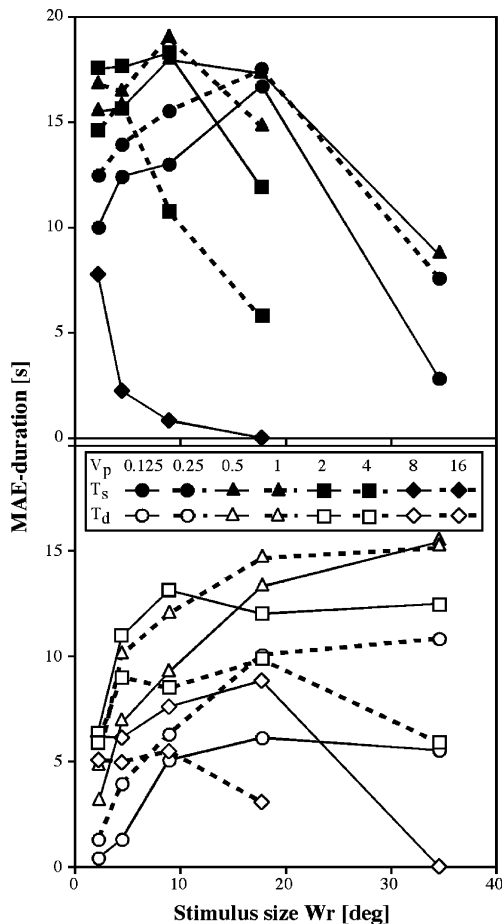


Fig. 6. Data from Fig. 4 are replotted as a function of angular stimulus size, to see whether there is an optimal stimulus size for either of the MAEs or both. Closed symbols for the sMAE and open symbols for the dMAE-duration. As explained more fully in the text, we conclude from these results that the optimal angular stimulus-size depends on pixel-size and screen-speed and is not a simple parameter that directly reflects fixed lateral interactions in the visual field.

$D = 225$ mm corresponds already to $48.6^\circ/s$, 8 ppf to about 97 and 16 ppf to about $194^\circ/s$. In this very high speed range even the dMAE decreases toward zero. In general the dMAE appears to be at or close to its optimum for stimulus-sizes of around 20° (Fig. 6), and about constant for larger sizes, provided the retinal speed is not prohibitive.

Our results show that Granit's (1927, 1928) suggestion of an optimal angular stimulus size for the sMAE should be reformulated. For any given motion stimulus there always appears to be some range of optimal angular stimulus-sizes if only the viewing-distance is varied. However, this range can sometimes be large and the optimum rather flat. Moreover, the value of the optimum angular subtense depends upon screen-speed, screen-size and spatial frequency content of the stimulus. This might explain the strong contrast between Granit's finding of a decrease of sMAE-duration for decreasing distance (increasing stimulus-size) and Freud's (1964) finding of an increase. Either finding can be replicated over some range of distance changes for an appropriate choice of spatial frequency content, screen-speed, and screen-size. Similarly, Costello (1960) reported (for the spiral sMAE) that the sMAE reduces for decreasing viewing-distance and constant angular size. Fig. 6 shows that this would also hold for our stimuli at low speeds, but that the reverse might be found for higher speeds. Of course, this reasoning from our broadband results to results and interpretations for moving gratings and spirals is hazardous. It is known from electrophysiology that moving gratings strongly stimulate simple cells in the primary visual cortex of cats and monkeys, whereas moving RPAs more strongly (and in some cases exclusively) stimulate complex cells, at least in the cat (e.g. Edelstyn & Hammond, 1988; Hammond, 1991; Hammond & MacKay, 1975, 1977; Hammond & Pomfrett, 1989; Vajda, Lankheet, van Leeuwen, & van de Grind, 2002; van Wezel, Lankheet, Fredericksen, Verstraten, & van de Grind, 1997; van Wezel, Lankheet, Verstraten, Marée, & van de Grind, 1996; but see Casanova, Savard, Nordmann, Molotchnikoff, & Minville, 1995). Therefore there is a possibility that broadband results (adaptation of complex cells?) might not be directly indicative of results that would hold for narrow-band stimuli (adaptation in simple cells?). Yet, to the extent that receptive field properties of the retina, or of common integration areas beyond V1 play a dominant role, one might nevertheless expect analogous or in some cases even identical results for broadband and narrow-band stimuli.

Assuming for a moment such a direct analogy between results for narrow-band and broad-band stimuli, one might be inclined to suggest that the viewing distance invariance for the sMAE at low speeds (Figs. 2–4) 'follows' from previous narrow-band studies. Pantle (1974), for example, reported that MAE-duration did

not depend on spatial frequency or speed, but solely on the temporal frequency of moving periodic stimuli (see also Ashida & Osaka, 1994, 1995; Wright & Johnston, 1985). Because the temporal frequency of our stimuli was not varied as viewing-distance changed, viewing-distance invariance of the sMAE-duration could be viewed as mirroring fixed temporal tuning of the sMAE. One problem with this reasoning is, however, that a decreasing viewing distance leads to an increasing eccentricity of the moving texture's outer edges. Previous results (van de Grind, Verstraten, & Zwamborn, 1994; Wright & Johnston, 1985) suggest that unchanging performance can only be expected if the pixel sizes at all eccentricities stand in equal ratios to the local acuities. This means that the interaction of a changing angular size of the stimulus with retinal inhomogeneity must play a role, and that a fixed temporal frequency tuning cannot in itself provide an explanation for the viewing-distance invariance of sMAEs. The explanation must therefore be more complicated. In addition temporal frequency tuning has not been shown to hold for a sMAE induced by moving RPAs (broadband stimuli). In fact, the relationship between narrow-band and broad-band results still needs to be worked out, and we expect it to be far from straightforward. For example, although RPAs have an approximately white power spectrum up to a frequency equal to the inverse angular pixel size, it is not necessarily correct to reason in terms of the frequency contents of this spectrum. Such reasoning neglects the phase spectrum, that is position information, and is only sensible if the processing system is linear (Westheimer, 2001). The linearity condition is certainly not met by the complex cells mentioned above, which just might be responsible for the detection of RPA-motion.

Until these problems are worked out, the safest summary of the present study is that viewing distance invariance for broadband stimuli (RPAs) holds for the sMAE at low speeds and for the dMAE at high speeds. At intermediate speeds dMAE increases and sMAE decreases as viewing-distance decreases, at least within the studied range of viewing distances. Given our cited previous work with moving RPAs it seems reasonable then to first of all conclude from these findings, that the low-speed system shows viewing-distance invariance only at low speeds, and the high-speed system only at high speeds. At medium speeds the low-speed system and high speed-system change sensitivity in opposite directions for decreasing viewing distance (third panel in Fig. 3). Therefore the second conclusion might be that the two systems, though having independent gain-controls, cooperate during motion detection, leading to an approximate distance invariance for *detection* tasks in the middle range of speeds as well (van de Grind et al., 1992). Many of these effects are most probably based on (1) properties of universal front-end (retinal) receptive fields

feeding into cortical motion sensors of various types, (2) the division of neurons across the two speed-tuned systems, and (3) the spatial distribution of differently sized front-end cells across the retina (see also van de Grind et al., 1986, 1992). This makes it likely that our results are indicative of the above re-interpretation of findings by Granit and others, despite the fact that one cannot blindly trust a Fourier-based reasoning to translate broad-band into narrow-band results or vice versa.

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References

- Aitken, J. (1878). On a new variety of ocular spectrum. *Proceedings of the Royal Society of Edinburgh*, 10, 40–44.
- Anderson, S. J., & Burr, D. C. (1985). Spatial and temporal selectivity of the human motion detection system. *Vision Research*, 25, 1147–1154.
- Ashida, H., & Osaka, N. (1994). Difference of spatial frequency selectivity between static and flicker motion aftereffects. *Perception*, 23, 1313–1320.
- Ashida, H., & Osaka, N. (1995). Motion aftereffect with flickering test stimuli depends on adapting velocity. *Vision Research*, 35(13), 1825–1833.
- Basler, A. (1909). Über das Sehen von Bewegungen. III. Mitteilung. Der Ablauf des Bewegungsnachbildes. *Archiv für die gesammte Physiologie des Menschen und der Thiere*, 128, 145–176.
- Cameron, E. L., Baker, C. L., & Boulton, J. C. (1992). Spatial frequency selective mechanisms underlying the motion aftereffect. *Vision Research*, 32(3), 561–568.
- Casanova, C., Savard, T., Nordmann, J. P., Molotchnikoff, S., & Minville, K. (1995). Comparison of the responses to moving texture patterns of simple and complex cells in the cat's area 17. *Journal of Neurophysiology*, 74(3), 1271–1286.
- Castet, E., Keeble, D. R. T., & Verstraten, F. A. J. (2002). Nulling the motion aftereffect with dynamic random-dot stimuli: Limitations and implications. *Journal of Vision*, 2, 302–311.
- Costello, C. G. (1960). Further observations on the spiral after-effect. *Perceptual and Motor Skills*, 11, 324.
- Dureman, I. (1962). Factors influencing the apparent velocity of visual movement after-effects. *Scandinavian Journal of Psychology*, 3, 132–136.
- Edelstyn, N. M. J., & Hammond, P. (1988). Relationship between cortical lamination and texture-sensitivity in complex neurones in the striate cortex in cats. *Journal of Comparative Neurology*, 278, 397–404.
- Freud, S. L. (1964). The physiological locus of the spiral after-effect. *American Journal of Psychology*, 77, 422–428.
- Granit, R. (1927). Über eine Hemmung der Zapfenfunktion durch Stäbchen-erregung beim Bewegungsnachbild. *Zeitschrift für Sinnesphysiologie*, 58, 95–110.

- Granit, R. (1928). On inhibition in the after-effect of seen movement. *British Journal of Psychology*, 19, 142–157.
- Hammond, P. (1991). On the response of simple and complex cells to random dot patterns: A reply to Skottun, Grosz and De Valois. *Vision Research*, 31(1), 47–50.
- Hammond, P., & MacKay, D. M. (1975). Differential responses of cat visual cortical cells to textured stimuli. *Experimental Brain Research*, 22, 427–430.
- Hammond, P., & MacKay, D. M. (1977). Differential responsiveness of simple and complex cells in cat striate cortex to visual texture. *Experimental Brain Research*, 30, 275–296.
- Hammond, P., & Pomfret, C. J. D. (1989). Directional and orientational tuning of feline striate cortical neurones. Correlation with neuronal class. *Vision Research*, 29, 653–662.
- Hiris, E., & Blake, R. (1992). Another perspective on the visual motion aftereffect. *Proceedings of the National Academy of Sciences USA*, 89, 9025–9028.
- Kinoshita, T. (1909). Über die Dauer des negativen Bewegungsnachbildes. *Zeitschrift für Sinnesphysiologie*, XLIII, 434–442.
- Over, R., Broerse, J., Crassini, B., & Lovegrove, W. (1973). Spatial determinants of the aftereffect of seen motion. *Vision Research*, 13, 1681–1690.
- Pantle, A. (1970). Adaptation to pattern spatial frequency: Effects on visual movement sensitivity in humans. *Journal of the Optical Society of America*, 60(8), 1120–1124.
- Pantle, A. (1974). Motion aftereffect magnitude as a measure of the spatio-temporal response properties of direction-sensitive analyzers. *Vision Research*, 14, 1229–1236.
- Thalman, W. A. (1921). The aftereffect of seen movement when the whole visual field is filled by a moving stimulus. *American Journal of Psychology*, 32, 429–440.
- Vajda, I., Lankheet, M. J. M., van Leeuwen, T. M., & van de Grind, W. A. (2002). On the velocity-tuning of area 18 complex cell responses to moving textures. *Visual Neuroscience*, 19, 651–659.
- van de Grind, W. A., Koenderink, J. J., & van Doorn, A. J. (1986). The distribution of human motion detector properties in the monocular visual field. *Vision Research*, 26(5), 797–810.
- van de Grind, W. A., Koenderink, J. J., & van Doorn, A. J. (1992). Viewing-distance invariance of movement detection. *Experimental Brain Research*, 91, 135–150.
- van de Grind, W. A., van Hof, P., van der Smagt, M. J., & Verstraten, F. A. J. (2001). Slow and fast visual motion channels have independent binocular rivalry stages. *Proceedings of the Royal Society London B*, 268, 437–443.
- van de Grind, W. A., Verstraten, F. A. J., & Zwamborn, K. M. (1994). Ensemble models of the movement aftereffect and the influence of eccentricity. *Perception*, 23, 1171–1179.
- van der Smagt, M. J. (1999). *Integration and segregation mechanisms in human motion vision*. Ph.D. thesis, Utrecht University, ISBN 90-393-2100-0.
- van der Smagt, M. J., Verstraten, F. A. J., & van de Grind, W. A. (1999). A new transparent motion aftereffect. *Nature Neuroscience*, 2(7), 595–596.
- van der Smagt, M. J., Verstraten, F. A. J., & van de Grind, W. A. (2000). Do motion aftereffects depend on test-pattern temporal frequency? *Perception*, 28c(Suppl).
- van Wezel, R. J. A., Lankheet, M. J. M., Fredericksen, R. E., Verstraten, F. A. J., & van de Grind, W. A. (1997). Responses in complex cells in cat area 17 to apparent motion of random pixel arrays. *Vision Research*, 37(7), 839–852.
- van Wezel, R. J. A., Lankheet, M. J. M., Verstraten, F. A. J., Marée, A. F. M., & van de Grind, W. A. (1996). Responses of complex cells in area 17 of the cat to bi-vectorial transparent motion. *Vision Research*, 36(18), 2805–2813.
- Verstraten, F. A. J., van der Smagt, M. J., Fredericksen, R. E., & van de Grind, W. A. (1999). Integration after adaptation to transparent motion: static and dynamic test patterns result in different aftereffect directions. *Vision Research*, 39(4), 803–810.
- Verstraten, F. A. J., van der Smagt, M. J., & van de Grind, W. A. (1998). Aftereffect of high-speed motion. *Perception*, 27(9), 1055–1066.
- Watanabe, A., Mori, T., Nagata, S., & Hiwatashi, K. (1968). Spatial sine-wave responses of the human visual system. *Vision Research*, 8, 1245–1263.
- Westheimer, G. (2001). The Fourier theory of vision. *Perception*, 30, 531–541.
- Wohlgemuth, A. (1911). On the after-effect of seen movement. *British Journal of Psychology, Monograph Supplement*, 1, 1–117.
- Wright, M. J., & Johnston, A. (1985). Invariant tuning of motion aftereffect. *Vision Research*, 25(12), 1947–1955.