

# Nulling the motion aftereffect with dynamic random-dot stimuli: Limitations and implications

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We used biased random-dot dynamic test stimuli to measure the strength of the motion aftereffect (MAE) to evaluate the usefulness of this technique as a measure of motion adaptation strength. The stimuli consisted of noise dots whose individual directions were random and of signal dots moving in a unique direction. All dots moved at the same speed. For each condition, the nulling percentage (percentage of signal dots needed to perceptually null the MAE) was scaled with respect to the coherence threshold (percentage needed to perceive the coherent motion of signal dots without prior adaptation). The increase of these scaled values with the density of dots in the test stimulus suggests that MAE strength is underestimated when measured with low densities. We show that previous reports of high nulling percentages at slow speeds do not reflect strong MAEs, but are actually due to spatio-temporal aliasing, which dramatically increases coherence thresholds. We further show that MAE strength at slow speed increases with eccentricity. These findings are consistent with the idea that using this dynamic test stimulus preferentially reveals the adaptation of a population of high-speed motion units whose activity is independent of adapted low-speed motion units.

**Keywords:** motion adaptation, integration, segregation, aliasing, eccentricity, density

## Introduction

After adaptation to motion in a given direction for a period of time, a stationary pattern appears to move in the opposite direction. This illusory motion, known as the motion aftereffect (MAE) or waterfall illusion (for an overview, see [Mather, Verstraten, & Anstis, 1998](#)) can also be observed when the test stimulus presented after adaptation is random dynamic visual noise (RDVN). This RDVN stimulus consists of dots whose individual directions are random across time (noise dots). [Hiris & Blake \(1992\)](#) emphasized that the MAE experienced with a RDVN test was a spatially global percept in which all the dots seemed to move in the same direction. More importantly, [Blake & Hiris \(1993\)](#) reported that this dynamic MAE can be perceptually nulled if a certain percentage of these dots, the so-called signal dots, coherently move opposite to the MAE direction (this biased DVN was introduced by [Newsome & Paré, 1988](#)). By nulling, they meant that the aftereffect experienced with a biased DVN (with an appropriate percentage of coherent dots) could not be distinguished from the percept elicited by an unadapted RDVN: that is, in both cases, the stimulus appeared as randomly moving dots without any global direction. The percentage of coherent dots needed to achieve perceptual nulling, i.e., absence of a global motion direction, was taken as an index of MAE

strength. This percentage was usually around 40% in their work.

This technique aims at avoiding some problems associated with previous null test methods ([Pantle, 1998](#)). In the simplest method, the whole test stimulus is moved in a direction opposite to that of the MAE, and its speed is increased until it appears stationary. The main theoretical problem in this case is that there is no clear relationship between the speed and the strength of a MAE. In a second class of methods, the test stimulus is dynamic. For instance, the test can be a grating whose phase shifts each frame by 180 deg. Without adaptation, the test appears either as a stationary flickering stimulus or as a bi-stable stimulus whose direction alternates across time between rightwards and leftwards. After adaptation in one direction, the probability of perceiving the test as moving in the opposite direction is increased. This effect is measured by slightly reducing or increasing the phase shift until the test appears either as a stationary flickering stimulus or as a bi-stable stimulus without any net preferred direction. Although rarely acknowledged as a limitation, the multistability of the test stimulus in this class of methods is obviously one serious methodological problem because it implies, among other things, a large inter- and intra-subject variability ([Ashida & Osaka, 1995](#)). Using a biased DVN as the test stimulus does

overcome these problems because it contains only one nominal speed and is not directionally bi-stable.

Despite these advantages, we believe that the nulling technique introduced by [Hiris & Blake \(1992\)](#) raises a few questions. The first aim of this work is to define more clearly the conditions in which nulling percentages truly reflect MAE strength rather than other factors. Our first observation is that the nulling percentage alone is not an accurate measure of MAE strength as it depends, for a given condition, on the effectiveness of signal dots in carrying unidirectional motion energy among the noise dots ([Barlow & Tripathy, 1997](#)). We therefore systematically measured motion coherence thresholds for the different conditions investigated ([Newsome, Britten, & Movshon, 1989](#)), and we expressed MAE strength as the ratio of the nulling percentage to the motion coherence threshold.

When we started using this technique, it appeared that observers had difficulty performing the task in some conditions. The main problem being that the MAE could not be satisfactorily cancelled: the aftereffect experienced with the biased DVN never appeared to be a set of randomly moving dots without any net direction. Instead, signal dots appeared to be sliding over the noise dots as soon as the percentage of signal dots exceeded the coherence threshold by a small amount. To address this problem, we found it useful to characterize more explicitly the mechanisms underlying the nulling technique. It was first noted that nulling the MAE with a biased DVN, in contrast with other nulling methods, relies on the integration of motion signals (noise and signal dots) scattered across space ([Vidnyanszky, Blaser, & Papathomas, 2002](#)). Truly nulling the MAE implies that the signal dots added in the test stimulus to cancel the aftereffect are not perceptually segregated from the noise dots. To interpret this observation, results pertaining to the issue of motion transparency have to be considered. Factors determining whether dots moving in different directions produce motion transparency or not were first investigated by [Qian, Andersen, & Adelson \(1994\)](#). They showed that motion transparency induced by two sets of dots moving in opposite directions can be suppressed by manipulating the spatial relationships between dots in the following way: dots were paired so that the two dots in each pair moved in opposite directions and were in close proximity (about  $0.2^\circ$ ). Additionally, dots moved over a short distance (i.e., with a short lifetime). In other words, when each pair of dots was contained within a small area, transparency was abolished. By increasing this area, transparency gradually reemerged. To explain these results, [Qian et al. \(1994\)](#) suggested that motion signals extracted within small areas by V1 cells go through a motion opponent suppression stage before being spatially pooled by MT units (the integration stage). Pairing the dots as they did yields strong mutual suppression of oppositely moving dots, and thus no input to MT cells.

This framework offers a convenient way of explaining the mechanisms at work in the nulling technique. Being able to find a null point implies that motion signals elicited by coherent and noise dots are integrated at the suppressive stage. And this is possible only if signal dots (or at least a portion of them) happen to be spatially paired by chance with the noise dots that elicit MAE activity. Therefore, we have assumed that our initial difficulty in observing a true null point was caused by a parameter that decreased the probability of these pairings. More precisely, our hypothesis is that the density of the dots, which was low in our initial measurements, is the key parameter. Our general point is that the nulling method is not very effective at low densities, i.e., when the probability of chance pairings is low, because signal dots added in the test stimulus are not efficiently combined or paired with the noise dots. The consequence is that the nulling percentage measured with low densities is small, i.e., close to the coherence threshold, because it mainly reflects a motion transparency threshold. Signal dots thus produce motion transparency before the MAE is completely cancelled, and consequently the nulling percentage underestimates MAE strength. In contrast, the nulling method should be more effective at higher densities, i.e., when each added signal dot is likely to be paired with noise dots underlying the MAE. Motion transparency thresholds should now be much higher than coherence thresholds, which are known to be relatively unaffected by density ([Barlow & Tripathy, 1997](#)). It has indeed been shown that increasing density does increase the probability of pairings occurring by chance and therefore impairs motion segregation ([Mestre, Masson, & Stone, 2001](#)). Therefore, we predict that nulling percentages measured at high densities will be higher than at low densities because they will be more related to the perceptual nulling of the MAE.

We found another problematic aspect of this nulling technique when we tried to replicate the initial findings of [Hiris & Blake \(1992\)](#). These authors reported high nulling percentages (about 40%) with stimuli moving at 2 %/s (the sole speed they used), whereas we obtained very low values (<5%) in preliminary experiments using the same speed. We therefore tried to find the relevant factors causing this discrepancy. The factor that turned out to be important was the spatio-temporal sampling of the moving dots.

In summary, we hope this work will help future MAE researchers use the DVN nulling technique efficiently.

## General Methods

### Stimuli

Stimulus sequences were produced by a computer-controlled graphics board (VSG 2/3; Cambridge Research Systems Ltd., UK) displayed on a Sony 21" FD

Trinitron (1392 columns X 1026 lines, refresh rate: 69 Hz).

Animation sequences were created online by displaying current dots on the monitor while simultaneously drawing the dots for the next frame in video memory. All signal dots were repositioned in the same direction (upward or downward) at a fixed distance, whereas noise dots were repositioned at a fixed distance but in random directions from frame to frame. Adaptation stimuli contained 100% signal dots (upward or downward). A wrap-around procedure was used to reposition dots reaching any border of the square aperture. The viewing distance was 228 cm (each pixel subtended 0.007°). The screen subtended 9.7° X 7.2°. The dots subtended 0.028° (4 X 4 pixels). The luminances of the dots and the background were 69 and 13.8 cd/m<sup>2</sup>, respectively.

## Procedure

### Nulling percentage

The procedure was the same for all experiments. On each trial, the adaptation pattern was presented for 10 s (60 s for the first trial of the block) and, after an interval of 500 ms, the test pattern was displayed for 1 s. Successive trials were separated by an interval of 1 s. After the test pattern disappeared, observers pressed one of two buttons to indicate the direction (upward or downward) of the dots that appeared to have a global motion. Formulated in this way, the task could be applied to the two different kinds of percepts experienced in our work: (a) In some cases, when MAE strength was low, the dot signals were perceived as moving transparently against a background of jittering noise dots. Then observers indicated the direction of the perceptually segregated signal dots. (b) When all the dots (noise + signal) appeared to move coherently, observers indicated the direction of this global motion.

We measured a nulling percentage, i.e., the proportion of signal dots moving in a given direction that produced on average as many upward as downward responses. This percentage was either positive, indicating that the signal dots moved in the same direction as the adaptation stimulus (i.e., opposite the MAE), or negative when the signal dots moved opposite to the adaptation stimulus. Therefore, a 0% corresponded to RDVN.

On each trial, the direction and the percentage of signal dots were controlled by a 0.5 staircase procedure. An upward response decreased the percentage of signal dots presented on the next trial, whereas a downward response increased the percentage. The initial step (16%) used to vary the percentage was halved after the first and the second reversals. After these two reductions, the step was constant (4%). The starting value of a staircase was randomly chosen between -8% and +8%. Two 0.5 staircases were randomly interleaved within an

experimental block. A block ended after 8 reversals in each of the two independent staircases. The mean of the last 6 reversal points was taken as the 0.5 threshold. Error bars (shown in the top graphs) for the nulling percentages represent standard errors.

### Coherence thresholds

We also measured coherence thresholds without prior adaptation (Newsome et al., 1989). On each trial, the direction and the percentage of signal dots were controlled by two randomly interleaved staircases which converged respectively toward 0.29 and 0.71 probabilities of perceiving upward motion (Levitt, 1971). Observers indicated if net perceived direction was upward or downward. A block ended after 8 reversals in each of the two independent staircases. For each staircase, the mean of the last 6 reversal points was taken as the threshold. Thresholds reported here were defined as half the difference between both thresholds (0.71 and 0.29). Calculated errors for the coherence thresholds were standard errors. The coherence thresholds were used to scale the nulling percentages. The errors (shown in the bottom graphs) for these ratios were calculated by summing the percentage errors for the nulling value and the coherence threshold.

## Experiment 1

The purpose of this experiment was to test our prediction (see “Introduction”) that the sensitivity of the DVN nulling method to reveal MAE strength can be enhanced by increasing the density of the dots.

### Stimuli

Stimuli were centered on the middle of the screen (0° eccentricity). The dot speed was constant (1.5 °/s): the position of the dots changed by 3 pixels (stepsize: 0.021°) every 14.5 ms, i.e., the effective position change rate was the same as the refresh rate of the monitor (69 Hz). Dots had a limited lifetime of 200 ms. The angular size of the square aperture containing the dots was 1.5°. Adapt and test stimuli had either the same or different densities, which were chosen from two values (39 dots/deg<sup>2</sup> or 311 dots/deg<sup>2</sup>), thus resulting in four different combinations.

## Results and Discussion

The top graphs of Figure 1 show the nulling percentages measured for both observers. Data for upward and downward adaptation have been collapsed. When the density is the same for both the adapt and test stimuli, nulling percentages are small for the low density, whereas they become larger for the high density (gray bars).

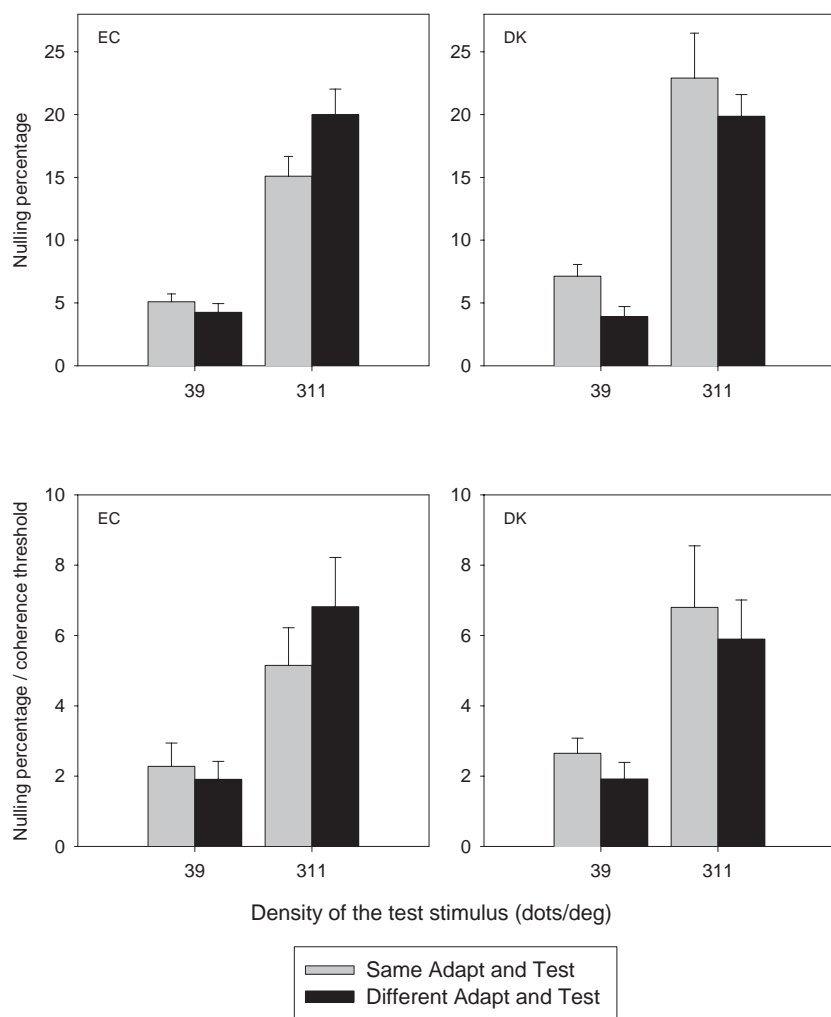


Figure 1. Results of Experiment 1 for two observers: Effect of the density of the dots. The dots moved at 1.5 °/s in 1.5° X 1.5° aperture centered on the fovea. In the top graphs, percentage of signal dots required to null the MAE is plotted against two different densities of the test stimulus. The adaptation and the test stimulus could have the same density (gray bars) or different densities (black bars). The nulling percentage is always higher when the test stimulus has the highest density, irrespective of the density of the adaptation stimulus. In the bottom graphs, this pattern of results remains the same when nulling percentages are divided by coherence thresholds measured with the two different densities.

Does the increase of the nulling percentage reflect an increase in MAE strength due to motion energy of the adapt stimulus being higher with the higher density? To answer this question, we performed a cross-adaptation experiment. As shown by the black bars, the results show that the increase in nulling percentage is mainly due to the density of the test stimulus: adapting with a high density stimulus and testing with a low density stimulus still produces small nulling percentages, whereas low density adaptation with high density testing entails large nulling percentages. The larger values obtained with the higher test density, irrespective of the adapt density, are difficult to account for in terms of different MAE strengths. In contrast, these results are consistent with our hypothesis (see “Introduction”). It seems that the density of dots in the test stimulus affects the probability that signal and noise dots be spatially paired by chance (Qian

et al., 1994). With a high density in the test stimulus, signal and noise dots have a high probability of their motion being integrated due to their spatial proximity. Therefore, nulling percentages are more likely to reflect a true nulling of the MAE. However, with a low density, signal and noise dots do not efficiently cancel each other so that nulling percentages reflect motion transparency thresholds and, therefore, underestimate MAE strength.

This global pattern of results remains unchanged when nulling percentages are divided by motion coherence thresholds measured in the two density conditions (bottom graphs). This results from the small effect of dot density on the detection of signal dots, as would be expected from previous results (Barlow & Tripathy, 1997), and indicates that the large differences in nulling percentages are not due to a reduced efficiency of the signal dots in the high-density condition.

## Experiment 2

The nulling percentages measured in Experiment 1 seemed to us much smaller than the initial values (about 40%) reported by [Hiris & Blake \(1992\)](#). In Experiment 2, we started to investigate the reasons for this discrepancy. We first discarded speed because these authors used a 2°/s speed similar to ours (1.5°/s). Density of the dots was not a good candidate: actually, Experiment 1 showed that density increases nulling percentages and this would predict very small values in the work of [Hiris & Blake \(1992\)](#) because they used a smaller density (12 dots/deg<sup>2</sup>) than our smallest.

The first factor that we considered as a good reason for the discrepancy was eccentricity because the authors presented their stimuli in the periphery (about 4 deg) compared to our foveal presentation. Therefore we measured nulling percentages in Experiment 2 as a function of eccentricity. We also tried to mimic the experimental conditions used by [Hiris & Blake \(1992\)](#) as closely as possible (especially density).

### Stimuli

Two hundred moving dots were presented within a square aperture subtending 4° X 4° (diameter: 3.25 deg in

[Hiris & Blake, 1992](#)). This resulted in a dot density of 12.5 dots/deg<sup>2</sup> (close to the density of 12 dots/deg<sup>2</sup> as used by [Hiris & Blake, 1992](#)). Dot lifetime was 500 ms. The speed of the dots was the same as in the previous experiment. Stimuli could be presented at 1 of 3 different eccentricities: 0°, 4° or 7°. The midpoint of the distance between the fixation point and the square aperture was centered on the middle of the screen (i.e., the fixation point was to the left and the aperture to the right).

### Results

The results for both observers are similar and are shown in [Figure 2](#). Adapting and testing in the fovea yield a very weak nulling percentage (top graphs). Increasing eccentricity, however, produces an increase of the null point. Scaling these data with the motion coherence thresholds obtained at the 3 eccentricities does not change the pattern of results (bottom graphs). This indicates that the effect of eccentricity is not primarily due to the signal dots being less efficient, as would be expected, for example, from the loss of spatio-temporal acuity in the periphery ([van de Grind, van Doorn, & Koenderink, 1983](#)).

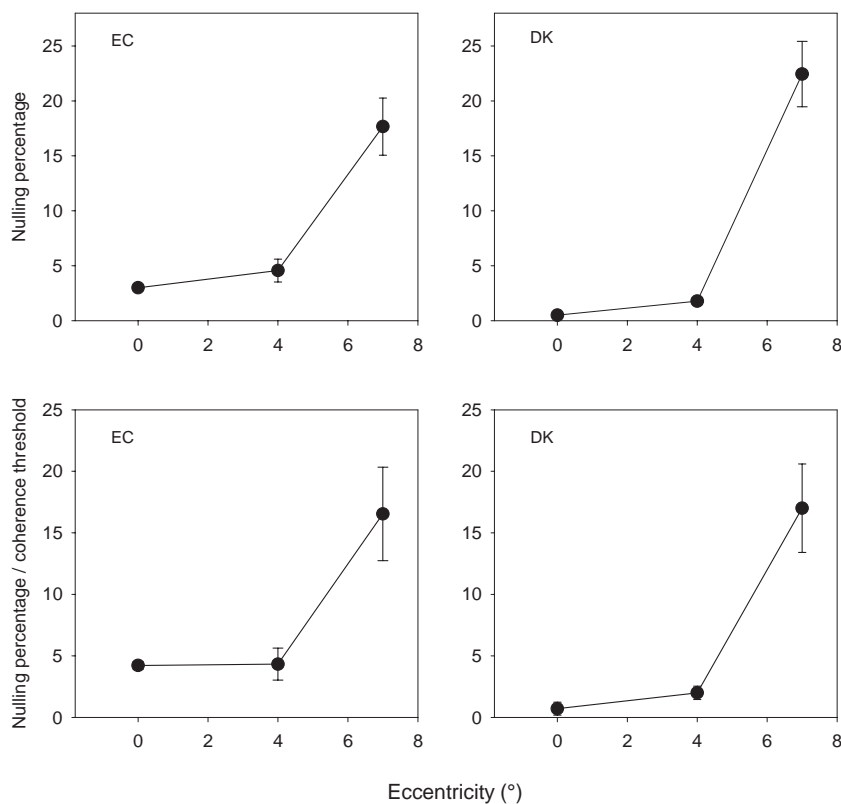


Figure 2. Results of Experiment 2 for two observers: Effect of eccentricity. The dots moved at 1.5 °/s within a 4° X 4° aperture. Observers fixated a point located at different eccentricities relative to the middle of the aperture. In the top graphs, the percentage of signal dots needed to null the MAE is plotted as a function of eccentricity. The same effect of eccentricity can be seen in the bottom graphs, where nulling percentages have been scaled with respect to coherence thresholds measured for the 3 eccentricities.

## Discussion

These results seem to indicate that MAE strength increases with eccentricity. This effect is at first sight not easy to interpret because the trend of our data is opposite to that reported by [van de Grind, Verstraten, & Zwamborn \(1994\)](#). These authors reported that increasing eccentricity for a constant retinal velocity up to around 10 °/s reduces MAE strength. Their conclusion was that reduced MAE in the periphery resulted from increasing scarcity of low-speed sensors at increasing eccentricities ([van de Grind, Koendering, & van Doorn 1986](#)). This idea is quite plausible because they used a static test pattern that was supposed to preferentially reveal the activity of low-speed units.

To interpret our results, it is necessary to rely on recent advances on mechanisms underlying the MAE. It has been suggested that two populations of motion detectors tuned to fast and slow speeds have independent involvement in generating a MAE, depending on the nature of the test stimulus ([Verstraten, van der Smagt, & van de Grind, 1998](#); [van der Smagt, Verstraten, & van de Grind, 1999](#); [Verstraten, van der Smagt, Fredericksen, & van de Grind, 1999](#); [van de Grind, van Hof, van der Smagt, & Verstraten, 2001](#)). A static test pattern will produce an aftereffect that will mainly depend on the degree of adaptation of low-speed units. This would explain the previously mentioned result that MAE strength is reduced in the periphery with a static test pattern ([van de Grind et al., 1994](#)). In contrast, when the test pattern is dynamic, the MAE will preferentially reveal the adaptation state of higher speed units. In our case, the test pattern is indeed dynamic as all the dots are in motion. Moreover, the spectrum of DVN stimuli contains higher speeds than the nominal speed due to the correspondence problem introducing spurious pairings between successive frames ([Barlow & Tripathy, 1997](#)). To interpret the increase in MAE strength with eccentricity, we propose that the DVN test stimulus is more likely to reflect adaptation of high-speed units. Thus, at 0° eccentricity, MAE strength is weak both because adaptation speed is low and because high-speed units are scarce in the fovea. In contrast, the larger number of high-speed units at higher eccentricities ([van de Grind et al., 1986](#)) proportionally increases the number of adapted units and causes a stronger MAE.

In summary, our tentative conclusion is that our findings can be accommodated with those of [van de Grind et al. \(1994\)](#) if we adopt the recent framework that two independent populations of motion detectors (low- and high-speed tuned) underlie the MAE. The relevant difference in the two studies is the nature of the test stimulus. Dynamic test stimuli, as in our study, tend to increase MAE strength in the periphery, whereas static test stimuli have the opposite effect. Finally, regarding the initial purpose of the experiment, we note that the nulling percentage values (even with the 7° eccentricity)

are still much lower than the high values reported by [Hiris & Blake \(1992\)](#). We investigated this issue further in the next experiment.

## Experiment 3

In the previous experiment, we found that eccentricity was not the factor accounting for the high nulling percentages reported by [Hiris & Blake \(1992\)](#). In this experiment, we tested whether the crucial factor to replicate their finding was the spatio-temporal separation travelled by the dots on each frame (for a constant speed of 1.5 °/s).

### Stimuli

Apart from spatio-temporal aliasing, stimuli were the same as in the previous experiment with the foveal presentation. The dot speed was constant (1.5 °/s) and was obtained in two ways: (a) In the *smooth* condition, the position of the dots changed by 3 pixels (stepsize: 0.021°) every 14.5 ms, i.e., the effective position change rate was the same as the refresh rate of the monitor (69 Hz). (b) In the *jittering* condition, the position of the dots changed by 12 pixels (stepsize: 0.084°) every 58 ms, i.e., the effective position change rate was one fourth of the monitor refresh rate (69 Hz/4= 17.25 Hz). This condition is similar to that used by [Hiris & Blake \(1992\)](#). Although not mentioned in their study, they actually used an effective position change rate of 67 Hz/4=16.75 Hz ([Hiris, personal communication, 2000](#)). Adaptation and test patterns were either smooth or jittering, resulting in four possible conditions.

### Results

The pattern of results is the same for both observers ([Figure 3](#)). First, when both the adaptation and the test patterns contain jittering (spatio-temporally aliased) dots, i.e., as in [Hiris & Blake \(1992\)](#), with about the same speed, we can replicate the results reported by these authors. Namely, the percentage of dots needed to null the MAE when looking at the biased DVN is around 50% for both observers (gray bar with an asterisk). However, still using the same speed (1.5 °/s), the results are completely different when the adaptation and test patterns are both in smooth motion. In this case, the nulling percentage is very low (3% for E.C., and 0.5% for D.K.; the gray bars on the left of each graph).

We also checked whether the low percentage obtained in the smooth condition could primarily arise because the smooth adaptation pattern was not as efficient in producing a MAE as the jittering adaptation pattern. To test this hypothesis, we again measured the nulling percentage obtained with a smooth test pattern (dot speed still at 1.5°/s), but we now used a jittering adaptation pattern. The results, however, show that the percentage is still very low (black bars on the left). The

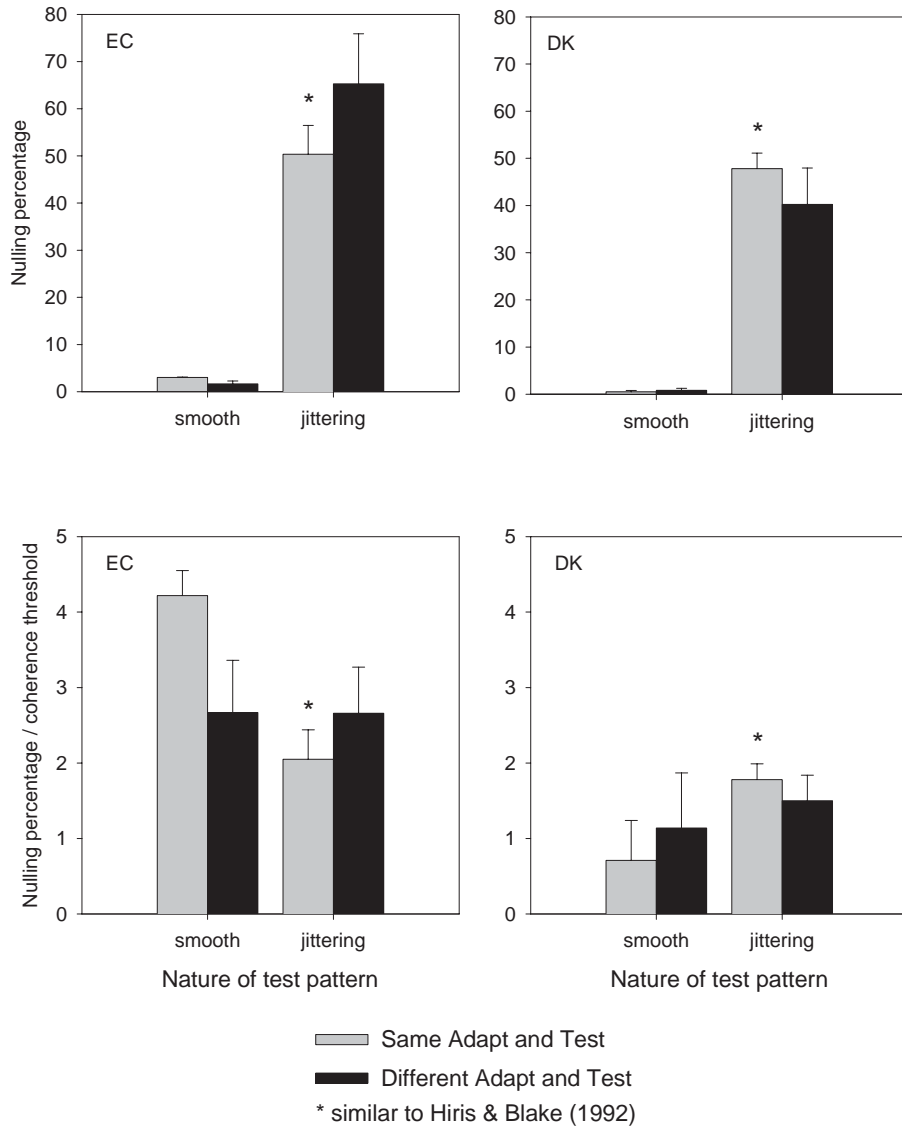


Figure 3. Results of Experiment 3 for two observers: Role of aliasing. Motion of the dots was either smooth or jittering (see text). Adaptation and test patterns were either identical (black bars) or different (gray bars). In the top graphs, the percentage of signal dots needed to null the MAE is plotted for the four possible combinations. A strong nulling percentage is only observed when the test pattern is jittering, whether or not the adaptation pattern is smooth or jittering. In the bottom graphs, the nulling percentage values are divided by the coherence thresholds measured when the stimulus was either smooth or jittering. The dots moved within a 4° square aperture at a speed of 1.5 °/s (viewing distance: 228 cm). Observers fixated a point in the middle of the aperture.

spatio-temporal characteristics of only the test seem to be relevant here. To strengthen this idea, we reversed the adapt/test characteristics so that the test was now jittering and the adaptation pattern was smooth. This change produced a dramatic increase of the nulling percentage for both observers (black bars on the right), and shows that using a jittering test (whatever the adapt pattern) is the necessary condition to obtain a high nulling percentage

To test whether these large values truly reflect an increase in MAE strength, they have been divided by the motion coherence thresholds measured for the two different spatio-temporal conditions in the bottom graphs

of Figure 3. Plotted in this way, the previous large difference between the jittering and the smooth condition is no longer visible. It turns out that the directional ambiguity associated with the jittering condition renders the signal dots highly inefficient as shown by the very large coherence thresholds (around 25%-30%). Thus, a nulling percentage of 50% is only twice as large as the coherence threshold. In other words, the large nulling percentages observed in the jittering condition, and reported by Hiris & Blake (1992), actually reflect a very weak MAE. For observer E.C., this jittering MAE is even weaker than the MAE measured when both the adapt and test stimuli are smooth.

## Discussion

Blake & Hiris (1993) studied the effect of “perceived smoothness” on the strength of the dynamic MAE. The motion, which they called smooth, corresponds to our jittering condition. It is likely that their “smooth condition” was actually the smoothest they could get at that time with their own animation sequences. However, displacing the dots by  $0.07^\circ$  with a sampling frequency of about 17 Hz, as they did, definitely produces aliased motion. This can be observed directly or predicted from previous results (Morgan, 1979; Watson, Ahumada, & Farrell, 1986). Blake & Hiris (1993) showed that making the adaptation pattern even jerkier reduces the dynamic MAE strength (with a constant test pattern). This is easy to explain because aliasing of the unidirectional adaptation velocity introduces motion energy in the direction opposite to the nominal adaptation direction, thus reducing the imbalance of activity between opposite directions. In this respect, aliasing was so strong in our jittering condition that perceived motion during the adaptation phase alternated between the nominal adaptation direction and the opposite direction.

In sum, with the low speed used here ( $1.5^\circ/\text{s}$ ), high nulling percentage values of the order of 50% or more can be obtained only if the test stimulus is spatio-temporally aliased. These high values, however, do not indicate a strong MAE but rather a poor efficiency of the signal dots.

## General Discussion

To measure MAE strength, Hiris & Blake (1992) introduced a nulling paradigm based on stimuli developed by Newsome & Paré (1988). The idea was that signal dots moving coherently against a background of noise dots could be used to null the MAE so that the final percept looked like isotropic noise (random dynamic visual noise [RDVN]): the nulling percentage of signal dots was taken as a direct measure of MAE strength. According to authors Blake & Hiris (1993, p. 1591), using this technique would make it “quite simple to manipulate potentially interesting variables such as speed or dot density while still varying signal strength.” However, when we started our preliminary investigations along these lines, a few unexpected difficulties arose. The aim of this work is to understand these potential problems and show that this technique is indeed a useful means for measuring the MAE, provided these problems are taken into account.

In all experiments, we measured a coherence threshold (i.e., the threshold percentage allowing motion detection of the coherent signal dots without prior adaptation) for the different conditions investigated. This aimed at ensuring that conditions which elevated nulling percentages did not actually produce a decreased effectiveness of the signal dots (Barlow & Tripathy, 1997).

We have first shown that increasing the dot density of the test stimulus increases nulling percentages. This effect is, however, difficult to interpret in terms of MAE strength mainly because adapting with a low density and testing with a high density still entail large nulling percentages. Moreover, this effect is not the consequence of the diminished efficiency of the signal dots at higher densities. We interpret this finding as evidence that MAE strength is underestimated with low-density test stimuli, whereas it is more properly measured with high densities. At low densities, we assume that nulling percentages (about twice the motion coherence threshold in Experiment 1) reflect a motion transparency threshold that is reached, although the MAE is not completely cancelled. In this case, observers report that the test stimulus does not really look like isotropic noise but rather like two sets of dots transparently moving over noise dots. This would result from the low probability of signal dots being spatially paired with the noise dots that elicit MAE activity (Qian et al., 1994). At high densities, however, the probability of these spatial pairings is higher so that motion transparency thresholds are significantly increased (Mestre et al., 2001). Consequently, a greater proportion of noise dots eliciting MAE activity can now be nulled by signal dots without producing motion transparency. This entails larger nulling percentages, which should provide less underestimated measurements of MAE strength. These findings concerning the effect of density have two consequences for future MAE studies, based on this nulling technique. First, as a rule of thumb, it is recommended to use test stimuli having the highest density possible to increase the sensitivity of the nulling method. Second, results from MAE studies using this nulling technique should be compared only insofar as they have the same density. More generally, as indicated in the “Introduction,” factors that tend to favor spatial integration of scattered motion signals (vs. segregation) should not be confused with factors that influence MAE strength.

We then tried to establish whether adapting and testing with a low speed entails strong or weak MAEs when using the RDVN nulling technique. The question arose because Hiris & Blake (1992) reported very strong MAEs with slow-speed patterns ( $2^\circ/\text{s}$ ), whereas our preliminary investigations showed only weak MAEs with a similar speed ( $1.5^\circ/\text{s}$ ) and apparently similar conditions. We have shown that Hiris & Blake’s (1992) finding, i.e., large nulling percentages (about 40%), holds only if the motion of the test dots is spatio-temporally aliased. This result, however, does not reflect a strong MAE but rather the very low efficiency of signal dots as indicated by high-coherence thresholds. Weak MAEs are also observed with slow-speed nonaliased motion ( $1.5^\circ/\text{s}$ ) presented in the fovea. Altogether, low-speed stimuli presented in the fovea, whether aliased or nonaliased, produce nulling percentages that are only 1-4 times as large as their corresponding coherence thresholds.

At moderately larger eccentricities (7°), nulling percentages are now 15 times as large as the coherence thresholds (still using a 1.5 °/s speed). At first sight, this dramatic increase may appear in conflict with previous results showing that MAE strength decreases with eccentricity (van de Grind et al., 1994). However, MAE strength in this latter study was assessed with a static test stimulus. To accommodate both findings, we propose to interpret them in the light of recent convergent findings pointing out that the nature of the test stimulus, either static or dynamic, is an important factor in assessing the characteristics of MAE (e.g., Ashida & Osaka, 1995; Nishida & Sato, 1995). In one line of research, it was shown that the direction of the MAE of transparent motion, or the MAE duration, as a measure of adaption, is highly dependent on the kind of test pattern used (Verstraten et al., 1998; van der Smagt et al., 1999; Verstraten et al., 1999; van de Grind et al., 2001). This has been interpreted as evidence that two types of motion detectors, tuned to fast and slow speeds (Anderson & Burr, 1985), have independent roles when a MAE is experienced. When the test pattern optimally activates high-speed units, the MAE will reveal the adaptation state of only these units. In contrast, a static test pattern will produce an aftereffect that will mainly depend on the degree of adaptation of low-speed units. Based on this framework, we have proposed that the increase of MAE strength with eccentricity occurs in our work because the test stimulus is dynamic and thus preferentially reveals the activity of high-speed units. Because the prevalence of high-speed units increases with eccentricity (van de Grind et al., 1986), high-speed energy available in the dynamic test stimulus is more likely to produce MAEs in the periphery. Conversely, as low-speed units become scarcer in the periphery, measuring MAE strength with a static test should preferentially reveal adaptation of low-speed units. This would explain why weaker MAEs are observed when eccentricity is increased (van de Grind et al., 1994).

Finally, we propose that the biased DVN nulling method could be fruitfully used to confirm and refine the hypothesis of the Dutch group that two different populations of motion detectors have independent roles in generating the MAE. We believe that the underpinnings of the dichotomy between static and dynamic stimuli need further investigation. Notably, a few questions are still unclear regarding the key finding that using a dynamic test pattern yields strong MAEs for adaptation speeds that are much higher than those reported when using a static test pattern (Verstraten et al., 1998). In this latter study, as in all relevant studies of this group, it is important to note that the dynamic test stimulus is a high-density array of pixels flickering between black and white at high rates, thus containing motion energy within a broad band of velocities. It is unknown whether the advantage of dynamic test stimuli resides in the large range of speeds they contain, or in the presence of certain particular high speeds. It seems that the DVN nulling method could be

efficiently used to tackle this issue. The reason is that the spectrum of the test stimulus is restricted around its nominal velocity as all the dots move at the same speed. Thus, the adaptation speed and the test speed can be independently varied so that their mutual relationships could be investigated in an extensive parametric study. One prediction is that the biased DVN test stimulus should be rendered more dynamic by increasing its speed. Our own preliminary measurements indeed show that moderately increasing speed of both adaptation and test stimuli dramatically increases MAE strength: at 6 °/s, nulling percentages are about 10 times as large as coherence thresholds (vs. ratios of 2-4 at 1.5 °/s).

In summary, the biased DVN nulling paradigm cannot be regarded as an easy-to-use procedure to assess MAE strength. As Anstis writes (Anstis, 1986), "The MAE, like piano music, is easy to record badly but hard to record well." With the introduction of this new nulling technique, it seemed that this recording problem was solved. However, as with other nulling methods, some difficulties must be overcome, and we have tried to resolve some of them in this work. One promising line of research with this method would be to better characterize the mechanisms allowing dynamic test stimuli to generate strong MAEs at high speeds.

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