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# ISI PRODUCES REVERSE APPARENT MOTION

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**Abstract**—A moving random-dot stimulus was presented in two sequential frames separated by an interstimulus interval (ISI) during which the field was spatially uniform with luminance equal to either the average luminance of the stimulus field (grey) or that of the black dots (black). In Experiment 1, black ISIs did not affect perception of motion direction but grey ISIs produced motion in the direction opposite to the physical displacement (reverse motion). In Experiment 2, the contrast of the stimulus was reversed simultaneously with the displacement of the random-dot fields so that reverse motion would be seen with no ISI [Anstis & Rogers, *Vision Research, 15*, 957, 1975]. In this condition, grey ISIs reversed the reverse motion to produce a veridical perception. Finally, in Experiment 3, we examined whether the negative image that follows the stimulus offset was the source of the reversal in motion direction. A gradual offset of the stimulus necessarily reduces the amplitude of the negative response at stimulus offset and also reduced the frequency of seeing reverse motion, suggesting that the apparent reversal of motion direction with ISI can be attributed to the negative phase of a biphasic impulse response function. A simulation of the temporal response to the displacements of random-dot fields demonstrated that the negative phase of a biphasic impulse response function is sufficient to produce the reverse motion. We therefore claim that there is a significant biphasic temporal response function that precedes the analysis of motion in the visual system. This indicates that the overall temporal response function of the visual system is the result of a cascade of functions from early through late stages and that only a portion of the overall temporal response function can be attributed to stages involved in motion analysis.

ISI    Reverse motion    Random-dot kenematogram    Temporal response function

## INTRODUCTION

The sequential presentation of two random-dot fields, which have a small displacement one from the other (random-dot kinematograms), produces a compelling impression of motion (Anstis, 1970; Julesz, 1971; Braddick, 1974). Several authors (see Anstis, 1980; Braddick, 1980) have suggested that these random-dot stimuli activate motion mechanisms at a low level in the visual system, the so-called short-range motion mechanism (Braddick, 1974) that is distinct from higher-level processes.

We demonstrate in this report that motion is seen in the opposite direction to that of physical displacement of the random dots (reverse motion) if a uniform grey field is briefly interposed between kinematograms. Braddick (1980) also reported reverse motion effects in a circular array of dots and we believe that the same phenomenon is responsible for both effects. We shall attribute this effect to the negative phase of a biphasic visual impulse response function and we shall argue that motion detection must therefore follow the site of this response function and that, consequently, only part of the overall impulse response function can be involved in motion analysis.

Reverse motion has also been reported in a different context. Anstis and Rogers (1975) demonstrated that if a stimulus image is simultaneously displaced and reversed in contrast (Anstis, 1970; Anstis & Rogers, 1975) the perceived direction of motion is opposite to that of the physical displacement. To explain the reversal of motion direction, Anstis and Rogers (1975) showed that if they low-pass filter the intensity profile of their stimulus, the profile actually shifts in the direction opposite to the physical displacement. This is easily understood in the case of a sinewave where a contrast reversal is equivalent to a 180 deg phase shift. A contrast reversal (+180 deg) plus, say a 90 deg phase shift produces a 270 deg shift and this is identical to a −90 deg shift, a shift in the opposite direction. The effect is nevertheless

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counterintuitive when observed on a random-dot field containing many spatial frequencies, and Anstis and Rogers (1975) concluded that the motion system must use a more low-pass filtered image than the form system.

We suspected that reverse motion reported by Anstis and Rogers (1975) and that which we observed without reversing contrast were related. The evident link would be if the initial random-dot field left a brief, negative after-image when it was replaced by a uniform field and this negative image then combined with the following positive field to produce motion in the wrong direction. The negative image may be the result of the negative phase of the visual impulse response function. The biphasic impulse response function has been considered to explain temporal inhibition obtained by the measurements of detection threshold for double (or triple) pulses (Bergen & Wilson, 1985; Ikeda, 1965; Rashbass, 1970). Such an impulse response function is also predicted from the band-pass profile of the temporal modulation transfer function measured with sinewave gratings (Bergen & Wilson, 1985; Kelly, 1971a, b; Roufs, 1972a, b). It is possible that the negative phase of the impulse response function reverses the contrast of a stimulus image at a low level of visual processing that precedes motion detection and that a grey ISI is necessary for this negative image to reach an effective amplitude. The negative image would then produce reverse apparent motion when followed by the shifted positive version of the stimulus (Anstis & Rogers, 1975).

Experiment I explored the effect of ISI to show that appropriate durations of ISI reversed the motion direction of random-dot kinematograms if the luminance level of the ISI field was grey. In Experiment 2, the effect of the ISI was explored for a stimulus that, like that of Anstis and Rogers (1975), produced reverse motion with no ISI: random dots were simultaneously reversed in contrast and spatially shifted. This second experiment examined whether an ISI might reverse the reverse motion (Anstis, 1970; Anstis & Rogers, 1975). Experiment 3 used gradual reductions of stimulus contrast to attenuate the negative phase of the impulse response function.

## EXPERIMENT 1: MOTION REVERSAL WITH ISI

The first experiment investigated the direction of perceived motion when a random-dot field was displaced with various ISIs. Either a grey or black uniform field was presented during the ISI.

### Method

*Stimuli and apparatus.* Stimuli were square fields of random dots generated on a cathode ray tube (30 Hz frame rate, interlaced fields) by a computer-controlled image processor. This stimulus subtended a visual angle of 4.8 deg, and was surrounded by a uniform grey field of $8 \times 8$ deg. The random-dot field was composed of a square matrix of $76 \times 76$ dots (0.06 deg width $\times$ 0.07 deg). Half of the dots were black (1.6 cd $m^{-2}$) and half were white (37.0 cd $m^{-2}$). Two random-dot patterns were used for a trial: the first pattern was generated arbitrarily and shifted three dots (0.19 deg) either left or right to make the second. The edges of the random-dot fields were stationary, and therefore some dots disappeared at one edge of the screen in the second pattern, and others appeared at the opposite edge. A blue and white bull's-eye (0.9 deg diameter) was located at the center of the stimulus field to serve a fixation spot. The ISI field was spatially uniform with luminance equal to either the luminance averaged over the display (grey ISI) or that of the black dots (black ISI). The ISI field replaced the random-dot field with the surround of grey field unchanged.

*Procedure.* The sequence of a trial was as follows. The observer first fixated the bull's-eye, and then moved a joystick either left or right when he/she was ready for the trial. The signal from the joystick initiated the display of the first random-dot pattern. The first random-dot pattern was presented for 1 sec, then replaced by the uniform ISI field. ISI was randomly chosen in each trial as an integer number of video fields totaling either 0.0, 17, 33, 50, 67, 83, 133 or 167 msec. The ISI field was followed by the second pattern which was also presented for 1 sec. The observer then identified the direction of motion of the random-dot field in a two-alternative forced choice (left or right). In the grey ISI condition the observers reported that they sometimes saw two different motions, one directed to left and the other toward right. In such cases, they reported the direction of stronger motion. The direction of the displacement was randomly determined from trial to trial. The luminance level of the ISI field was constant throughout a session (either grey or black). Each session comprised 128 trials: 16

trials (eight trials for rightward displacement and the other eight for leftward) for each of eight ISIs. A new random-dot pattern was generated for each trial.

*Observers.* Three male observers, SS, PF, MA and one female observer, JR participated in this experiment. All observers had normal or corrected-to-normal visual acuity. Two observers, SS and PF, completed four sessions and the other observers, MA and JR, completed two sessions for each of the grey and black ISI conditions.

### *Results and discussion*

Figure 1 shows the percentage of responses in the direction of the physical displacement (forward motion) as a function of ISI separately for the four observers. Open circles represent results for the grey ISI and filled circles represent those for the black ISI. The broken line at 50% across each panel shows the random responses. Each point was derived from 64 observations for SS and PF, and 32 observations for MA and JR. A representative standard error is shown by a vertical line for the lowest datum point in each panel.

For the 0.0 msec ISI, observers perceived forward motion on almost 100% of the trials. On the other hand, all observers responded in the reverse direction at more than chance level (forward motion was seen less than 50% of trials) for ISIs between 17 and 67 msec when the grey level of luminance was used for the ISI field. This indicates that they saw motion in the opposite direction to the physical displacement for these values of ISI. One can see that the response functions seem to have two negative peaks at around 30 and 70 msec, although the depth of these peaks varies dependent on observers: the peak for shorter ISI is not clear for the data of SS and that for longer ISI is not very clear for MA. For ISIs longer than 100 msec, responses are at chance level, indicating that no motion was seen.

For the black ISI field, observers responded in the forward direction at higher than chance level or around chance over the whole range of ISIs used. The observers saw motion in the same direction as the physical displacement whenever they saw motion. The dark field interposed between random-dot patterns did not produce reverse motion. It should be noted, however, that three observers reported motion in the reverse direction at slightly more than chance level (less than 50% for forward motion) for an ISI near one of the negative peaks of the results

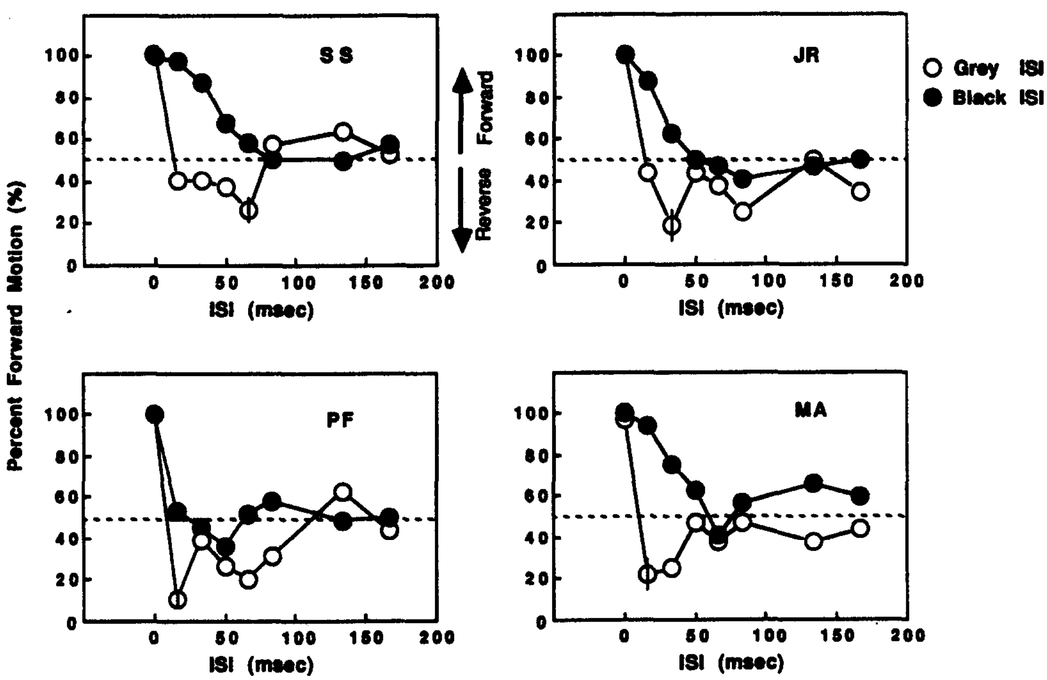


Fig. 1. Percentage of responses reporting displacement in the forward direction as a function of inter-stimulus-interval (ISI). Open circles are results for the grey ISI condition and filled circles are for the black ISI condition. The four panels show data from four different observers. A representative standard error for an ISI is shown, a vertical bar in each panel. The broken line across each panel shows the chance level of the response (50%).

for the grey ISI (i.e. 50 msec for PF, 67 msec for MA and 83 msec for JR). There might be therefore slight reversals of motion direction even for black ISIs. For ISIs longer than 100 msec, responses were around chance level, consistent with the results for the grey ISI.

## EXPERIMENT 2: REVERSAL OF CONTRAST IN KINEMATOGRAMS

Experiment 2 used random-dot kinematograms in which the second stimulus was a negative contrast version of the first one so that reverse motion was seen *without* an ISI (Anstis, 1970; Anstis & Rogers, 1975). Our experiment examined whether a grey ISI would reverse the direction of the motion produced by opposite contrast random-dot kinematograms as it did for the normal random-dot kinematograms in Experiment 1.

A double reversal of motion (i.e. no reversal) would be expected in this stimulus if the source of the reverse motion produced by the grey ISI in Experiment 1 was the inversion of image contrast due to the negative phase of the impulse response function. The impulse response function inverts the contrast of the first pattern following its offset and the second pattern is actually presented in negative contrast. Since both patterns have the same contrast (negative), the motion relationships of a normal kinematogram should hold.

### *Method*

The stimulus configuration was the same as that in Experiment 1 except that the second random-dot pattern was reversed in contrast in addition to being shifted. White dots in the first pattern therefore became black in the second pattern and black ones became white. Only a grey ISI was used. Other details of the method were the exactly same as that in Experiment 1. The same four observers participated in this experiment.

### *Results and discussion*

The percentage of forward motion responses is plotted against ISI in Fig. 2. For 0.0 msec ISI, all observers responded in the forward direction at less than chance level (although, in the case of PF, the difference was not significant), indicating that reverse motion was perceived. When grey ISIs between 17 and 67 msec were interposed between the random-dot fields, observers saw motion in the forward direction at percentages higher than chance level. The responses in the forward direction indicate a double reversal of the motion. Interestingly, two peaks seen in the results here are at approximately the same ISIs as the minima of results for the normal kinematograms shown in Fig. 1. These results are consistent with the possibility that the same mechanism produced the reversal of forward motion (Experiment 1) and the reversal of reverse motion here.

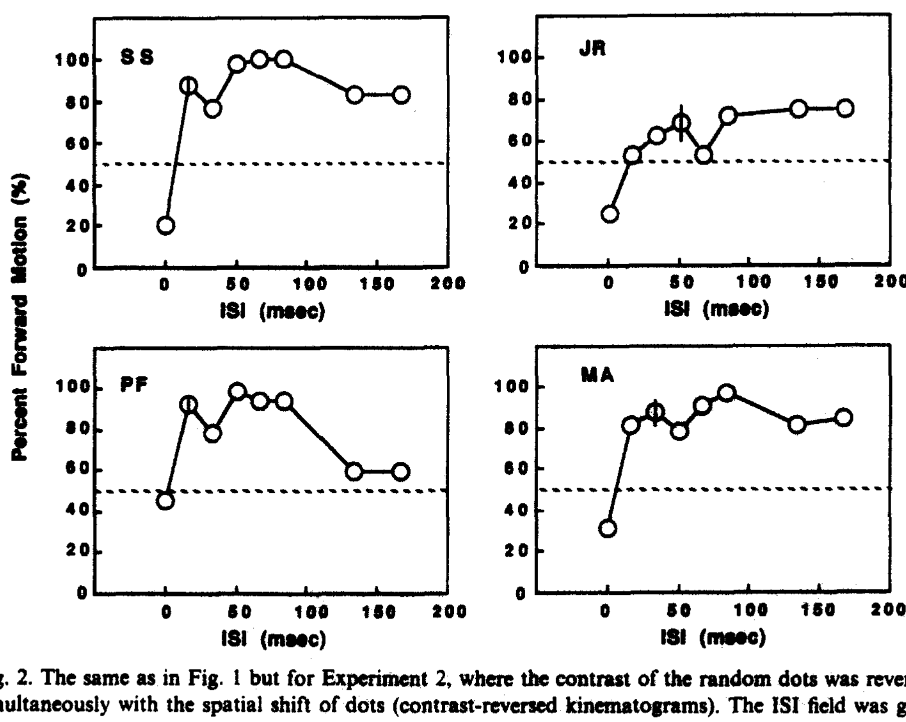


Fig. 2. The same as in Fig. 1 but for Experiment 2, where the contrast of the random dots was reversed simultaneously with the spatial shift of dots (contrast-reversed kinematograms). The ISI field was grey.

For the ISIs longer than 100 msec, detection of forward motion remained above chance level. This is inconsistent with the results of Experiment 1, which show that no motion was seen for ISIs longer than 100 msec. The maximum ISI for which low-level (or short-range) motion can be seen has been suggested to be about 100 msec (Baker & Braddick, 1985; Braddick, 1973; Lappin & Bell, 1976). We have no explanation for this perception of motion at long ISIs seen in this experiment.

## EXPERIMENT 3: THE EFFECT OF GRADUAL STIMULUS OFFSET

Experiment 3 examined whether the negative phase of the visual impulse response function might be the factor that reverses the contrast of images following stimulus offset and that this reversal in contrast produces reverse motion as does a reversal of physical contrast (Anstis & Rogers, 1975; and the results for 0.0 msec ISI in Experiment 2). In order to examine the effect of the negative response of temporal mechanisms, the first random-dot field was terminated gradually using multi-step (three- or six-step) reduction of contrast, instead of one steep change of contrast from 100% (black and white random-dot field) to 0% (uniform grey), which was used in Experiments 1 and 2. Since a gradual stimulus offset will reduce the amplitude of the negative phase of the impulse response function, a gradual offset may also reduce the frequency of seeing the reverse motion, if, in fact, the negative phase of the impulse response function is the source of the reversal of motion direction.

### *Effect of multi-step stimulus offsets on negative response*

Prior to the experiment, we modeled the effect of multi-step stimulus offsets on the amplitude of the negative response that follows the offset. The temporal response for an experimental stimulation can be predicted by assuming a impulse response function psychophysically determined by Bergen and Wilson (1985). The mathematical formula of the function is:

$$F(t) = (t/9.5)^4 \times \exp(-t/9.5)(0.042 - 0.00034t^{1.5}), \quad (1)$$

where $t$ represents time and the coefficients are from one of two sets predicted for results of two different stimuli in their experiments. The set that we use is more appropriate for transient phenomena. In equation (1), absolute level of response in the original equation of Bergen and Wilson (1985) has been normalized so that the response for a steady uniform white field (the steady white response) becomes 1.

The temporal response function of the visual system is a compound function resulting from the cascade of several sequential stages. The function measured by Bergen and Wilson (1985) represents the overall temporal response function and so will in fact not be appropriate for the early biphasic response function that we believe is responsible for the image contrast reversal in our stimuli. Since the overall function is a convolution of the individual functions of the component stages, the early function that interests us must have a more rapid response than that described by equation (1). The function of equation (1) is nevertheless sufficient for purposes of demonstration.

In Experiment 3, the contrast of the dots was reduced linearly in either three or six steps at each video field of the CRT (16.7 msec) until the contrast reached 0.0% (33% in each step for three-step stimulus offset and 17% for six-step stimulus offset). Figure 3 shows the temporal responses for a single pulse (impulse) and for single-, three- and six-step stimulus offsets as predicted by equation (1). The level of 1 of the responses corresponds to the steady white response. The value of the negative peak for three-step stimulus offset is 80% of that for single-step stimulus offset and the minimum value for six-step stimulus offset is 53%. The three- and six-step stimulus offsets should therefore have reduced the amplitude of the negative phases. Figure 3 also shows that the time at which the negative response reaches a minimum is about 50 msec after the stimulus offset independently of the number of offset steps. The same ISIs used in Experiment 1 would therefore be appropriated to investigate the effect of these gradual stimulus offsets.

### *Method*

Both the grey and black ISI conditions were repeated using gradual stimulus offsets of the first random-dot pattern for normal random-dot kinematograms. After the presentation of 1 sec of the first random-dot pattern, the contrast of the dots was reduced linearly in either three or six steps. The procedure was the identical to that in Experiments 1 and 2. The same four observers participated in this experiment.

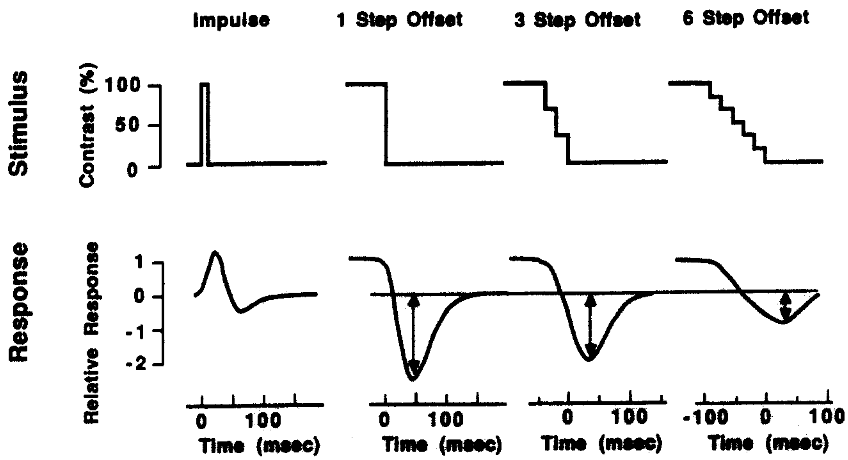


Fig. 3. The temporal responses predicted by equation (1) for the offset of a white dot (bottom panels) with different numbers of steps (top panels). The response level is normalized so that the responses before the stimulus offset is 1 (steady white response).

*Results and discussion*

Figure 4 shows functions for frequency of seeing forward motion vs ISI. Open circles represent results for the grey ISI and filled circles represent for the black ISI. For the grey ISI, unlike the results for single-step stimulus offset (Fig. 1), responses are mostly above chance level except for one observer, PF. Observer PF responded significantly below chance level for some ISIs in both six- and three-step stimulus offset conditions. However, the frequency of responses indicates that reverse motion is reduced with the increase of stimulus offset steps for PF as for the others. Providing a gradual stimulus offset reduced the tendency to see motion in the reverse direction for all observers.

Figure 4 also shows that multi-step stimulus offsets reduced the difference of results between the grey and black ISIs. For the single-step stimulus offset condition, the frequency of reports of forward motion between the grey and black ISI sometimes differed by more than 60 percentage points (see Fig. 1). In contrast, for multi-step stimulus offsets, responses for the grey ISI were similar to those for the black ISI, especially when the six-step stimulus offset was used. The effect of luminance level in ISI field, which was critical for the determination of the motion direction in the single-step stimulus offset condition, declined with the number of steps in the first-pattern offset.

In order to show the perceived direction of motion as a function of the number of stimulus offset steps (Fig. 5), responses between 17 and 67 msec ISIs were pooled together and the percentage of forward motion within this period was plotted against the number of steps in the stimulus offset (the single-step data are from Experiment 1). Figure 5 shows that the response for forward motion is greater for three- and six-step stimulus offsets than that for single-step stimulus offset, indicating that motion reversals were reported less frequently when the first pattern was terminated gradually. These results support the assumption that the reverse motion is attributed to the negative phase of the impulse response function and that this negative response is strongest following an abrupt stimulus offset (Fig. 3).

The increase of the number of steps in the stimulus offset from three to six, however, did not have the same effect for all observers. Forward motion is seen more for six-step stimulus offset than three-step stimulus offset for SS and PF as predicted from the reduction of the negative response that follows the stimulus offset, while the opposite effect is seen for JR and MA. However, for these two observers with six-step stimulus offsets and ISIs greater than 0 ms, the motion responses are scattered very close to chance levels (see Fig. 4). The results for these observers may indicate only that the stimuli have reached the limits of temporal resolution for a motion response and not that the strength of the negative phase of the image following stimulus offset has increased for six-step as opposed to three-step stimulus offset.

## SIMULATION OF TEMPORAL RESPONSE FOR DISPLACEMENT OF RANDOM DOTS

A simulation was performed to demonstrate that the impulse response function can produce

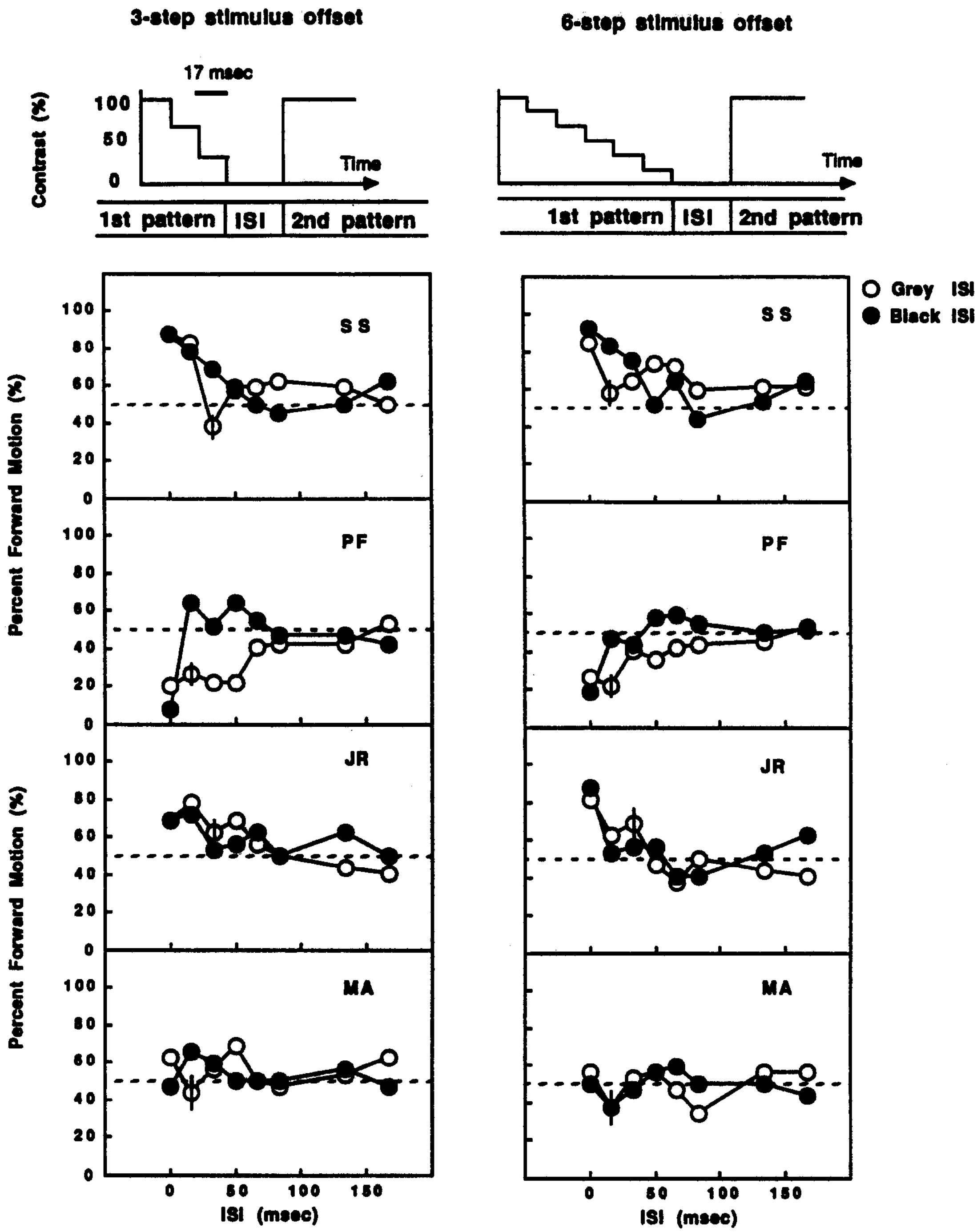


Fig. 4. The same as Fig. 1 but for multi-step stimulus offsets (Experiment 3). Left: three-step stimulus offset. Right: six-step stimulus offset. Top two panels show the schematic view of the contrast change of the stimulus in the different conditions.

motion reversal in random-dot kinematograms. In the simulation, a horizontal row of dots was used as a stimulus. First, the random-dot stimulus was blurred spatially using a Gaussian filter to attenuate components with wavelengths shorter than 0.38 deg, twice the displacement size. This Gaussian filter attenuates spatial frequency components higher than 2.6 cycle $deg^{-1}$ (the half-amplitude frequency). Image components with spatial frequencies higher than this undergo phase shifts of 180 deg or more during the displacement, and this complicates the task of determining the direction of motion for any analysis that uses bandpass detectors that operate above this frequency. For the sake of simplicity, we have filtered these components out of

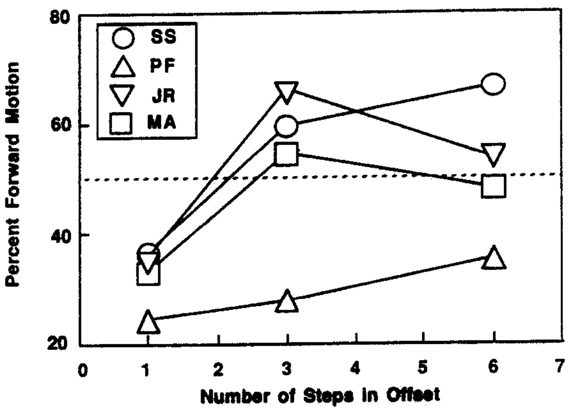


Fig. 5. Percentage of responses for the direction of displacement as a function of offset-step number, provided by pooling data for ISIs between 17 and 67 msec from Figs 1 and 4. Difference symbols represent different observers. The broken line shows chance level of response.

the image and it might be argued that the visual system does the same.

Secondly, the spatially smoothed image was filtered temporally using the impulse response function of equation (1). The filtered response is normalized so that the response for a steady uniform white field (the steady white response) becomes 1 and that for a steady uniform black field (the steady black response) becomes $-1$.

Figure 6 shows response images in a space–time plot with time running down the page, for a filtered random-dot row. Time is shown with respect to the onset of ISI. The stimulus is also shown at the left of each simulated response. The 0.19 deg displacement of stimulus is rightward. White areas in response images indicate the response value of 1 or more and black areas indicate that of $-1$ or less.

*Grey ISI*

Figure 6a shows simulated responses for the condition in which a grey-luminance ISI interposed 70 msec. One can see features that shift leftward (i.e. a left and downward orientation of contiguous white and black regions). For example, the black patch labelled C appears to have the black patch labelled D as its nearest neighbor as indicated by the arrow. The patch D corresponds to the displaced patch A and the patch C is a negative response to white patch B following its offset.

*Contrast-reversed kinematogram*

For the contrast-reversed kinematograms in Experiment 2, the negative response that follows the stimulus offset now produces forward motion. As shown in Fig. 6b, the impulse response function reverses the contrast of the first pattern while the grey ISI is being presented. This therefore produces the same contrast as the second pattern. Consequently, this stimulation is almost identical to the displacement of random-dot fields with neither ISI nor reversal in contrast. Forward motion is expected in this condition, and indeed, this was the case in Experiment 2.

*Discussion*

The simulation demonstrated the reversal of motion due to the negative phase of a biphasic impulse response function. This indicates that a biphasic temporal filter must exist prior to the extraction of motion. Some motion models use temporal filters which approximate the overall temporal response function measured psychophysically as a part of the system properties of the motion analysis (e.g. Adelson & Bergen, 1985, Watson & Ahumada, 1985). However, our demonstration shows that it is more appropriate to use only a portion of the overall temporal response function to build motion detectors.

Although this stimulation did reveal that a biphasic response function is sufficient to reverse the motion in the stimulus, it did not address the observed difference in effect of grey and black ISIs. In fact, a similar reversal of motion would be predicted in both cases for the linear filtering we have used here.

Why then, would be presence of a grey ISI be so much more effective than a black one in eliciting reverse motion? The answer may lie with the saturation of the negative repsonse at stimulus offset. For a grey ISI, both light and dark parts of the stimulus change by equal and opposite amounts so that they both become grey. For a black ISI, however, only the white areas of the stimulus change and they change by twice the amount. If the negative response at stimulus offset were limited in some way (could not become blacker than black) so that it could not produce a response twice the amplitude of that occurring in the corresponding areas for the grey ISI, the negative contrast image produced at stimulus offset would have less contrast for a black ISI than for a grey ISI. While we feel that this is a reasonable explanation of our result, further experiments would be necessary for confirmation.

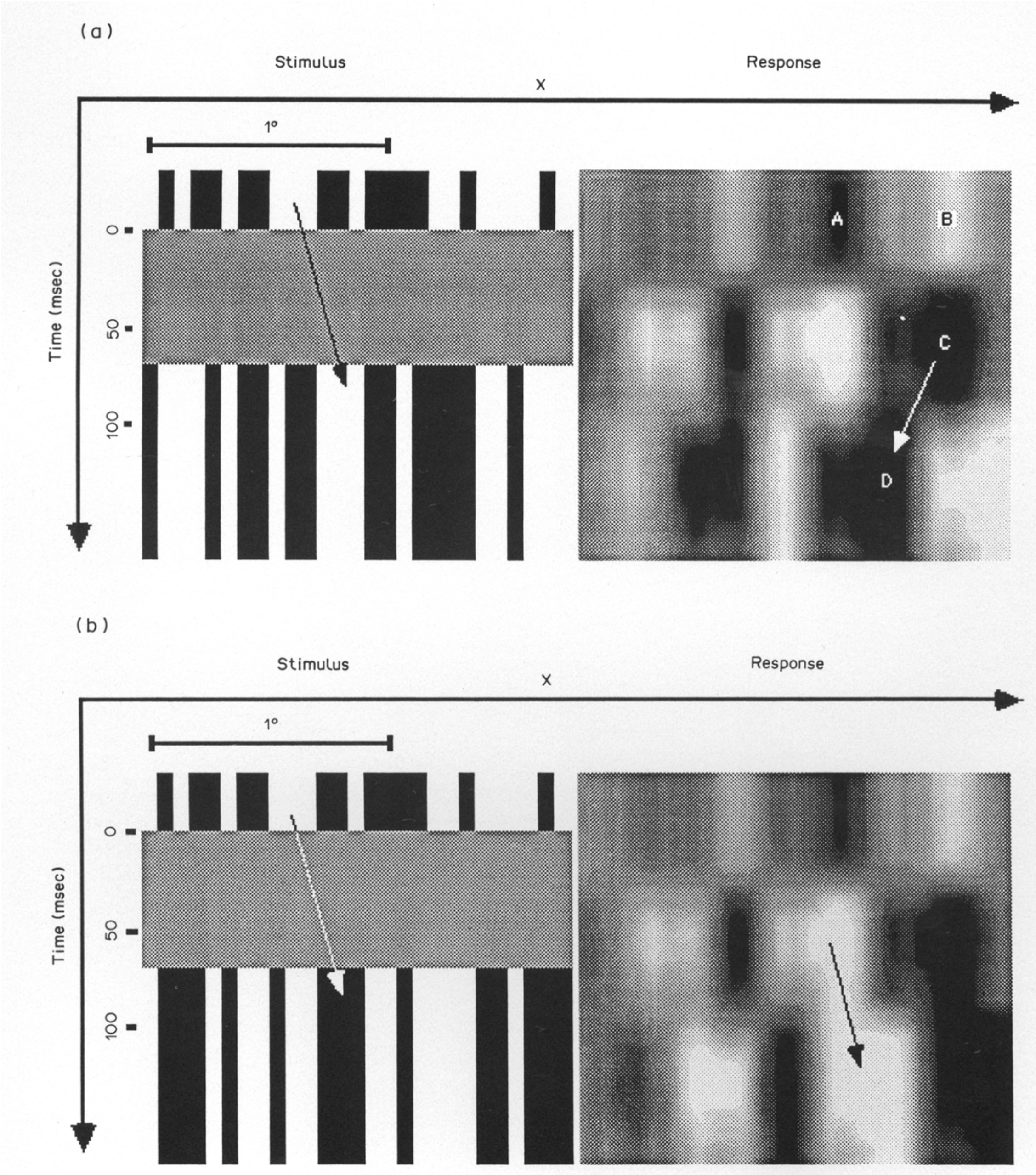


Fig. 6. Temporal responses predicted from equation (1) for the displacement of a row in a random-dot field. Stimulus is shown in the left of each response image. $x$-axis show horizontal position in space and $y$-axis shows time with respect to the onset of the ISI field. The same pattern is displaced 0.19 deg to rightward: (a) 70 msec ISI with a grey field for a normal kinematogram; (b) 70 msec ISI with a grey field for a contrast-reversed kinematogram. Arrows indicate physical displacement on the left and energy displacement in filtered image on the right.

## GENERAL DISCUSSION

We showed that the direction of motion was reversed when a uniform grey ISI was interposed between the fields of a random-dot kinematogram that was either normal (positive–positive) contrast version (Experiment 1) or a reversed (positive–negative) contrast one (Experiment 2). The reduction of the frequency of seeing reverse motion when gradual stimulus offsets were used suggested that this reversal of motion direction can be attributed to the negative phase of a biphasic impulse response function (Experiment 3). A simulation of the temporal response for displacements of random-dot fields demonstrated that the negative phase of a biphasic impulse response function can produce an energy shift in the opposite direction to that of the physical displacement of random dots.

The reversal of motion direction seen with an ISI has been previously reported using either square wave (Braddick, 1980) or sine wave (Pantle, Eggleston & Turano, 1985) gratings. These reverse motions for periodical stimuli may also be attributed to the negative phase of an impulse response function. For a periodical stimulus, the reversal of a image in contrast is equivalent to a 180 deg phase shift. Thus, if the physical displacement is a 90 deg phase shift, for example, the spatial displacement between the reversed image of the first pattern and the second pattern produces a combined 270 deg shift and this is identical to a $-90$ deg shift, a shift in the opposite direction. As is the case for random-dot kinematograms, the negative phase of a biphasic impulse response function predicts the reverse motion for periodical stimuli.

Bishof and Groner (1985) also reported reverse motion using a single row of random dots arranged circularly around an annulus. However, in their stimulus, reverse motion occured at displacements just beyond $D_{max}$ without any ISI other than the refresh rate of the CRT. They were able to predict the reversal of motion direction under these conditions using the motion model of Marr and Ullman (1981). This same model does not predict a reversal of motion for these conditions with two-dimensional patterns, however, so that as Bishof and Groner point out, their motion reversal may be unique to one-dimensional patterns and therefore seems to be different phenomenon from ours.

It is surprising that the reversal of motion direction due to ISI has not been previously reported with random-dot kinematograms. This is probably because black ISIs, which do not reverse direction of motion as shown in Experiment 1, were used in most experiments where the effect of ISI was explored (Baker & Braddick, 1985; Lappin & Bell, 1976).

The luminance level of the ISI field was varied in Braddick (1973), and thus, the ISI field was grey in some conditions. The experimental conditions was, however, different in many ways from our experiments: the size of stimulus field (2.9 deg) was smaller than ours (4.8 deg); the displacement size (0.093 deg) was smaller than ours (0.19 deg); the exposure duration of each random-dot field (100 msec) was shorter than ours (1 sec); and, there were random dots surround of stimulus field in this experiment. Our preliminary observations showed that each of these factors—smaller stimulus field (or stimulus at less eccentric in the visual field), smaller displacement, shorter exposure duration or presence of surround dots—made reverse motion weaker.

## CONCLUSION

An ISI reversed the direction of perceived motion for the displacement of a random-dot field when the luminance level of the ISI field was the same as the average luminance of the random-dot field. This reverse motion can be attributed to the negative image produced by a biphasic impulse response function following the offset of the initial field of the stimulus. This negative image combines with the displaced positive field (the second field) to produce reverse apparent motion as a result of the presence of physical energy in that direction in the stimulus (Anstis & Rogers, 1975; Adelson & Bergen, 1985). Our data therefore indicate that there is a significant biphasic temporal response function that precedes the analysis of motion in the visual system. Since the overall temporal response function is the result of a cascade of functions from early through late stages, only a portion of the overall temporal response function can be legitimately attributed to stages involved in motion analysis.

An early biphasic function which precedes motion analysis may be the result of processing in the retinal ganglia and lateral geniculate nuclei, both structures that precede the cortical regions where motion extraction begins. The reverse motion phenomenon we report may provide a means to examine the spatial and temporal characteristics of this early response function.

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