

RELATIVE MOTION INDUCED BETWEEN STATIONARY LINES

K. NAKAYAMA¹ and C. W. TYLER

Smith-Kettlewell Institute of Visual Sciences, 2232 Webster Street, San Francisco, CA 94115, U.S.A.

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Abstract—Simple harmonic motion of two moving lines can induce a relative motion between two adjacent stationary lines. There is both a maximum and minimum stimulus amplitude within which this motion can be seen and this depends on frequency. For a wide range of low frequencies the lower amplitude limit for induced motion is inversely proportional to frequency, suggesting that the phenomenon requires a minimum threshold velocity independent of amplitude. Furthermore, there is a relatively steep high frequency cut-off in the lower limit of induced motion, occurring between 2 and 5 Hz, which is a much lower frequency than that for real motion. The upper amplitude limit for induced motion has an entirely different characteristic (slope of -2 on log-log coordinates), indicating that the upper limit is not limited by velocity alone but by both velocity and amplitude. In comparison to real motion, the upper velocity limit for movements of 1° or less is very low (less than $1^\circ/\text{sec}$). Subsidiary experiments using constant velocity stimuli support the above conclusions. The results are interpreted in terms of hypothetical velocity-sensitive neurons having a center-surround organization with respect to velocity and a range of receptive field sizes, with preferred velocity increasing for increasing field sizes.

INTRODUCTION

In 1929, Duncker observed that if a stationary dot is surrounded by a moving background, the dot will appear to be moving. He called this phenomenon "induced movement" and implied that our perception of motion was not simply dependent on the absolute velocities of isolated points but was dependent on Gestalt factors, the total relationship between points (Duncker, 1929).

After nearly 50 years, there has been a revival of interest in induced or relative motion, stemming primarily from the realization that this seemingly "higher order" phenomenon can be interpreted in terms of neurons having excitatory and inhibitory inputs with respect to stimulus velocity. From a spatial analysis of the motion after-effect, Richards (1971) suggested that there exist velocity-sensitive neurons with a center-surround organization. Other studies indicate that there is an inhibitory interaction between neighboring regions of the visual field sensitive to velocity (Loomis and Nakayama, 1973; Holmgren, 1974; Walker and Powell, 1974; Tynan and Sekuler, 1975; Anstis and Reinhardt-Rutland, 1976), much like that postulated by Mach in his analysis of brightness (Mach, 1866). In addition, there is also the implication that relative motion is involved with other fundamental aspects of visual information processing such as figure-ground organization and depth perception (Julesz, 1971; Nakayama and Loomis, 1974).

As a way of further exploring the nature of induced movement, we have initially chosen frequency analysis, a method which has been successful in characterizing the spatio-temporal limitations of real movement and apparent movement (Tyler and Torres, 1972; Tyler, 1973), as well as delineating some aspects

of motion perception in rigid objects (Tyler, 1974). Because it requires the interpretation of surround information, and is thus more spatially dispersed, our initial thought was that induced motion might have a selective reduction in high frequency sensitivity (see Cervetto, Fiorentini and Maffei, 1969).

METHODS

The visual display used to generate induced motion consisted of four horizontal parallel lines displayed on the face of a CRT. The lines were spaced 1° apart, were 10° in length and had a luminance of approximately 0.5 cd/m². The two outer lines were driven in simple harmonic motion in counterphase by a sinusoidal generator in a configuration shown in Fig. 1. When the frequency and amplitude are within the appropriate range (see later), there is an induction of motion of the two stationary inner lines. For example, when the outer lines are moving apart, the two inner lines appear to be moving closer together and the reverse occurs when the outer lines are moving closer. Thus, two lines which are themselves stationary appear to be moving relative to each other. It should be noted

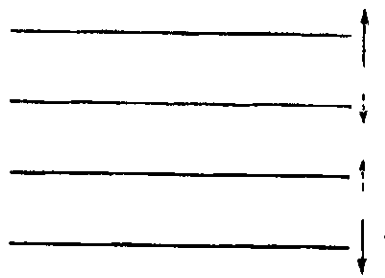


Fig. 1. Schematic of stimulus arrangement. The two inner lines are stationary. Counterphase motion in the two outer lines induces the sensation of counterphase motion in the inner stationary lines, in a direction opposite to the nearest outer line.

¹ To whom reprint requests should be addressed.

that this symmetric configuration eliminates the confounding effects of eye tracking, and shows that the motion induction is the result of visual interactions, rather than an oculomotor effect.

The experimental task required that the observer fixate the center of the display (viewing distance = 57 cm) and set the minimum amount of movement of the outer lines so that the induced movement of the two center lines was just at threshold. This defined the lower amplitude limit for the induction of motion and could be obtained for each frequency. Early in our experiments, however, we found that in addition to this lower limit there was an upper limit as well. By increasing the amplitude of the motion of the outer lines above threshold, the induction was increased, reaching a maximum, and then decreased to an upper limit beyond which the observer could not see any induced motion whatsoever. Thus we were able to see the effect of frequency on this upper, as well as lower limit, providing, at least for this configuration, a relatively complete characterization of the spatio-temporal boundaries of induced motion.

RESULTS

Real movement

We first describe the sensitivity of the observer to real movement in order to provide the basis from which to characterize induced movement. For these experiments, the observer fixated between the two stationary center lines and adjusted the amplitude of the moving outer lines so that these outer lines were just at the motion threshold. Under these conditions, the outer lines are 1.5° from the foveal center. For analytical purposes, the thresholds are plotted in double logarithmic coordinates (filled circles, Fig. 2). These results, replicating the work of Tyler and Torres (1972) for peripheral vision, show that at low frequencies the relation between peak-to-peak threshold amplitude and frequency is reciprocal, having a slope of -1 . Other expected features of the curve are a minimum threshold around 2 Hz and lack of sensitivity beyond 20 Hz. The slope of -1 between 0.2 and 1.0 Hz is of considerable interest because it is consistent with the view that the threshold is set exclusively in terms of the maximum velocity in the stimulus. This can be best appreciated by noting that

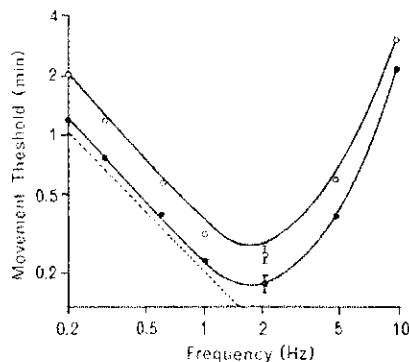


Fig. 2. Comparison of triangular (open circles) and sinusoidal (filled circles) waveforms. Threshold amplitude plotted in terms of frequency. The upper solid curve represents a theoretical prediction of triangular data based on the hypothesis of a minimum velocity threshold. This theoretical curve is displaced 0.19 log units above the sinusoidal curve. Dashed line has a slope of -1 .

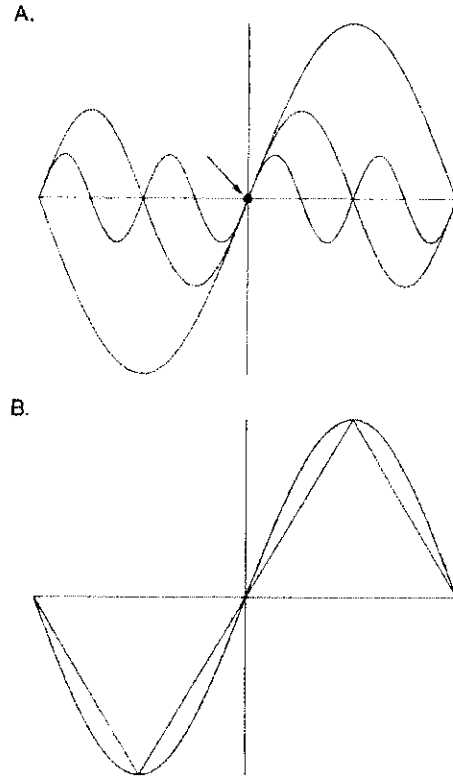


Fig. 3. (A) Sinusoids where amplitude and frequency are reciprocal. Note that all share a common maximum slope (velocity); see arrow. (B) Comparison of sinusoidal and triangular waveforms of the same frequency and amplitude. Maximum slope (velocity) of sinusoid is 1.57 times that of triangle.

sinusoids having an inverse amplitude vs frequency relation show a common peak velocity (Fig. 3A); hence, all points along the reciprocal line (dashed line) in Fig. 2 have the same peak velocity. Over low frequencies, at least, the detection of motion seems dependent on a minimum retinal velocity, regardless of frequency or amplitude.

In order to further clarify and support this concept of a sensitivity based on velocity, we compared threshold amplitude of motion for both sine and triangle waves, exploiting the fact that sine waves of the same amplitude and frequency have a peak velocity of 1.57 times that of triangle waves (Fig. 3B). Therefore, if sensitivity to a minimum velocity is the essential feature we should expect triangle waves to raise the threshold by a factor of 1.57 (0.19 log units). These results (open circles, Fig. 2) are quite close to this prediction, with triangle waves having a higher threshold, not only along the whole of the low frequency portion of the frequency spectrum, but along the high frequency portion as well. This finding provides additional support for the view that the detection of motion is limited by a threshold velocity, independent of frequency and amplitude.

For comparison with induced movement, the real movement sensitivity was measured for four observers (Fig. 4, filled circles). Each shows similar characteristics to those described above.

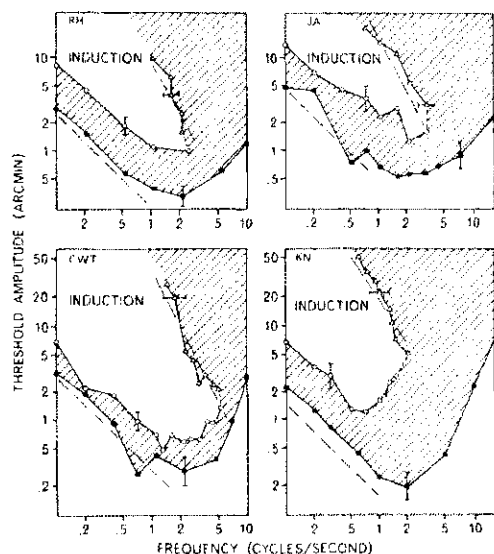


Fig. 4. Frequency characteristics of real and induced motion for four observers. Filled circles (lower curve) show peak-to-peak threshold amplitude to see real motion in the outer lines. Open circles show the lower threshold limit for induced motion; open triangles show the upper threshold limit for induced motion. Lower dashed line represents a slope of -1 , upper dashed line represents a slope of -2 . Shadow area represents conditions where real motion is seen, but induced motion is not. Induced motion is restricted to the tongue-shaped area of the graph labeled "induction".

Induced motion

Lower limit. Before describing the frequency limitations for induced motion, it is necessary to discuss some phenomenal characteristics of the relative induced motion. Under optimal conditions at an intermediate frequency and amplitude (see below), there is a compelling appearance of motion in inner lines which is counterphase to the nearest outer line. As the parameters are changed away from these optimal conditions, the movement sensation diminishes such that when it is just perceptible there is just the faintest "breathing" of the inner two lines. This "breathing" criterion was used to determine the induced movement threshold in three observers. The fourth observer (CWT) utilized a different criterion, noting that during induced motion the four lines all appeared to move as a peculiar compressing and expanding object, with each inner line appearing to move in phase with the further outer line, rather than in opposition the adjacent outer line. The use of this criterion might account for the greater range of induced motion sensitivity for CWT. Interestingly, however, the overall frequency characteristics of his response remain identical to the others, despite the criterion difference (see below).

The lower threshold for induced motion required the observer to set the outer lines to a minimum amplitude sufficient to detect apparent motion in the stationary inner lines. The most conspicuous aspect of this lower threshold (open circles, Fig. 4) is a clear indication of a reduced high frequency sensitivity for induced motion. Whereas real motion remains visible

beyond 10 Hz, induced motion is much more frequency-limited, with an upper limit between 1.5 and 5 Hz for the four observers. This point had been observed qualitatively in the original observations of Duncker (1929). The reduced temporal resolution of induced motion may be understood in terms of our original hypothesis postulating the interactive role of a surround and center mechanism sensitive to velocity. Presumably it reflects our initial supposition that higher order processes requiring more neural integrations are likely to show greater bandwidth limitations.

Despite this great difference between real and induced movement, there is also an important similarity. The low frequency portions of both curves are essentially parallel, sharing the same slope of -1 , with the threshold amplitude curve for induced motion displaced up by a factor of approximately 3 (varying from 2 to 4 for the four observers). Thus, at least for the low frequency portion of the lower limit, induced motion, like real motion, appears to depend exclusively on a threshold velocity.

Upper limit. As mentioned previously, there is an upper amplitude limit, as well as a lower amplitude limit to induced motion. In other words, increasing the amplitude beyond a point leads to a subjective decrease of movement induced in the stationary lines until a point beyond which induced movement could not be obtained. In order to determine the upper limit most easily and accurately, threshold limits in this region were taken by holding amplitude constant and having the observer vary oscillation frequency in the outer lines. Although obtained by varying frequency instead of amplitude, the results obtained are essentially equivalent and can be plotted on the same amplitude vs frequency coordinates, with error bars oriented horizontally rather than vertically. Plotting both upper and lower amplitude limits produces a looped curve, similar to those found for the frequency characteristics of other functions with upper and lower limits (Tyler, 1973, 1975). The upper portion of the looped curve (triangles, Fig. 4) represents this upper limit, showing a clear dependence on frequency. Instead of showing a slope of -1 like the lower limit, the slope of the upper limit is much steeper, following a slope of approximately -2 .

Initially, we were puzzled by this relatively steep slope. In terms of a classical systems analysis approach, a slope of -2 on a log frequency vs log amplitude graph (Bode plot) is generally indicative of a mechanism limited by a sensitivity to a second derivative, or in our terms, an acceleration. [Since the acceleration of a sine wave rises as the square of frequency ($d^2 \sin \omega t / dt^2 = -\omega^2 \sin \omega t$) all points on a line with slope of -2 share a common peak acceleration.] The phenomenal characteristics of the movement induction, however, did not support this concept. In fact, for low rates of high amplitude oscillation the illusion of movement in stationary lines was the weakest during the reversal of direction just where the acceleration of the inducing lines was greatest.

An alternative explanation suggests itself, however, if we explore some spatial implications of our threshold vs frequency curves by relating them to properties of velocity-sensitive neurons. Since points comprising

the upper curve in Fig. 4 designate the amplitude where the phenomenon of induced motion is seen to be at threshold, it should be clear that each point corresponds to given sinusoidal amplitude and frequency having a definable peak velocity, which is equivalent to:

$$V = 2\pi Af \quad (1)$$

where V = peak velocity, A = amplitude and f = frequency. Note that in this case, amplitude is defined as the height of the sine wave above the mean value, a value one-half of the peak-to-peak amplitude plotted in Figs 2 and 4. Thus, it is possible to compute the peak velocity of the threshold stimulus for each frequency, providing a threshold velocity as well as threshold amplitude for each frequency. Because the physiological characteristics of neurons showing motion selectivity are generally described in terms of amplitude and velocity, rather than in terms of frequency, we replotted the data for CWT from the upper limit and the low frequency portion of the lower limit, in terms of amplitude and velocity (Fig. 5). The lower filled circles represent the lower threshold velocity vs amplitude characteristics computed in the same manner.

Not surprising is the fact that the lower limit is essentially flat, reflecting our earlier conclusion that threshold velocity is not related to amplitude. The upper velocity limit computed in the same manner does not remain constant, however, but increases substantially for larger stimulus excursions (open circles, Fig. 6). Clearly, there is a relationship between the upper velocity limit and the amplitude of the movement. The data conform to the function $V \propto A^{1/2}$, which is shown as the dashed line in Fig. 5.

In order to verify this mathematically derived velocity vs amplitude relationship directly, we remeasured the upper limit using velocity rather than amplitude as the dependent variable. We also changed the repetitive presentation to single non-periodic episodes of linear motion. In this subsidiary ex-

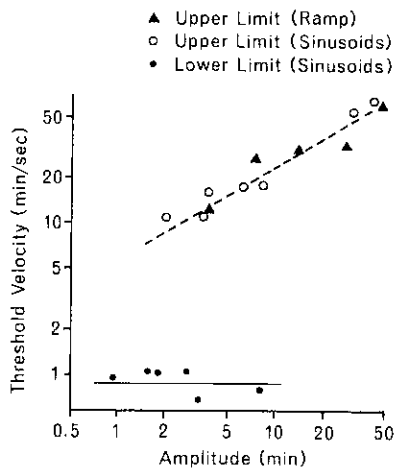


Fig. 5. Threshold velocity as a function of amplitude. Filled circles are data calculated from the lower amplitude limit and open circles are from the upper amplitude limit (from KN's data in Fig. 4). Filled triangles from the ramp experiments (see text). Dashed line represents slope of $+\frac{1}{2}$ in log-log coordinates.

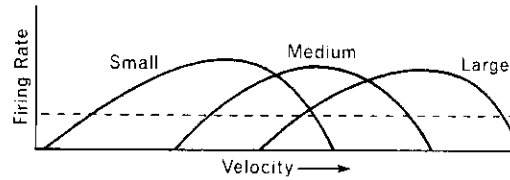


Fig. 6. Hypothetical characteristics of movement-sensitive neurons used to understand the upper and lower velocity limit for induced movement. Firing rate of three neurons with differing size receptive fields is plotted as a function of stimulus velocity. Assuming that cells with these characteristics feed into neurons with a center-surround organization with respect to velocity, we postulate that it takes a minimum threshold firing rate of a lower order velocity cell to activate the surround mechanism of the cell which mediates induced movement, and the dashed line represents a threshold firing level necessary to elicit this induced motion. Since the smallest receptive fields have the best sensitivity to the lowest velocities, they alone determine the lower threshold limit for induced motion. The upper limit is determined by the combined characteristics of neurons with differing receptive field sizes (see text).

periment, the spatial aspects of the stimulus arrangement were identical to that of Fig. 1. For a given trial, the outer lines were moved towards the inner lines over a preset distance (amplitude). For each amplitude of stimulus motion, the distance of the outer lines was adjusted such that it was always at the same average distance of 1° from the inner lines during its motion. After each presentation, the observer adjusted a knob on a ramp generator which could increase or decrease the velocity of the movement, enabling us to obtain a maximum threshold velocity for induced motion at a particular amplitude of motion.

The filled triangles of Fig. 6 show that these data fall within the variance of the data derived from the amplitude vs frequency plot, with peak velocity rising as the amplitude of the movement is increased. This provides a direct confirmation of our derived velocity vs amplitude relationship, supporting our notion that the maximum velocity which can induce motion is determined by the amplitude of the motion.

DISCUSSION

The common slope of -1 in the threshold vs frequency curves for both real and induced motion suggests a shared underlying property, each requiring a minimum velocity, regardless of both frequency and amplitude over a 10-fold range. The minimum velocity for real motion here is in the range of 25–50 arc sec/sec, which is comparable to other reports (Leibowitz, 1955). The minimum velocity to see induced motion is higher—approximately 60–120 arc sec/sec. Thus, it appears that, although it takes a minimum velocity to see real or induced motion, it clearly takes a higher minimum to see induced motion.

The threshold dependence of real motion on velocity, demonstrated under our experimental conditions, further delineates the retinal region over which this exclusive sensitivity to velocity is apparent. Tyler and Torres (1972) reported the existence of some sensitivity to position in the fovea, inferring this from

the less than -1 slope in the amplitude vs frequency relation, and they found a velocity sensitivity at 5° eccentricity in the periphery as inferred by the slope of -1 . Our current results show that at 1.5° eccentricity the slope is also -1 , suggesting that sensitivity to position is essentially absent only 0.5° outside of the fovea, despite the fact that a stationary reference marker is only 1° away.

The upper limit is clearly different from the lower limit, having a steep negative slope of -2 on the amplitude vs frequency curve. The upper part of the looped function closely resembles the upper amplitude/frequency limitations previously described for apparent (ϕ) movement (Tyler, 1973). This raises the interesting possibility that ϕ movement and induced movement are functions of the same movement system in the brain, which itself is quite distinct from the neural system processing real movement.

Considered in terms of velocity, the upper velocity threshold is highly dependent on amplitude, ranging from 10 arc min/sec to 50 arc min/sec as amplitude is increased. This relationship holds both for periodic and for single constant velocity ramps.

The higher thresholds for induced motion as compared to real motion deserves some comment. Whereas some investigators have shown lower thresholds for the perception of induced motion (Duncker, 1929) and others have noted wide individual differences (Mack, Fisher and Fendrich, 1975), we show a consistent 2-4-fold increase in threshold for induced motion in comparison to real motion. The discrepancy is likely to lie in differences in stimulus configuration. The above studies used only the simplest configuration—one stimulus moving relative to another. Thus, the velocity of a point has a fundamental physical ambiguity, depending on the choice of a coordinate reference frame, and there is always a constant relative motion between the two stimuli irrespective of the coordinate frame that is chosen. In this case, the attribution of motion to one or the other stimulus depends on a number of egocentric factors—eye movements, as well as one's body frame of reference. With our configuration, as well as with those reported by others, however (Loomis and Nakayama, 1973; Gogel, 1977), there is no such ambiguity. No matter what the choice of coordinate reference frame, moving or stationary, there is an absence of relative motion between the inner two lines; yet we persist in perceiving a relative motion between them. It should not, therefore, be considered surprising that the characteristics of induced motion with only one set of stimuli moving in relation to another set should be different than that obtained in our case. Because motion induced between stationary lines is difficult to attribute to the observer's frame of reference and because it varies quite systematically with frequency and amplitude, we think it appropriate to attempt an explanation at a neural level.

Neurophysiological interpretation

As part of a hypothetical neurophysiological model to account for our results, we make the following assumptions:

(1) Induced motion is mediated by neurons having a center-surround organization with respect to velocity.

(2) Induced motion requires a minimum threshold signal input into these inhibitory surrounds.

(3) Movement cells with small receptive fields are sensitive to a slower range of velocities than movement cells with larger receptive fields.

Single unit recordings indicate that a substantial proportion of visual neurons are selective for velocity and direction. (See Grüsser and Grüsser-Cornehls, 1973, for a review.) Furthermore, some of these neurons have inhibitory surrounds which are also velocity-sensitive (Sterling and Wickelgren, 1969; Bridgeman, 1972; Collett, 1972; Frost and Wong, 1977). In general, the peak response of velocity-sensitive neurons varies with the velocity of the stimulus, rising monotonically from a minimum over a fairly wide range, but then eventually falling as the velocity is increased (Grüsser and Grüsser-Cornehls, 1973; Pettigrew, Nikara and Bishop, 1968; Movshon, 1975). Thus, the velocity response characteristics of single neurons also have an upper and lower limit, and the range over which cells are sensitive varies widely, depending on the cell type and the species. For example, the optimal velocity for on-off ganglion cells in the rabbit is very slow, $0.1^\circ/\text{sec}$ (Barlow, Hill and Levick, 1964), whereas it is approximately 5000 times faster for some complex cells of the mammalian cortex. Within any neuro-anatomical recording area there is a tendency for neurons to show variation in the range of velocity and this range tends to be correlated with receptive field size. Thus, cells having the largest receptive fields are often the ones sensitive to the highest stimulus velocities (Grüsser and Grüsser-Cornehls, 1973; Movshon, 1975). Figure 6 summarizes some of these properties of velocity-sensitive visual neurons, showing the peak firing rate as a function of velocity for three hypothetical neurons having three different size receptive fields.

We suggest that induced movement requires a minimum amount of signal to be fed into the inhibitory surrounds of movement-sensitive neurons (dashed line, Fig. 6). Thus, if a velocity sensitive neuron had an impulse vs velocity characteristic like that seen in Fig. 6, it should be clear that there would need to be a minimum velocity of the target to produce induction if such neurons stimulated the surrounds of cells mediating movement induction. Neurons with the smallest receptive fields, and hence the ones having a sensitivity to the lowest velocity, will determine the lower amplitude limit of our frequency response plots, since many of these smaller units could be distributed over a wide region. Thus any slow movement, as long as it has the minimum velocity, can be expected to stimulate at least one of such a class of units and thereby lead to induced motion. Moreover, the threshold amplitude vs frequency characteristics (slope of -1) also follow from the properties of these most sensitive units with small receptive fields.

To explain the upper velocity limit for induced motion, we utilize the relationship of the size of the receptive field to its upper velocity sensitivity (Fig. 6). Smaller amplitude movements with a high velocity will not induce motion because such motion is above the velocity limit for cells with small receptive fields and is not of sufficient amplitude to summate over

the receptive field of larger units having a higher velocity sensitivity. Larger amplitude movements, with the same velocity, however, while still not stimulating cells with small receptive fields, will stimulate cells with larger receptive fields. Thus, the existence of differing size receptive fields, with larger receptive fields being correlated with higher maximum velocities, accounts for the rising velocity amplitude relationships seen for the upper limit.

A notable difference between real and induced motion is the restricted set of conditions under which induced motion is elicited. In comparison to real movement, the limitations of induced motion are very great (Fig. 4). The upper velocity limit is especially striking, being so limited that velocities over 1/sec for an amplitude of about 1° are already too great to induce motion. Given the broader range of velocity and frequencies over which real motion can be seen, it seems that the mechanisms mediating induced motion constitute only a limited subset of mechanisms which are motion-sensitive, mechanisms which have particular sets of characteristics. Given the current distinction between X and Y cells (Enroth-Cugell and Robson, 1966), it would be of interest to determine whether or not induced motion can be attributed to X cells, the set having the lower range of velocity sensitivities.

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