

## INTERATTRIBUTE APPARENT MOTION

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**Abstract**—Apparent motion can be seen between two alternating stimuli even if they are defined with respect to their background by attributes other than luminance (such as color, or texture). We measured motion strength as the maximum separation between two alternating stimuli which produced an impression of motion, for conditions in which the two stimuli were defined by the same attribute (intra-attribute) as well as conditions in which they were defined by different attributes (interattribute). The attributes used to define the stimuli were luminance, color, texture, relative motion, or stereopsis. The results indicate that motion was seen for all the intra-attribute conditions about equally well. The results also show that interattribute motion could be seen for all combinations studied. The motion strength in these cases was about 80% of that for the intra-attribute conditions. The process responsible for this motion perception must therefore be able to combine information from different attributes.

Motion perception    Vision    Apparent motion    Multiple representations

### INTRODUCTION

If a stimulus presented at one location is alternated with a second stimulus presented at a different location, a compelling impression of movement is produced, provided that the temporal and spatial parameters are appropriate (Wertheimer, 1912; Korte, 1915; Wallach, 1959; Anstis, 1970, 1980; Kolers, 1972; Ullman, 1979). Rather than two stimuli appearing to flicker on and off at separate locations in this display, a *single* object is seen to oscillate rapidly back and forth. In a way, the message of the motion percept and, in particular, of the perceived path of the motion, is "I was there before but I am here now." Treisman (1986) captures this aspect of object identity in her notion of "object files" that are opened when an object appears and keep position and other information up to date as the object moves and changes.

Although the perception of motion implies that the initial and final stimuli are taken to be the same object, apparent motion can be easily produced when the stimuli differ radically in shape or color. Kolers and von Grünau (1976) reported that observers resolved differences in shape between the initial and final stimuli by perceiving one transforming itself smoothly into the other during the flight. Differences in color were resolved by an abrupt transformation. In fact, several studies have shown that the shape and surface attributes of stimuli have little effect

upon motion affinity (Kolers, 1972; Ullman, 1979; Ramachandran, Ginsburg & Anstis, 1983). More recently, Green has used a more sensitive two-alternative forced-choice test of stimulus affinity in motion competition displays (Green, 1986; Green & Odom, 1986) and does report effects of stimulus orientation, spatial frequency, depth plane, and color on the strength of apparent motion. Shecter, Hochstein and Hillman (1988) used a similar technique and were also able to measure an effect of shape (circle, triangles, or rings) on motion affinity. It is clear in their data that while the effects of shape are measurable, they are relatively small.

Although the general result is that stimulus qualities have only small effects upon the strength of apparent motion, the study by Ramachandran et al. (1983) reported an important exception: motion strength between two filled objects was greater than that between a filled object and an outline one. The authors attributed this result to the low spatial resolution of the motion system. That is, the motion system would merely match stimuli at a blob level while ignoring finer details. Filled objects would appear as similar blobs after low-pass filtering but an outline stimulus would lose a great deal of its contrast and would be a weak competitor for motion. This interpretation could explain previous failures to find an effect of stimulus qualities upon motion strength since low-pass images would lose many of the shape

and texture attributes that researchers had attempted to manipulate.

Prazdny (1986) challenged the hypothesis of a low-pass motion system by demonstrating that there was a stronger motion signal between two filled shapes than between a filled and outline shape even when the shapes were presented as stereograms or as kinematograms. Prazdny (1986) argued that low-pass filtering of the luminance image would simply render invisible the fine dot textures on which stereograms and kinematograms depend. A motion system that analyzed only low-pass luminance images would therefore not respond at all to stereo-defined or motion-defined stimuli. Since Prazdny showed that these stimuli not only produced compelling motion but also duplicated the "filled shape" versus "outline shape" effect reported by Ramachandran et al. (1983), he concluded that the motion system could not be analyzing just the low-pass luminance image.

Prazdny's results do demonstrate that low-pass luminance filtering could not precede the motion response to stimuli defined by fine textures. On the other hand, rather than indicating that there is no low-pass filtering at all, the similarity of the results for the different visual attributes suggests that low-pass filtering may occur in each stimulus domain, once the shape has been extracted from the image. The extraction of the stereo-defined or texture-defined shapes might depend on high spatial frequencies, but once the shapes are extracted, the perception of motion is based on low-pass versions of those shapes.

Other studies have also shown that apparent motion can be produced between stimuli that would be invisible to a luminance-based analysis. For instance, Ramachandran, Rao and Vidyasagar (1973) showed that apparent motion was visible between two texture-defined squares which were uncorrelated in the point-by-point luminance textures that defined them. Petersik, Hicks and Pantle (1978) reported that apparent motion could be seen between alternating squares defined by relative motion. Lelkins and Koenderink (1984) examined the perception of motion created by displacement of areas undergoing dot replacement and presented a high-order motion detector that could respond to their stimuli. Julesz (1971) observed that the alternation of two squares defined by dynamic random-dot stereograms also produced strong apparent motion. Lu and Fender (1972), Ramachandran and Gregory (1978) and

Cavanagh, Boeglin and Favreau (1985) all reported apparent motion between alternating squares defined by equiluminous color. It has also been observed that when stimuli are defined by dynamic random noise (Prazdny, 1987) or binocular disparity (Julesz & Papathomas, 1988), motion can be seen with stimuli that appear to float in front of the background but not with stimuli that appear as holes in the background.

Clearly, apparent motion can be produced by the pairing of stimuli defined by attributes other than luminance. The perception of motion with these displays may depend on a system that identifies forms and then matches them across time and space. These are the properties of the long-range motion system, as described by Anstis (1980) and Braddick (1980). Conversely, the perception of motion for these attributes may depend on directionally selective receptive fields similar to those described by Barlow and Levick (1965) or Reichardt (1961), except that these receptive fields would respond to high-level attributes. Chubb and Sperling (1988) and Lelkins and Koenderink (1984) have described second-order motion detectors for flickering stimuli that are based on higher-order center-surround receptors coupled to Reichardt-style correlation mechanisms.

In this paper we examine the relative strength of motion for different stimulus attributes as well as the motion strength for displays where the first stimulus is defined with respect to the background by one attribute and the second by a different attribute (e.g. a disk defined by color followed by a disk defined by texture).

We evaluated five different stimulus domains: luminance, color, texture, relative motion and stereopsis. Physiological evidence suggests that there may be a specialization of function in different cortical areas for at least some of the stimulus attributes that we are studying. For example, Zeki (1971, 1978), Allman and Kaas (1975), van Essen (1985), van Essen and Maunsell (1983) and others have reported that monkey area V4 appears to be specialized for the analysis of color, and area MT for motion. In functional terms, these cortical areas may be thought of as way stations of an intertwined set of processing pathways, each analyzing and representing a different aspect of the visual world. Stimuli defined by the five attributes that we have chosen to study may selectively activate individual pathways. If apparent motion can be seen between stimuli that are defined in separate

pathways, it suggests that the motion process responsible for this perception must be able to integrate information from these different pathways.

The strength of apparent motion was measured by alternating the position of a disk between the extreme left and the extreme right side of the display. At each exchange, the entire background was reversed in contrast so that transients in the image were not localized to the disk where they could have served as a common cue for motion. Observers decreased the distance between the left and right positions until apparent motion was seen. The disks were defined by one of the five stimulus attributes and the left and right presentations of the disk could be defined by the same attribute or by different attributes. All possible combinations of the five stimulus attributes for the two disk positions were used with the exception of combinations of color and stereo (the red/cyan anaglyph glasses used for stereo interfered with the color stimuli). In addition, we used two versions of the stereo- and motion-defined stimuli, one in which the disks appeared to float in front of the background and one in which they appeared as holes in the background. Prazdny (1987) and Julesz and Papathomas (1988) reported that these latter stimuli did not produce impressions of apparent motion.

## METHODS

### *Subjects*

Three experienced psychophysical observers (two men and one woman) from the Psychology Department of the Université de Montréal participated in the experiment. The average age was 28 (range from 21 to 39 years). Subjects were screened for color vision and perception of depth from binocular disparity and all had normal or corrected vision.

### *Stimuli*

The test stimuli were disks presented on a textured background. They were generated by a Grinnell GMR-270 image processor and presented on a Conrac 5411 RGB video monitor. The disks were 1.5 deg in diameter and the entire display subtended 14 deg from a viewing distance of 1.04 m. A 0.5 deg fixation bull's-eye was present, centered in the top half of the screen, and the left and right positions of the disk were at equal distances from the centre of the screen, 3 deg below the fixation point, and

separated by a distance controlled by the observer. In all cases, the background was filled with a random dot texture, with individual texture elements being 0.06 deg square, 50% white and 50% black, and having a Michelson contrast between the light and dark elements of 50%. The mean luminance of the background was 33 cd/m<sup>2</sup>.

The luminance-defined disks were filled with the same texture as that of the background but with a higher mean luminance, producing a Michelson contrast between the mean luminances of the disks and the background of 11.1% (the contrast between the light and dark texture elements within the disks remained at 50%). The disks for the four other stimulus attributes all had the same mean luminance as that of the background.

The color-defined disks were filled with the same texture as that of the background except that their color was yellow (CIE *x*, *y* coordinates, 0.44 and 0.48 respectively). The luminance of the yellow disks was set to a predetermined point equiluminant with the background for each observer individually (described below).

The texture-defined disks were a uniform gray of the same mean luminance as the textured background.

The motion-defined disks were filled with a texture identical to that of the background, and either the texture of the background moved while that of the disks remained static or vice versa. In the first case, the disks appeared to lie in front of a drifting background, while in the second case, the disks appeared as a hole through which a moving field could be seen. These two versions of the motion-defined disks will be called "near" and "far", respectively. The moving texture drifted leftward at a speed of 3.5 deg/sec.

The stereo-defined disks were filled with the same texture as that of the background and appeared either in front or behind the background plane. The disks had either a 0.12 deg crossed or uncrossed disparity between the cyan and red random dots filling it (equivalent to a depth difference of about 3.5 cm at the viewing distance used), while there was a 0.0 deg disparity between the cyan and red random dots filling the background area. The disks appeared to float in front of the display screen in the crossed disparity condition but appeared as windows through which a rear field could be seen in the uncrossed case. These two versions of the



stereo-defined disks will be called "near" and "far", respectively. The stereo image was viewed through red/cyan stereo glasses to separate the left and right eye images which, when fused, appeared black and white.

### Procedure

**Equiluminance.** Before starting the experiment, an equiluminance setting for color-defined stimuli was established for each observer individually. The observer was shown a static display of one of the color stimuli described above and adjusted the luminance of the yellow color to the point of minimum visibility. This adjustment was performed four times and the average value was used to set the equiluminance of the color condition in the main experiment. We also verified that stimuli defined by a luminance difference (as in the luminance condition) were not visible until the contrast between the mean luminances of the background and of the stimulus reached about 5%. This high threshold was due to the presence of the 50% contrast random-dot texture and ensured that even if the luminances of the background and of the yellow color were not exactly matched in the color condition, the stimuli would be visible only because of the color difference and not because of any residual luminance difference.

**Experimental conditions.** The display alternated between the disk on the extreme left and that on the extreme right side of the screen at a rate of 2 Hz, a 250 msec exposure for each disk with no interstimulus interval. At each exchange, the entire background was reversed in contrast (we also ran control conditions where the background texture, rather than reversing contrast, was replaced with a new random texture at each exchange and found no systematic differences in settings). While fixating the bull's-eye that was 3 deg above the line of motion between the two disk positions, the observer decreased the distance between the two disks by tilting a response lever until apparent motion was just seen. The left and right positions moved symmetrically toward the center of the display. The response lever was of the velocity type so that the speed with which the observer made the disks approach each other depended on the angle through which the lever was tilted. Observers generally moved the disks slowly and took several pauses in order to evaluate the stimulus before continuing. Once motion was seen, the observer pressed a response button and

the task began again with the two disks placed once more at the left and right extremes of the display screen.

There were five stimulus attributes but two of them, stereo and motion, had two different versions, stereo "near" and "far" and motion "near" and "far". The number of conditions needed to examine all combinations, two at a time, was therefore 28, including the seven conditions where both disks were defined by the same attribute. The two conditions pairing color with stereo "near" or "far" were not tested because of the interference of the colored glasses required for stereo viewing with the colored stimulus. Within each of the 26 conditions, at least 20 trials were run. If two different attributes were involved in the condition, it was run once (10 trials) with one stimulus attribute on the left and the other on the right and a second time (10 trials) with the positions exchanged.

## RESULTS

### Intra-attribute

Figure 1 shows the interdisk separations for which apparent motion just became visible as a function of stimulus attribute. These are the data averaged over three subjects for only those conditions where both disks were defined by the same attribute. These intra-attribute data show

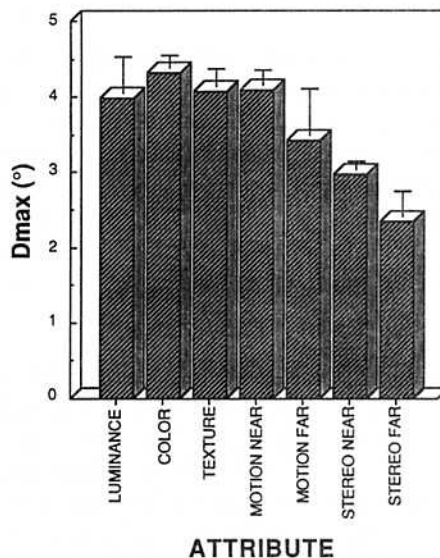


Fig. 1. Results averaged over the three subjects for the intra-attribute conditions. The measure ( $D_{\max}$ ) refers to the maximum distance at which motion could be seen between the two stimuli. The thin lines on each column represent the standard error ( $\pm 1$  SE).

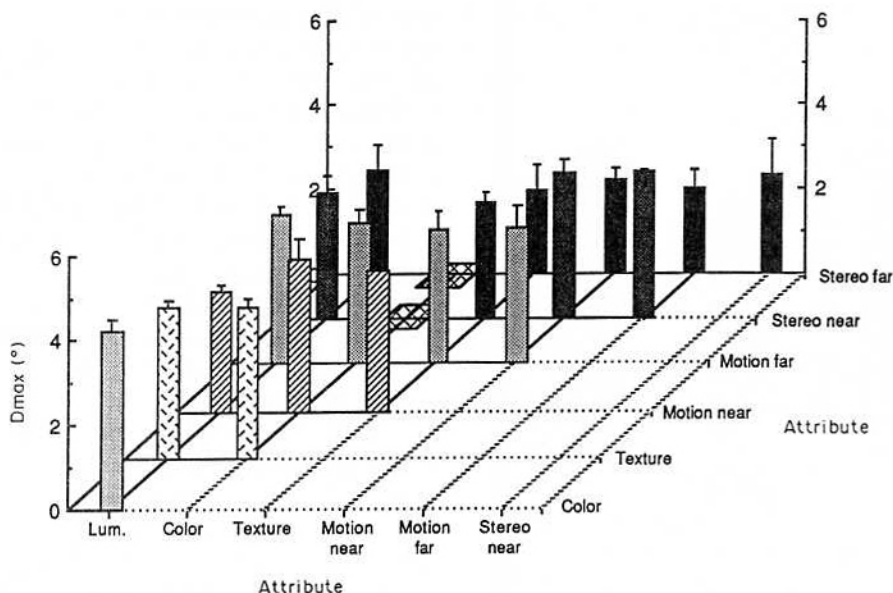


Fig. 2. Results averaged over the three subjects for the interattribute conditions. The horizontal axis and the axis in depth refer to the attribute by which each stimulus of a pair differed from the background. Of the 21 possible combinations, 19 were examined. Since observers wore red/cyan glasses to view the stereo anaglyphs, stereo could not be combined with color. These two conditions were therefore omitted and are indicated on this graph by flat cross-hatched squares. All other conventions are as in the preceding figure.

that apparent motion was visible for all stimulus attributes including stereo "far", where the disks appear as holes. Although there is some additional motion strength for the stereo disk in front compared to in back, this is not statistically significant [ $t(2) = 2.61$ ; NS], contradicting Prazdny's (1987) and Julesz and Pappathomas' (1988) reports that no apparent motion is visible for stimuli that appear as holes the background. A similar result is seen for the motion "near" and motion "far" data [ $t(2) = 1.15$ ; NS].

Overall, there was not a large variation in motion strength between the different attributes. The strongest stimulus (color) was not quite twice as strong as the weakest stimulus (stereo "far"). However, it is difficult to determine whether this variation was due to qualitative differences between the processing of motion for these different attributes or simply to differences in the effective contrast of the stimuli, which we did not attempt to equate.

*Interattribute.* Figure 2 shows the interdisk separations for which apparent motion just became visible as a function of the two attributes involved. The main point to be noted in this figure is that apparent motion was visible for all combinations and that there was no particular pairing that was a great deal better or worse than the others. The overall values of

interdisk separation in these conditions were generally somewhat less than those for the intra-attribute conditions (Fig. 3). The ratio of the average separation for the intra-attribute conditions to that for the interattribute conditions was 0.84 across the three subjects. For the individual observers, the intra-attribute separations were significantly greater than the interattribute separations for two of the three observers [ $t(6) = 6.02$ ;  $P < 0.001$  for SS;  $t(6) = 2.52$ ;  $P < 0.05$  for MA; and  $t(6) = 0.63$  (NS); for LM].

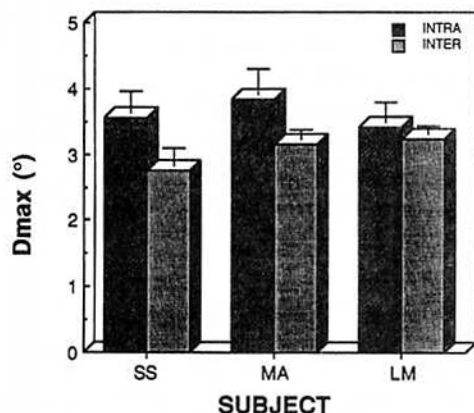


Fig. 3. Averaged results for the intra- and interattribute conditions for each individual observer. Conventions are as in the preceding figures.

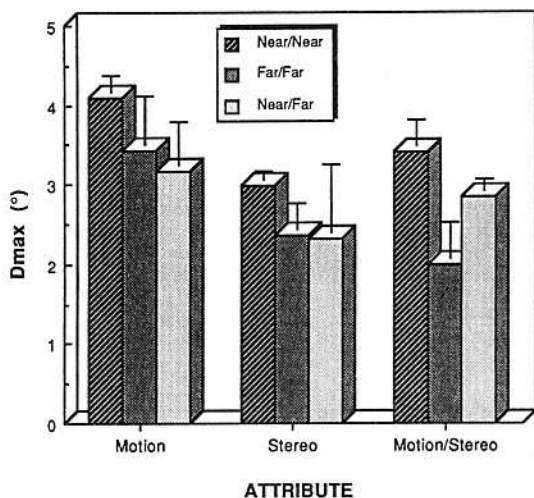


Fig. 4. Results averaged over the three observers for motion- and stereo-defined stimuli. The first two sets of columns represent  $D_{max}$  for the intra-attribute conditions of motion and stereopsis respectively, and the third set represents  $D_{max}$  for the interattribute conditions where one stimulus was defined by motion and the other by stereopsis. Conventions are as in the preceding figures.

There were large differences between individuals in the variability of motion strengths across the interattribute conditions. For observers LM and MA, the largest measured interdisk separation was a little more than twice the smallest, while for observer SS, the largest was five times the smallest.

Finally, we examined whether there was any specific affinity between stimuli when they both appeared in front or when they both appeared behind the background. Stimuli appearing in front or behind the ground plane occurred for the conditions of relative motion and stereopsis. Figure 4 shows the relevant data taken from Figs 1 and 2. Apparent movement between the two stereo disks behind the plane was weaker than that involving the two in front. Also, apparent movement between the motion and stereo disks was weaker when both were behind than for other combinations. However, no other pattern is evident and there is certainly no tendency for the two near and two far pairs to have greater strength than the combined near/far pairs.

## DISCUSSION

The results in the intra-attribute conditions showed that motion was visible for all the visual attributes that we examined. The strength of visual motion, as measured by the maximum displacement over which the motion could be

seen between the alternating disks, varied by a factor of less than two as a function of the attribute defining the disks. The visibility of motion for the stereo "far" and motion "far" conditions contradicts the results reported by Prazdny (1987) and Julesz and Pappathomas (1988), who claimed that apparent motion could not be seen between patches that appeared as holes in the background.

One might conclude from these intra-attribute results that similar systems responsible for motion perception may be available for several stimulus domains. However, our results also showed that motion could be seen between two disks that were defined by different attributes. This result indicates that the motion process must have access to an integrated representation in which stimulus definition is not relevant. That is, some detectors responsible for the perception of motion must be relatively insensitive to the attributes by which a stimulus differs from its background. These units should be able to match stimuli solely by spatio-temporal proximity.

One way to implement a motion system consistent with our data is through directionally selective units, such as those described by Barlow and Levick (1965) or Reichardt (1961), that receive information from all visual pathways (Fig. 5). Directionally selective units such as these could link together stimuli regardless of

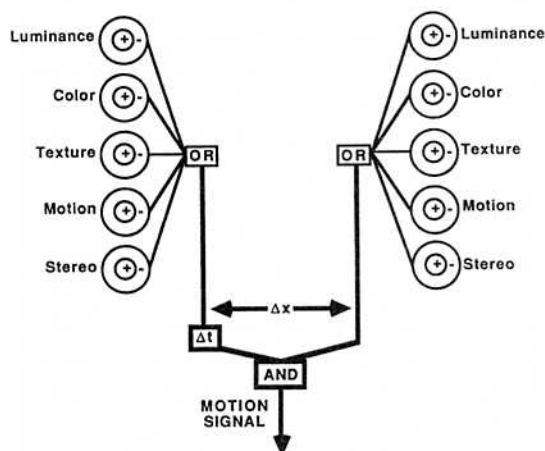


Fig. 5. Example of a directionally selective unit that could combine information coming from several visual pathways. Each set of center-surround units that are responsive to different attributes are spatially separated ( $\Delta x$ ) and a temporal delay ( $\Delta t$ ) is introduced in the signal coming from the left hand units. This arrangement renders the unit responsive to rightward motion when the signals from both sets of center-surround units are combined.

how they differ from their background. This suggestion extends previous descriptions of high-level motion detectors based on Reichardt-style crosscorrelation (Lelkins & Koenderink, 1984; Chubb & Sperling, 1988) to include a larger range of stimulus attributes. Spatially structured receptive fields have been demonstrated for luminance (Hubel & Wiesel, 1968), color (Michael, 1978a,b,c) and relative motion (Frost & Nakayama, 1983; Frost, Cavanagh & Morgan, 1988) but not explicitly for stereo (although see Poggio, Motter, Squatrito & Trotter, 1985) or texture (Hammond & MacKay, 1975; Nothdurft & Li, 1985). We have shown these receptive fields as concentric in Fig. 5 but they might have different organizations. Our data do not offer any insights into the possible shapes of these fields.

One could attribute the motion perception we have examined here to some unspecified long-range process (Braddick, 1980), but it is clear that any motion process must identify forms and match them over space and time. We feel that our suggested structure is the simplest of possibilities. On the other hand, the substantial variations seen for one observer (SS) in motion strength as a function of the attributes being paired implies some additional complexity in the motion analysis. It is not clear from our data whether this variability results from variations in the visibility of the stimuli defined by different attributes or from the preferences of the motion system for or against particular pairings of attributes.

Although we have shown that motion can be seen between two disks no matter what attributes define them, motion strength was greater in the intra-attribute compared to the interattribute conditions for two of the three observers. This difference implies there is some attribute-specific processing that is not captured in our model (Fig. 5) and which is undoubtedly the source of the orientation, spatial frequency, depth and color specific motion that Green has reported (Green, 1986; Green & Odom, 1986). Our data suggest that this attribute-specific contribution accounts for about 1/6 of the overall motion strength in our stimuli. To explain the advantage of intra-attribute conditions, we must assume that there are also motion detectors that independently detect displacement for each of the visual attributes. For simplicity, we assume that these would be based on Reichardt-style crosscorrelation of information from receptive fields that respond to one attribute only.

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## REFERENCES

- Allman, J. M. & Kaas, J. H. (1975). The dorso-medial cortical visual area: A third tier in the occipital lobe of the owl monkey (*Aotus trivirgatus*). *Brain Research*, *100*, 473–487.
- Anstis, S. M. (1970). Phi movement as a subtraction process. *Vision Research*, *10*, 1411–1430.
- Anstis, S. M. (1980). The perception of apparent movement. *Philosophical Transactions of the Royal Society, London B*, *290*, 153–168.
- Barlow, H. B. & Levick, W. R. (1965). The mechanism of directionally selective units in rabbit's retina. *Journal of Physiology, London*, *178*, 477–504.
- Braddick, O. J. (1980). Low-level and high-level processes in apparent motion. *Philosophical Transactions of the Royal Society, London, B*, *290*, 137–151.
- Cavanagh, P., Boeglin, J. & Favreau, O. E. (1985). Perception of motion in equiluminous kinematograms. *Perception*, *14*, 151–162.
- Chubb, C. & Sperling G. (1988). Drift-balanced random stimuli: a general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America A*, *5*, 1986–2007.
- van Essen, D. C. (1985). Functional organization of primate visual cortex. In Peters, A. and Jones, E. G. (Eds.) *Cerebral cortex* (Vol. 3, pp. 259–329). New York: Plenum Press.
- van Essen, D. C. & Maunsell, J. H. R. (1983). Hierarchical organization and functional streams in the visual cortex. *TINS*, *6*, 370–375.
- Frost, B. J. & Nakayama, K. (1983). Single visual neurons code opposing motion independent of direction. *Science, N.Y.*, *220*, 744–745.
- Frost, B. J., Cavanagh, P. & Morgan, B. (1988). Deep tectal cells in pigeons respond to kinematograms. *Journal of Comparative Physiology A*, *162*, 639–647.
- Green, M. (1986). What determines correspondence strength in apparent motion? *Vision Research*, *26*, 599–607.
- Green, M. & Odom, J. V. (1986). Correspondence matching in apparent motion: Evidence for three-dimensional spatial representation. *Science, N.Y.*, *233*, 1427–1429.
- Hammond, P. & MacKay, D. M. (1975). Differential responses of cat visual cortical cells to textured stimuli. *Experimental Brain Research*, *22*, 427–430.
- Hubel, D. H. & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology*, *195*, 215–243.
- Julesz, B. (1971). *Foundations of cyclopean perception*, Chicago: University of Chicago Press.
- Julesz, B. & Pappathomas, T. V. (1988). Asymmetries in binocular motion perception from disparity and rivalry differences. *Investigative Ophthalmology and Visual Science* (Suppl.), *29*, 266.
- Kolers, P. A. (1972). *Aspects of motion perception*. New York: Pergamon Press.



- Kolers, P. A. & von Grünau, M. W. (1976). Shape and color in apparent motion. *Vision Research*, 16, 329-355.
- Korte, A. (1915). Kinematoskopische Untersuchungen. *Zeitschrift Psychologie*, 72, 194-296.
- Lelkins, A. M. M. & Koenderink, J. J. (1984). Illusory motion in visual displays. *Vision Research*, 24, 1083-1090.
- Lu, C. & Fender, D. H. (1972). The interaction of colour and luminance in stereoscopic vision. *Investigative Ophthalmology*, 11, 482-489.
- Michael, C. R. (1978a). Color vision mechanisms in monkey striate cortex: Dual-opponent cells with concentric receptive fields. *Journal of Neurophysiology*, 41, 572-588.
- Michael, C. R. (1978a). Color vision mechanisms in monkey striate cortex: Dual-opponent cells with concentric receptive fields. *Journal of Neurophysiology*, 41, 572-588.
- Michael, C. R. (1978c). Color-sensitive complex cells in monkey striate cortex. *Journal of Neurophysiology*, 41, 1250-1266.
- Nothdurft, H. C., & Li C. Y. (1985). Texture discrimination: Representation of orientation and luminance differences in cells of the cat striate cortex. *Vision Research*, 25, 99-113.
- Petersik, J. T., Hicks, K. I. & Pantle, A. J. (1978). Apparent movement of successively generated subjective figures. *Perception*, 10, 563-572.
- Poggio, G. F., Motter, B. C., Squatrito, S. and Trotter, Y. (1985). Responses of neurons in visual cortex (V1 and V2) of the alert macaque to dynamic random-dot stereograms. *Vision Research*, 25, 397-406.
- Prazdny, K. (1986). What variables control (long range) apparent motion? *Perception*, 15, 37-40.
- Prazdny, K. (1987). An asymmetry in apparent motion of kinetic objects. *Bulletin of the Psychonomic Society*, 25, 251-252.
- Ramachandran, V. S. & Gregory, R. (1978). Does colour provide an input to human motion perception? *Nature, London*, 275, 55-56.
- Ramachandran, V. S., Rao, V. M. & Vidyasagar, T. R. (1973). Apparent movement with subjective contours. *Vision Research*, 13, 1399-1401.
- Ramachandran, V. S., Ginsburg, A. P. & Anstis, S. M. (1983). Low spatial frequencies dominate apparent motion. *Perception*, 12, 457-461.
- Reichardt, W. (1961). Autocorrelation, a principle for evaluation of sensory information by the central nervous system. In Rosenblith, W. A. (Ed.) *Principles of sensory communication* (pp. 303-317). New York: Wiley.
- Shecter, S., Hochstein, S. & Hillman, P. (1988). Shape similarity and distance disparity as apparent motion correspondence cues. *Vision Research*, 28, 1013-1021.
- Treisman, A. (1986). Features and objects in visual processing. *Scientific American*, 255(5), 114B-125.
- Ullman, S. (1979). *The interpretation of visual motion*. Cambridge, Mass: MIT Press.
- Wallach, H. (1959). Perception of motion. *Scientific American*, 201(1), 56-60.
- Wertheimer, M. (1912). Experimentelle Studien über das Sehen von Bewegung. *Zeitschrift Psychologie*, 61, 161-265.
- Zeki, S. M. (1971). Cortical projections from two prestriate areas in the monkey. *Brain Research*, 34, 19-35.
- Zeki, S. M. (1978). Functional specialization in the visual cortex of the rhesus monkey. *Nature, London*, 274, 423-428.