Roles of attention and form in visual motion processing: Psychophysical and brain imaging studies

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INTRODUCTION

It goes without saying that the human visual information processing system is very complex. Marr (1982) proposed that several principles should be taken into consideration to improve understanding of this complex system. These include the *modularity principle* and the *feedforward principle*. The modularity principle assumes that the visual system consists of several processes that are relatively independent of each other in early stages of visual processing (front-end processing). Therefore, each of these processes can be largely examined independently without considering the others. The feedforward principle assumes that the majority of visual functions can be understood without taking feedback effects into consideration.

While research that follows these principles has greatly contributed to understanding some important aspects of visual information processing, other important aspects of information processing have been relatively neglected, especially, interactions between different processes and feedback from higher to lower levels (however, see Grossberg & Mingolla, 1985; Koch & Davis, 1994).

Research on motion perception is not exceptional in this sense. Over the last decade, as in other aspects of visual processing, the majority of research on the processing of velocity of a moving object has mainly explored feedforward processing within the motion module (for a review, Hildreth & Koch, 1987; Nakayama, 1985; Snowden, 1992).

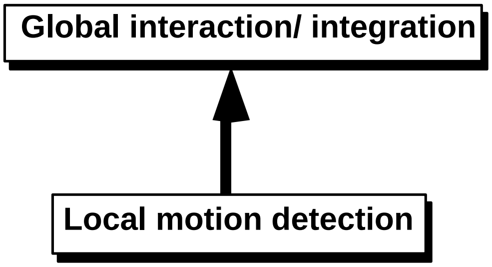


Figure 1 Two stage model

One of the most successful models made from this viewpoint is the *two-stage model*. As shown in Figure 1, this model assumes that visual motion processing includes two stages[1] of analysis (Adelson & Movshon, 1982; Hildreth & Koch, 1984; Movshon, Adelson, Gizzi & Newsome, 1986; Snowden et al, 1991; Welch, 1989). The first stage is supposed to measure *local components of motion*. The directions of locally measured motion components of an object have been reported to be orthogonal to the object's local contours (e.g., Gizzi, Katz, Shumer and Movshon, 1990; Movshon et al, 1986). These locally measured motion components, therefore, do not necessarily correspond to the perceived motion of the whole object. In the second stage, the locally measured motion signals for a single object are integrated. For example, as shown in Figure 2, when two moving gratings overlap, instead of moving in the two different directions orthogonal to the two gratings (Figure 2 (a, b)), they appear to make a "plaid", moving in one motion direction (Figure 2 (c)) (Adelson & Movshon, 1982; Movshon et al, 1986)[2].

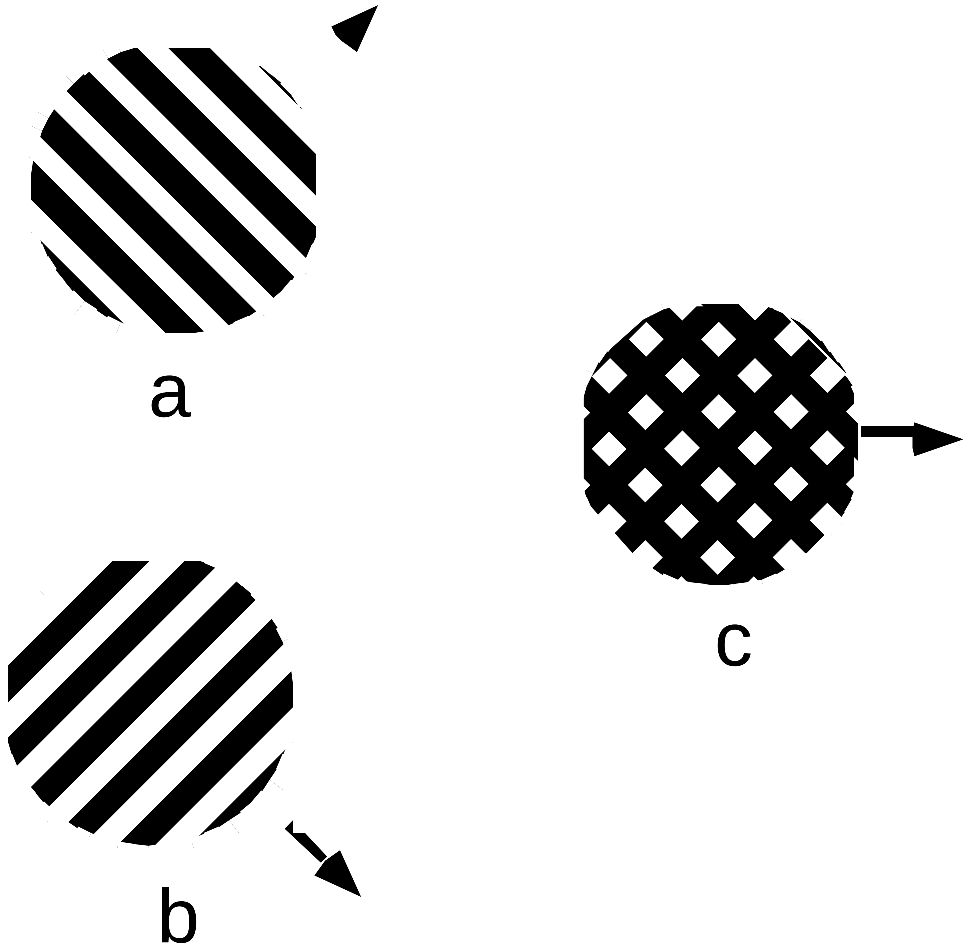


Figure 2: The gratings appear to move in the directions orthogonal to the stripes as in a and b. However, when these two gratings are superimposed, they appear to make a "plaid", moving in one motion direction (Adelson & Movshon, 1982).

The first stage seems to mainly involve V1 and to a certain extent MT, while the second stage of processing may occur at MT, but not at V1. Movshon et al (1986) found that when a plaid consisting of two moving gratings is presented, they found cells in V1 tuned to directions orthogonal to the gratings. However, no cell in V1 was found to be tuned to the integrated motion direction of the plaid. On the other hand, 40% of the cells in MT were found to be tuned to the motion directions orthogonal to the gratings, and 25% of the cells to the integrated motion direction (also see Rodman & Albright, 1987).

Snowden et al have also proposed the two stage model. Using a "transparent" stimulus composed of two sets of random dots moving in opposite directions, it has been reported that cells at V1 tuned to each of the two opposite motion directions gave a similar response to the transparent stimulus and the single surface stimulus composed only of the dots moving in one of the two directions. On the other hand, the activity of the cells in MT stimulated by the transparent stimulus was found to be constantly supressed[3]. That is, local velocities are detected in V1 and the signals of these velocities are interacted in MT (Snowden, Treue, Erickson and Andersen, 1991).

Although this two-stage model has made a great contribution to understanding early motion processing, it considers only feedforward processing within the motion module. In order to better understand motion processing, it should be examined from a viewpoint of visual processing as an interaction of interdependent processes. Recent physiological and anatomical studies show that there are massive reciprocal projections (De Yoe & Van Essen, 1988). These projections may be used in at least two ways in motion processing. The first is for carrying signals from higher-level to lower-level motion processing (feedback projections). When a subject is instructed to pay attention to a whole or part of a moving object, this kind of active attention should originate in a high-level stage of neural information processing (e.g., Corbetta et al, 1991; Posner & Corbetta, 1992) and may influence low-level visual processing. The second way is for reciprocal projections between motion and other types of information processing (inter-module projections). A signal which is sent from motion processing to another processing and that is modified there may be sent back to the motion module in order for the visual system to produce a unified surface reprsentation (Cavanagh, 1987; He & Nakayama, 1992) or representations that are consistent with each other. These two possible kinds of information—feedback projections and inter-module projections— flows should be considered in relation to the two-stage model.

Here, we will discuss our research on early motion processing in relation to both attention (feedback projections) and form processing (inter-module projections)

EFFECT OF ATTENTION ON EARLY MOTION PROCESSING —FEEDBACK PROJECTIONS—

There has been a good deal of controversy about whether or not attention influences very early stages of visual information processing. A considerable amount of work has suggested that attention influences relatively high-level processing, but not the feature analysis level. Treisman and her colleagues built a feature integration theory in which one role of attention is to integrate visual features that are independently processed at lower level stages (Treisman & Gelade, 1981). Neurobiologically, Moran & Desimone (1985) have found that the response of cells in areas V4 and the inferior temporal area (IT) of macaque mokeys to an unattended stimulus is dramatically reduced. However, they did not find such response reduction in cells in V1, where local measurement in various stimulus dimensitons occurs (Hubel & Wiesel, 1959; 1962). On the other hand, Motter (1993) found that the activity of orientation-tuned cells at V1 was enhanced when subjects (macaque monkeys) attended to a specific orientation.

With regard to the effect of attention on motion processing, Cavanagh (1991) found that motion can be driven by attention in the absence of low-level motion signals[4]. Culham and Cavanagh (1994) also found that motion capture is influenced by attention. These findings suggests that attention is quite influential in motion processing. Recently, it has been found attention modulates MT and MST in monkey by means of electrophysiology (Treue & Maunsell, 1996) and the human homologues of MT and MST by f-MRI technique (O'Craven & Savoy, 1995). However, it is not clear whether attention influences each of the first stage of motion processing where local component motion directions are measured and how attention influences the first and second stages.

In order to clarify these questions, the roles of attention in the first, local motion component measurement stage and in the second, integration stage should be examined. To accomplish this, several questions must be addressed: Can the visual system selectively attend to a locally-measured component motion? If so, does attention directly activate the local mechanism or unit for the component motion? Does attention alter the interactions of the signals from locally measured-component motions? Does attention operate on different stages of motion processing, depending on the nature of the task?

If these questions about the influence of attention on motion processing are clearly answered, we will attain a better insight not only into the role of attention in motion processing but also attention in general.

The role of attention in the first stage with f-MRI

The first question is whether attention can modulate component motion directions that are measured in the first stage. Assume that a complex object is shown moving at a velocity that is determined by the integration of locally measured component motions. If directing attention to a local contour of the complex object makes us perceive it moving in the direction orthogonal to the local contour, we may say that attention modulates the component motion.

The previous studies have used either moving random dots or a plaid pattern. Both stimuli contain problems to be used for the purpose of examining the effect of attention on local component motion.

Lankheet and Verstraten (1995) found that when the subject was asked to direct attention to one of two surfaces of random dots moving in opposite directions, the adaptation to the attended direction was higher. Although their finding itself is interesting and very important, using random dots causes a problem for our experiment in that it is not clear whether the subject directed attention to a local motion or a spatially integrated surface moving in a particular direction.

The plaid pattern is also problematic for the purpose of our study. It has been pointed out that the intersections of two gratings of a plaid pattern, which move in the same direction as the perceived motion direction of the plaid as a whole, may be used as a local tracking cue to the plaid motion (Gorea. & Lorenceau, 1991; Alais, Wenderoth, & Burke, 1994). Alais et al (1994) found that the inter-ocular transfer of the motion aftereffect to the integrated motion direction of a plaid pattern was not perfect, suggesting that the monocular motion unit for the motion direction identical to the integrated motion direction is actually involved when the integrated motion is perceived. This finding is in accordance with the view that intersections are used as a local tracking cue. Thus, the plaid motion may not be entirely determined by the internal integration of locally measured component motions.

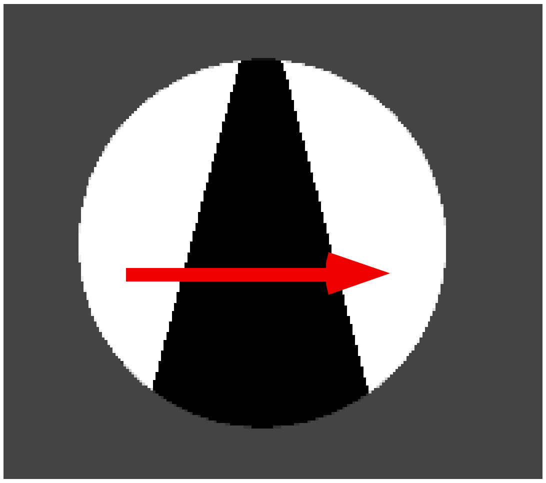


Figure 3 : The test stimulus consisting of the non-parallel stripes moving either to the leftt or to the right in a circular aperture.

In order to get around these potential problems to examine the effect of attention to a local component motion, Watanabe (1995) have developed a new stimulus that is shown in Figure 3. It consisted of a sequence of black wedges moving against a white background toward the right or the left in a circular aperture. The black wedges (0.5 cd/m^2 in luminance) were 30 deg in angular subtence and moved either to the right or left at a speed of 2.5 deg/sec within a white circular aperture (32.0 cd/m^2) against a dark gray background (16.0 cd/m^2). The radius of the circular aperture was 7.5 deg. A light gray cross (24.5 cd/m^2) was presented in the center of the circle as a fixation point. The motion of the wedges as a whole should be the result of the integration of the signals from component motions that are measured along the right and left contours of the stripes. Both the IOC hypothesis[2] and the vector summation hypothesis predict that the motion direction(s) of the wedges as a whole should be either rightward or leftward as represented by the arrow in Figure 3. In this new display, although indeed there are unambiguously moving features, namely the corners near the top or bottom of the aperture, they do not move in the same directions as the integrated motion direction. Thus, when the wedges are perceived to move in the integrated motion direction (either rightward or leftward), unlike the intersections in the plaid, these features should not be tracked as a local cue for the motion direction of the plaid as a whole.

When these wedges are observed without allocating attention to any particular place or any particular motion while fixating the fixation point in the center of the display, the wedges appear to move to the left or right in the true direction of motion. However, once attention is directed selectively at one of the wedge contours, the whole wedges appear to move in the direction orthogonal to the attended contour. In the experiment, after the disappearance of the wedge stimulus, the subject was instructed to adjust an arrow to the perceived motion direction of the wedge. The experimental result with 6 subjects (Figure 5) confirmed the observation. Eye movements were observed on a monitor [Panasonic wv-5410] connected to a camera [Panasonic wv-1850] directed at the right eye of the observer. No significant pursuit eye movements were observed throughout the experiments. Notice that the component motion direction detected at a contour is believed to be orthogonal to the contour (Movshon et al, 1986). Thus, these results suggest that attention modulates a local motion direction.

Next, we presented the subject with the test stimulus shown in Figure 2 and examined blood flow change (activation) by means of functional Magnetic Resonance Imaging (f-MRI) technique. So far we found that for all 6 subjects V1 was more activated when they directed attention at one of the contours of the wedge than when they observed the test stimulus passively (Miyauchi et al, 1995, 1996). This is shown in the functional map in Figure 4.

Such an increase in activation in V1 in the attention condition was not found with any subject when the same wedge was presented stationary. This result suggests that the V1 activation is due to attention to a local motion rahter than attention to a spatial location.

In another control experiment, we presented a black rectangle moving in the circular aperture with the same procedure as in the first experiment. The horizontal width of the rectangle was the same as the averge width of the wedge in Figure 2. In that case, no significant activation difference was found in V1 with any of the six subjects between the attention condition and the passive condition. Since the orientation of both side of the rectangle was vertical, the direction of the local motion should be the same as the direction of the integrated motion. Thus attention might not have to strongly activate the unit for the local motion direction. Similar results were reportedwith a monkey brain (Motter, 1991).

This finding shows that attention influences V1 where local motion directions are first measured (Movshon et al, 1986). How is V1 influenced by attention? One possibility is that the unit (in V1) which is responsible for a local motion was selectively more activated in the attention tasks. However, the mere fact of an activation increase in V1 may not filter out another possibility that this activation increase might be merely due to the general arousal of V1, for example, because of the difficulty of the attention task as compared with no attention task (see Wurtz et al, 1980).

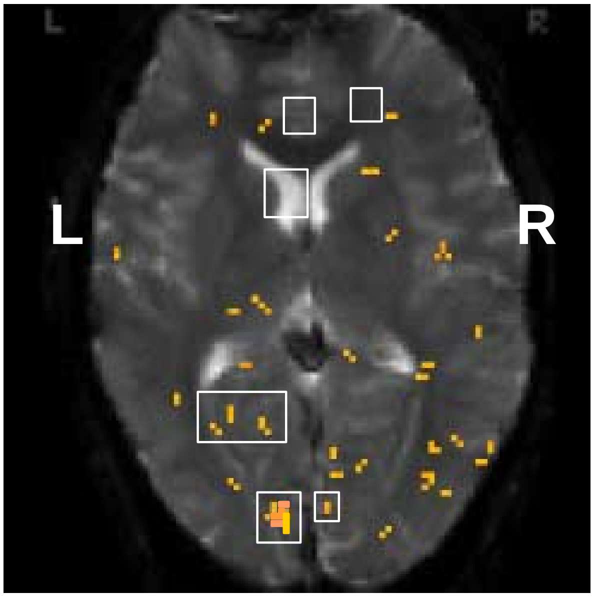


Figure 4 : Functional map of one observer (SM) overlaid on the anatomical map for the right side (right image) attention conditions after the no attention condition results have been subtracted.

In order to examine which possibility is more likely, Watanabe (1995) conducted psychophysical experiments that measured motion aftereffects. It is known that after we perceive an object moving in a direction for several minutes, a physically stationary object appears to move in the opposite direction to that of the previously viewed moving object. This motion aftereffect is usually thought to be due to the adaptation of a set of units tuned to the direction of a moving object. This adaptation in turn causes an inbalance between outputs from the two sets of units responsible for opposing motion directions (e.g., Anstis, 1986). Motion aftereffects have been regarded as a strong and objective measure used to infer the kind of inner motion process activated while the moving object was observed before the occurrence of the aftereffect (e.g., Alais, Wenderoth, & Burke, 1994). Several researchers have pointed out that attention can alter strength and direction of motion aftereffect (Chaudhuri, 1990; Lankheet & Verstraten, 1995; Verstraten et al, 1994). This suggest that attention influences motion processing. However, it was not clear which stage of motion processing is influenced by attention.

Watanabe (1995) compared the strength of motion aftereffects with inter-ocular viewing to that with monocular viewing, in both attention and non-attention conditions. On each trial, the same wedge stimulus as used for the f-MRI experiment (Figure 3) was presented as an adaptation stimulus for 1 min and was followed by a test stimulus consisting of black and white parallel stripes whose orientation was varied from trial to trial. The adaptation and test stimuli were presented either with monocular (same eye) or inter-ocular (one eye to another) viewing . As in the previous experiment, there were two attention conditions and one non-attention condition. The duration of the motion aftereffect was measured as an index of its strength. Before the experiment, each subject conducted approximatly 100 practice trials to reduce response variability.

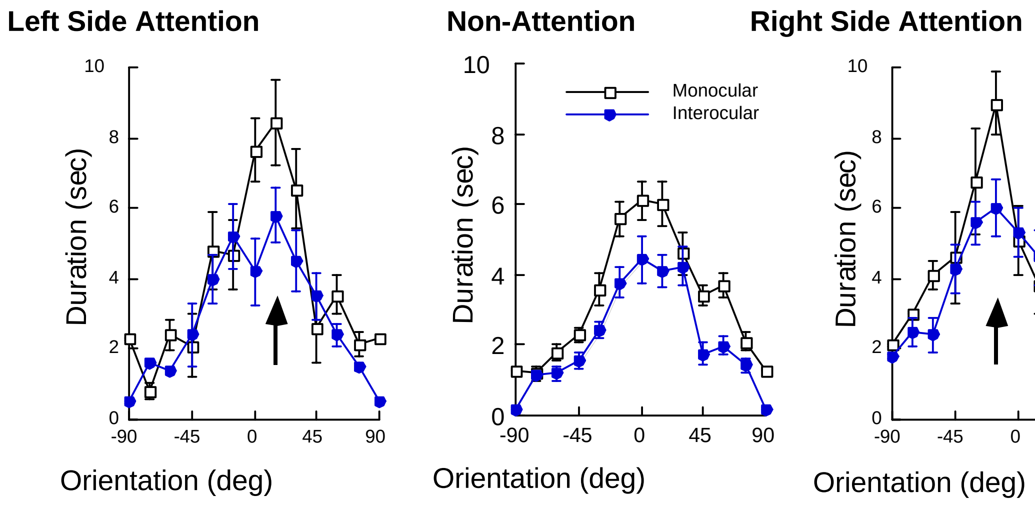


Figure 5: The duration of motion aftereffect as a function of orientation of the test stripes for the left side attention (left), the non-attention (center), and the right side attention (right) conditions. 0 and 90 (-90) deg represent vertical and horizontal orientations. The arrows represent the orientation of the side where attention was directed.

Figure 5 shows the duration of motion aftereffect as a function of test stripe orientation. In the attention conditions, strongest motion aftereffects were obtained when the orientations of the test stripes were orthogonal to the local motion directions which attention modulated, with both monocular and inter-ocular viewings. In the non-attention condition, the aftereffect was strongest when the orientation of the test stripes was orthogonal to the integrated motion direction (the rightward direction). These results show that motion aftereffects are modulated by attention to a local motion.

Second, in both the attention and non-attention conditions, the motion aftereffects were stronger with monocular viewing than with inter-ocular viewing. The difference in strength of the aftereffect between monocular and inter-ocular viewing in the non-attention condition may be attributed to the monocular units' activation, stimulated by the afferent stimulus information only with the monocular viewing (Wolfe & Held, 1981). However, the difference in the strength between the two viewings around the peak of the “tuning curves” was much larger in the attention conditions than in the non-attention condition. Furthermore, while the "tuning curve" for monocular viewing is as shallow as for inter-ocular viewing in the non-attention condition, the tuning curves were significantly steeper for monocular viewing than for inter-ocular viewing in the attention conditions.

These results suggest that the difference in strength and shape of the two curves in each attention condition may not be attributable just to the difference between the presence and absence of the adaptation of the monocular units to the afferent motion information. Presumably, the monocular units for attended motion directions were strongly activated. Attention seems to influence monocular units for relevant component motion directions.

Since a majority of monocular cells have been found in and before V1, these psychophysical results are in accord with the higher activation of V1 in the attention conditions with f-MRI. Furthermore, since the psychophysical results suggest the activation of a specific unit for relevant motion directions, they also eliminate the possibility that the activation of V1 found by f-MRI technique is due to the general arousal of V1.

The role of attention in the second stage of motion processing

As mentioned in the introduction, it has been suggested that locally measured motion signals interact and integrate at MT (Rodman & Albright, 1989; Movshon et al, 1986; Snowden, 1991). In the previous section, we showed that attention to a local motion activates the units in V1 which correspond to local component computations (Movshon et al, 1986).

An important question arises: Does attention to any kind of motion always activate V1 or does the stage of motion processing that is activated by attention depend on the featue of motion to which attention is directed?

We examined the blood flow change by means of the f-MRI technique when attention was directed to an integrated direction of motion, instead of a local motion direction. In the experiment, the subjects were presented with several bouncing balls (Figure 6(a)).

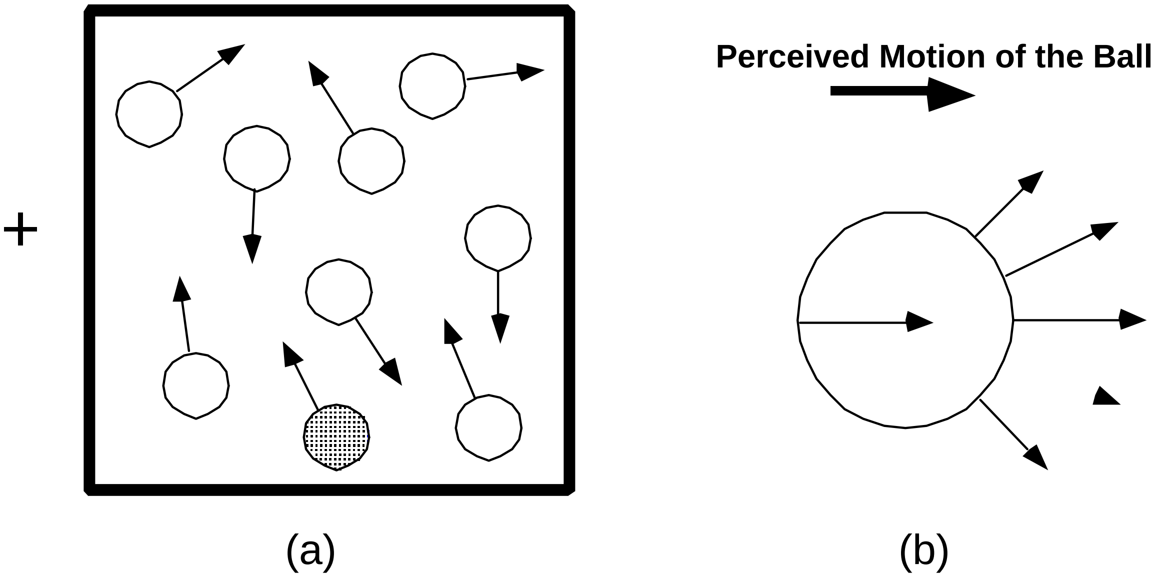


Figure 6: (a) Balls bouncing within a framewok were presnted. In the attention condition, the subject was instructed to direct attention to particular ball which blinked for a second before the onset of the measurement of the brain activity. In the passive condition, the subject was instructed to direct attention to no particular place. In both conditions, the subject had to fixate the fixation point which was presented either the right or the left side to the framework. (b) The perceived motion (represented by the bold arrow) of a bouncing ball is obtained as aresult of integration of local motions whose directions are perpendicular to local contours.

In the attention condition, the subject was asked to direct attention to one particular ball while fixating a point in the center of the display. In the non-attention condition, the subject was asked to watch the display passively while fixating the central point. As shown in Figure 6(b), the perceived motion direction of a bouncing ball should be obatained by integrating locally measured motion signals. Thus, directing attention at a single bouncing ball among many balls means directing attention to an integrated motion among many integrated motions. We found that MT/MST area was significantly more activated in the attention condition than in the non-attention condition. However, there was no significant difference found in the amount of activation in V1 between the two conditions (Miyauchi et al, 1995, 1996). Basically the same results were obtained when attention was directed to expanding/contracting motion that may be first measured in MST (Tanaka, Fukada & Saito, 1989) as a result of interactions and integrations of local motion units (O'Craven and Savoy, 1995).

Further study

We are now conducting a series of experiments by means of f-MRI and psychophysics in which the subject is instructed to direct attention to a different feature of motion with the same stimulus under each of several different conditions. Although this experiment is still underway, the preliminary results show that the location of an anactivated area due to an attention allocation depends on a task demand, that is, which feature of motion attention is directed to.

Conclusion for effects of attention on motion processing

The results of the experiments have the following implications: First, when attention is directed to a component motion direction, V1 is more activated. Second, the V1 activation may be attributed to the activation of the units in V1 for the local motion, but not to an overall activation in V1 caused by a general awareness. Third, when attention is directed to an integrated motion of an object, MT is more activated, but V1 remains at baseline. That is, the level of motion processing attention influences depends on features of motion to which attention is directed.

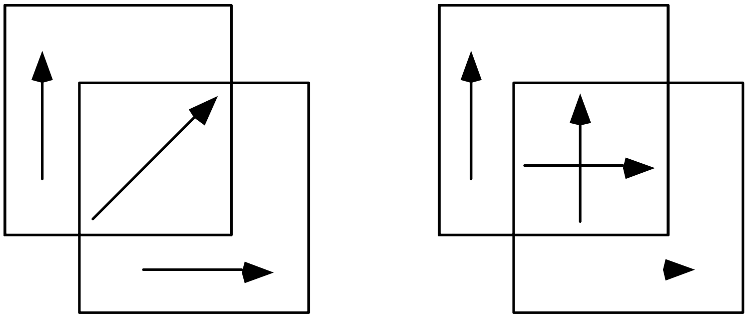
Why does the stage of motion processing that is influenced by attention vary under different experimental conditions? Remember that according to the two stage model, the earliest stage at which local motions are measured is V1 while the area at which the local motion signals interact and are integrated may be MT/V5 (Movshon et al, 1986; Rodman & Albright, 1989; Snowden et al,, 1991). Our findings suggest that attention influences a cortical area that is crucial for measuring or producing signals of a feature of motion (local component motion or global motion) to which attention is directed.

This makes several important implications regarding the relationship of attention to visual information processing in general. First, basic visual features such as motion signals in V1 can be modulated by attention. Several researchers have argued that visual search for basic features are in a relatively high-level stage of visual processing (Cavanagh, Arguin & Treisman, 1990; Bravo & Blake, 1990). Perhaps attention can reach down and modulae basic visual features in representations that come before the representation on which visual search occurs (Wolfe, 1996). Second, our results indicate that the units for a relevant mtion feature are activated. This suggests that attention enhances signals for a relevant feature, rather than just picking up the signals and/or filtering out irrelevant signals. Third, the visual system seems to activate the specific unit in a specific stage which is most responsible for the processing of a feature at whcih attention is directed.

INTER-MODULER INTERACTIONS BETEEN MOTION PROCESSING AND FORM PROCESSING

The previous section indicated a way of sending feedback signals from a high-level cortical area influence early motion processing. In this section, we will show a novel phoenomenon called *velocity decomposition* that may show how inter-cortical interactions occur— specifically, how motion processing interacts form and other kinds of processing to produce a unified surface representation or representations that are consistent with each other (Watanabe, 1997).

Watanabe (1997) showed that a transparency configuration makes two different interactions of motion signals occur in the same retinal region. He demonstrated that motion in one physical direction appeared to be decomposed into two component motions in a transparency configuration. Figure 7 (a) is a physical velocity map of the display that induces the velocity decomposition. It consists of random dots moving simultaneously in three different directions in three different regions—a central square and two flanking rotated "L" shapes. In this case, the velocity of the dots in the central square appeared to be decomposed into two component velocities; one identical to the velocity of the dots in the upper "L" and the other identical to the velocity of the dots in the lower "L", as illustrated in Figure 7 (b). In addition, one square with dots moving upward and another with the dots moving rightward appeared to overlap transparently in the central square[5].



(a) (b)

Figure 7: (a) Example of the stimulus that induces velocity decomposition. The three regions are defined by the different velocities of random dots. There are no black contour lines actually present as used in this figure. A velocity of the dots within the same area is represented as one vector. (b) Schematic description of perceived velocities. The velocity of the dots in the central square appears to be decomposed into two component velocities; one is the same as the velocity of the dots in the top "L" and the other is the same as that in the bottom "L".

Watanabe (1997) checked how these dots from the three regions interact. In an experiment, a fixation point was presented for 1 sec. From trial to trial, its location was varied from the center of the central square to a point 4.5 deg above the center. Then the test stimulus (Figure 7a) was presented for one sec. While the dots in the upper and lower "L"s constantly moved rightward and upward, respectively, the direction of dots in the

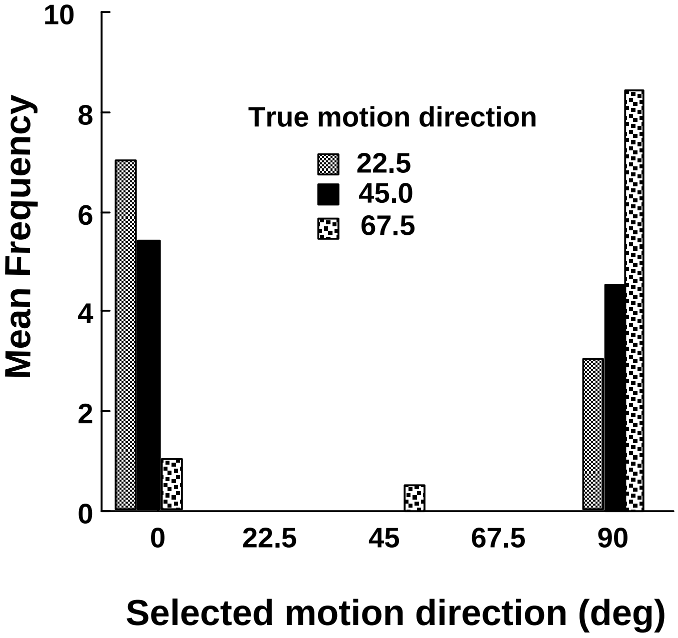


Figure 8: Mean frequency (n=2) as a function of the selected motion direction, for 22.5, 45.0 and 67.5 physically truemotion directions of the dots in the central square. 0, 45, 90 deg represent the upward, upper-rightward, and rightward motion directions.

central square was varied from trial to trial in 16 different directions ranging from 0 to 337.5 deg in 22.5 deg steps. 0, 90.0, 180.0, and 270.0deg represent upward, rightward, downward and leftward motion directions, respectively. The test stimulus was then followed by a set of arrows, each of which pointed in the 16 different directions. Individual dots existed for about 70 ms and then disappeared to be replaced by others at random locations so that the subjects could not trace individual dots to infer their physically true motion directions. This renewal scheme minimizes the probability that individual dot paths are being tracked (Andersen et al, 1990). The subjects were instructed to choose only one arrow that represented the perceived motion directions in the central square most appropriately.

In order to examine which motion direction the subjects saw for 22.5, 45.0 and 67.5 deg physical motion directions of the dots in the central square, the frequency of the motion direction the subject chose is shown for these three directions in Figure 8, respectively. The data were obtained when the location of the fixation point was 4.5 deg above the center of the central square. For 45 deg, they choose 0 and 90 deg nearly equally often. This result is in accord with the subject's verbal report that they actually saw 0 and 90 deg motions at the same time. However, since they were instructed to choose only one motion direction, they chose one of the two randomly. On the other hand, when the physical true motion directions were 22.5 and 67.5 deg, they saw 0 and 90 deg motion directions most frequently. What was common to all the three conditions was that with increasing eccentricity from the center of the central square, the frequency of the subject choosing 0 or 90 motion directions increased, although even with the foveal viewing the same but weaker tendency was observed.

Watanabe (1997) also conducted an experiment in which the speed of the dots in the central square of the same figure as in the previous experiment was systematically varied and found that velocity decomposition occurred most frequently when the velocity (direction and speed) of the dots in the central square is the vector sum of the velocities of the dots in the two "L"s. The same tendency was found with many other combinations of dot motion directions in the three areas.

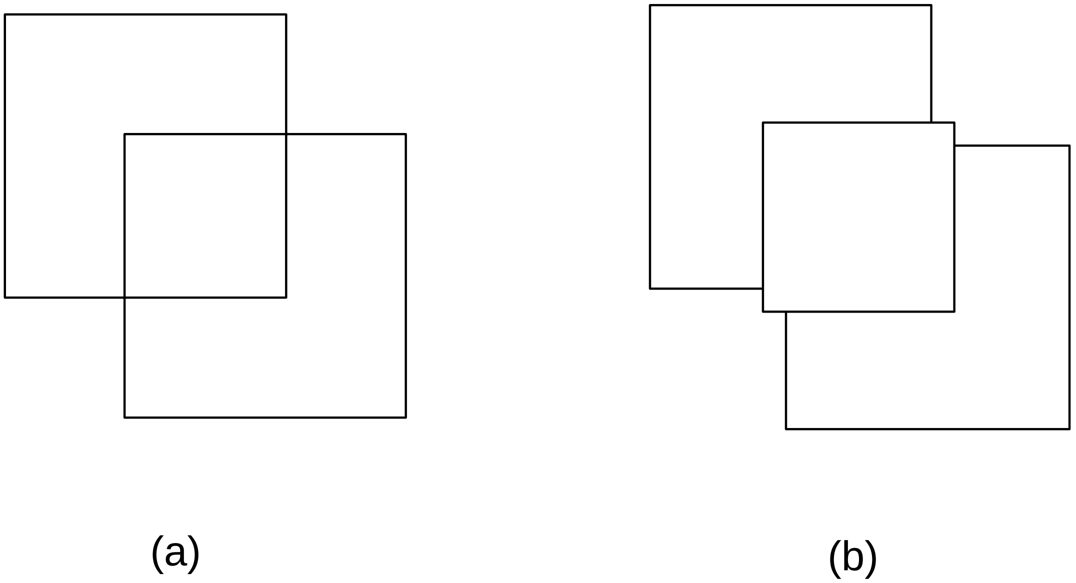


Figure 9: (a) A transparency cnfiguration. The two large squares appear to be overlapping in the region of a central small square. (b) An occulusion configuration. The central square appears to be opaque, occluding the two large squares.

Velocity decomposition has been observed in the transparency configuration shown in Figure 9 (a), in which two large squares appear to be overlapping in the region of the central small square. At times, the top large square appears to be transparent, overlying the bottom square. At others, the bottom appears to be transparent. Is the transparency configuration necessary for velocity decomposition?

In order to answer this question, the random dots were put in an occlusion configuration as shown in Figure 9(b), where the central square appears to be opaque, partially occluding the two large squares. In this case, no velocity decomposition was observed even if the velocity of the dots in the central square was the vector sum of the velocities of the two "L"s. The subject constantly chose 45 deg motion direction when this direction was presented in the central square. These results show that the transparency configuration is necessary for velocity decomposition[3].

How do velocity and surface decompositions occur? As mentioned above, the motion condition necessary for velocity decomposition is also necessary for surface decomposition and the figural configuration necessary for surface decomposition is also necessary for velocity decomposition. Since surface decomposition occurs in the figural configuration shown in Figure 9a, form processing should be involved in the surface decomposition. Thus, the results of the present study suggest that there is a strong reciprocal interaction between motion and form processings in order to produce a uified representation presentation (Cavanagh, 1987) or presentations consistent with each other. The information of a representation in form processing may influence and change a representation of motion. This change in motion representation might, in turn, influence the representation in form processing, and so on. This reciprocal interaction may be accomplished by inter-module projections.

What is happening within motion processing in relation to the two stage motion model while motion processing and form processing interact? There are at least two possibilities. One is that an interaction occurs between form processing and the second stage of motion processing. Velocity decomposition may be a result of two different global interactions of motion direction signals occurring at two different depth planes in the same retinal region. For the 22.5 and 67.5 degs, the motion of the dots in the central square seems to be assimilated to the motion direction of an "L" which is closer to the direction of the dots in the central square (see, Nawrot & Sekuler, 1990; Watanabe & Cole, 1995). Assimilation may be the result of large-scale interactions such as smoothing of different motion directions (Bulthof, Little & Poggio, 1989 ; Grossberg & Rudd, 1992; Hildreth, 1984; Yuile & Grzywacz, 1988). When the velocity of the dots in the central square was the vector sum of the velocities of the dots in the “L”s, the magnitude of the difference between the motion directions of the dots in the upper "L" shapes and that in the central square was the same as the magnitude between those in the lower "L"s and in the central square. When this velocity condition and the transparency configuration coincide, the two different assimilations of the dots in the central square to the directions of the dots in the two "L"s could occur at two different depth planes into which the central square was decomposed. On the other hand, any assimilation did not occur in the occlusion configuration that does not induce surface decomposition.

The other possibility is that the local motion signals only for the decomposed motion directions are relatively enhanced in the first stage of motion processing. The direction of local motion is suggested to be orthogonal to the local contour (Gizzi et al, 1990; Worgotter, 1991). Usually, local motion signals are integrated into one motion direction if these signals are regarded as properties of a single object. The speed of each motion component is proportional to the cosine of the angle between the true motion direction of the object and the local motion direction (Adelson & Movshon, 1982). When a circular dot is moving, for example, in the upper-right direction, the speed for the detected local motion for the true motion direction is the highest and much higher than those for the upward and rightward directions. However, in the surface decomposition configuration, the speeds of the local motions for the upward and rightward directions detected in each of the dots in the central square might be enhanced and the local motion signals might be integrated into these two directions.

CONCLUSION

A research on motion processing has mainly attempted to clarify only feedforward processing within the motion module. Indeed, research inspired by this framework has made a great progress and two stage motion processing has been largely accepted. However, a large number of reciprocal projections have been found between different cortical areas.

This chapter has shown our attempts to understand motion processing from a viewpoint of visual processing as an interaction of interdependent processes. First, we have shown how attention works on each of the two stages in motion processing. Using f-MRI technique, we found that attention directed to a local motion direction enhanced activity in parts of V1, whereas attention activated MT but not V1 when it is directed to a global motion direction. These findings have important implications for the role of feedback projections. The visual system seems to control the destination of feedback processing so well as to activate a specific unit for motion direction up to a specific stage of motion processing.

Second, we showed a phenomenon called velocity decomposition that may reveal reciprocal interactions between motion and other processings whose implimentation may be accomplished by inter-module projections.

Although only two examples are shown in this chapter, there may be many visual functions whose feedforward processing within a module are largely known but whose interactive aspects are a mistery. In the near future, more of these interactive aspects are expected to be clarified through research on visual processing from the viewpoint of visual processing as an interaction of interdependent processes.

FOOTENOTES

[1] Many computational models assume that the first stage can be divided into energy extraction through spatio-temporal filters and construction of a local velocity from the extracted energy (e.g., Adelson & Bergen, 1985; Grzywacz & Yuile, 1991; Heeger, 1987).

[2] There are two controversial hypotheses as to an integrated velocity. One is the "intersection-of-constraints" (IOC) hypothesis that assumes that an integrated motion is determined by the intersection of all the physically possible interpretations generated by locally measured component motions (Adelson & Movshon, 1982; Fennema & Thompson, 1979). The other is the vector summation hypothesis in which the integrated velocity is determined by summation of locally measured component motions that are orthogonal to the local contours (e.g., Mingolla, Todd & Norman, 1992; Yo & Wilson, 1992).

[3] The same transparency configuration causes brightness transparency (Beck, 1986; Beck, Pradzny, & Ivry,1984; Watanabe & Cavanagh, 1993) and texture laciness (Watanabe & Cavanagh, 1996).

[4] The way of how suppressive interactions occur was measured psychophysically, first, by Snowden (1990) and, more recently, by Verstraten, Fredericksen, van Wezel, Boulton and van de Grind (1996) with an improved measurement.

[5] In contrast, Lu and Sperling (1995) suggest that attention influences a saliency map rahter than

motion measurement. The saliency map is assumed to be in a lower stage than motion measurement.

REFERENCES

Adelson, E. H., & Bergen, J. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America A, 2*, 284-299.

Adelson, E. H., & Movshon, J. A. (1982). Phenomenal coherence of moving visual patterns. *Nature*, *30*, 523-525.

Alais, D., Wenderoth, P., & Burke, D. (1994). The Contribution of One-Dimensional Motion Mechanisms to the Perceived Direction of Drifting Plaids and their Aftereffects. *Vision Research*, *34*, 1823-1834.

Andersen, R. A., Snowden, R. J., Treue, S., & Graziano, M. (1990). Hierarchical processing of motion in the visual cortex of monkey. *Cold spring harbor symposia on quantitative biology*, *LV*, 741-747.

Anstis, S. (1986). Motion perception in the frontal lobe. In K. R. Boff, L. Kaufman, & J. R. Thomas (Eds.), *Handbook of Perception and Human Performance, Vol. 1. Sensory Processes and perception* (pp. 1-27). New York: John Wiley & Sons.

Beck, J. (1986). Perception of transparency in man and machine. In A. Rosenfeld (Eds.), *Human and machine vision II* (pp. 1-12). Orlando: Academic Press.

Beck, J., Pradzny, K., & Ivry, R. (1984). The perception of transparency with achromatic colors. *Perception Psychophysics.*, *35*, 407-422.

Bravo, M. & Blake, R. (1990). Preattentive vision and perceptual groups. *Perception*, *19*, 515-522.

Bulthoff, H., Little, J. & Poggio, T. (1989). A Parallel algorithm for real-time computation of optical flow. *Nature*, *337*, 549-553.

Cavanagh, P. (1991). Attention-based motion perception. *Science*, *257*, 1563-1565.

Cavanagh, P., Arguin, M. & Treisman, A. (1990). Effect of surface medium on visual search for orientation and size features. *Journal of Experimental Psychology: Human Perception & Performance.*, *16*, 479-192.

Chaudhuri, A. (1990). Modulation of the motion aftereffect by selective attention. *Nature*, *344*, 60-62.

Corbetta, M., Miezin, F. M., Shulman, G. L., & Petersen, S. E. (1991). Selective and divided attention during visual discriminations of shape, color, and speed; functional anatomy by positron emission tomography. *Journal of Neuroscience*, *11*, 2383-2402.

Culham, J. C. & Cavanagh, P. (1994). Motion capture of luminance stimuli by equiluminous color grating and by attentive tracking. *Vision Research*, *34*, 2701-2796.

DoYoe, E. A., & Van Essen, D. C. (1988). Concurrent processing streams in monkey visual cortex. *Trends in Neuroscience*, *11*, 219-226.

Gizzi, M. S., Katz, E., Schumer, R. A., & Movshon, J. A. (1990). Selectivity for orientation and direction of motion of single neurons in cat striate and extrastriate visual cortex. *Journal of Neurophysiology*, *63*, 1529-1543.

Gorea, A., & Lorenceau, J. (1991). Directional Performances with Moving Plaids: Component-related and plaid-related processing modes coexist. *Spatial Vision*, *5*, 231-252.

Grossberg, S. (1997). How is a moving target continuously tracked behind occluding cover? In *High-level Motion Processing* (Ed. T. Watanabe), Cambridge: The MIT Press.

Grossberg, S., & Mingolla, E. (1985). Neural dynamics of form perception: Boundary completion, illusory figures, and neon color spreading, *92*, 173-211.

Grossberg, S. & Rudd, M. E. (1992). Cortical dynamics of visual motion perception: short-range and long-range apparent motion. *Psychological Review*, *99*, 78-121.

Grzywacz, N. M., & Yuile, A. L. (1991). Theories for the visual perception of local velocity and coherent motion. In M. S. Landy & J. A. Movshon (Eds.), *Computational models of visual processing* (pp. 231-252). Cambridge: The MIT Press.

Heeger, D. (1987). A model for the extraction of image flow. *Journal of the Optical Society of America A*, *4*, 1455-1471.

Hildreth, E. C. (1984). *The measurement of visual motion*. Cambridge: MA: MIT Press.

Hubel, D. H., & Wiesel, T. N. (1959). Receptive fields of single neurons in the cat's striate cortex. *Journal of Physiology.*, *148*, 574-591.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. , ***160***, 106-154.

Koch, C., & Davis, J. L. (Ed.). (1994). *Large-scale neuronal theories on the brain*. Cambridge: The MIT press.

Lankheet, M. J. M., & Verstraten, F. A. J. (1995). Attentional modulation of adaptation to two-component transparent motion. *Vision Research*, *35*, 1401-1412.

Lu, Z.-L., & Sperling, G. (1995). Attention-generated apparent motion. *Nature*, *377*, 237-239.

Mingolla, E., Todd, J. T. & Norman, F. (1992). The perception of globally coherent motion. *Vision Research*, *32*, 1015-1031.

Miyauchi, S., Watanabe, T., Sasaki, Y., Takino, R. & Putz, B. (1995). Voluntary attention to motion can specifically activate either V1 or MT. *The proceedings of 10th Tokyo Institute of Psychiatry International Symposium*, Tokyo.

Miyauchi, S., Watanabe, T., Butz, B., Takino, R., & Sasaki, M. (1996). Voluntery attention to the motion of visually perceived objects can specifically active either V1 or MT. *Electroeucephalography and Clinical Neurophysiology.*, in press.

Moran, J., & Desimone, R. (1985). Selective Attention Gates Visual Processing in the Extrastriate Cortex. *Science*, *229*, 782-784.

Motter, B. C. (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2 and V4 in the presence of competing stimuli. *Journal of Neurophysiology*, *70*, 909-919.

Movshon, J. A., Adelson, E. H., Gizzi, M. S., & Newsome, W. T. (1986). The analysis of moving visual patterns. In C. Chagas, R. Gattas, & C. Gross (Eds.), *Pattern recognition mechanisms* (pp. 117-151). New York: Springer Verlag.

Nawrot, M., & Sekuler, R. (1990). Assimilation and contrast in motion perception: expolations in cooperativity. *Vision Research*, *30*, 1439-1451.

O'Craven, K. M., & Savoy, R. L. (1995). Attentional modulation of activation in human MT shown with functional magnetic resonance imaging (FMRI). *Investigative Ophthalmology & Visual Science*, *36*, 3923.

Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25-42.

Rodman, H. R., & Albright, T. D. (1989). Single-unit analysis of pattern-motion selective properties in the middle temporal visual area (MT). *Experimental Brain Research*, *75*, 53-64.

Sato, T. (1997). Dmax: relations to low- and high-level motion processes. In *High-level Motion Processing* (Ed. T. Watanabe), Cambridge: The MIT Press.

Snowden, R. J. (1992). The perception of visual motion. *Current Opinion in Neurobiology*, *2*, 175-179.

Snowden, G. R., Treue, S., Erickson, R. E., & Andersen, R. A. (1991). The response of Area MT and V1 neurons to transparent motion. *Journal of Neuroscience*, *11*, 2768-2785.

Stoner, G. R., & Albright, T. D. (1992). neural correlates of perceptual motion coherence. *Nature, 412,* 412-414.

Stoner, G. R., Albright, T. D., & Ramachandran, V. S. (1990). Transparency and coherence in human motion perception. *Nature*, *344*, 153-155.

Tanaka, K. (1997). Representation of visual motion in the extrastriate cortex. In *High-level Motion Processing* (Ed. T. Watanabe), Cambridge: The MIT Press.

Tanaka, K., Fukada, Y., and Saito, H. (1989). Underlying mechanisms of the response specificity of expansion/contraction and rotation cells in the dorsal part of the medial superior temporal area of the macaque monkey. *Journal of Neurophysiology, 62,* 642-656.

Treisman, A., & Gelade, G. (1981). A feature integration theory of attention. *Cognitive Psychology, 12,* 97-136.

Treue, S. & Maunsell, J. H. R. (1996). Attentional modulation of visual motion processing in cortical areas MTand MST. *Nature*, *382,* 539-541.

Tse, P., Cavanagh, P. & Nakayama, K. (1997). The role of parsing in high-level motion processing. In *High-level Motion Processing* (Ed. T. Watanabe), Cambridge: The MIT Press.

Yuile, A. L. and Grzywacz, N. M. (1997). A Theoretical Framework for Visual Motion. In *High-level Motion Processing* (Ed. T. Watanabe), Cambridge: The MIT Press.

Verstraten, F. A. J., Fredericksen, R. E., & van de Grind, W. A. (1994). Movement aftereffect of bi-vectorial transparent motion. *Vision Research*, *34,* 349-358.

Verstraten, F. A. J., Fredericksen, R. E., van Wezel, R. J. A., Boulton, J. C. & van de Grind, W. A. (1996). Directional motion sensitivity under transparent motion conditions. *Vision Research, in press,*

Watanabe, T. (1995). Motion aftereffects show that attention may selectively activate local motion units located in V1. *Investigative Ophthalmology & Visual Science*, *36* , 634.

Watanabe, T. (1997). Velocity decomposition and surface decomposition —reciprocal interactions between motion and form processing—, *Vision Research*, in press.

Watanabe, T. & Cavanagh, P. (1993). Surface decomposition accompanying the perception of transparency. *Spatial Vision*, *7*, 95-111.

Watanabe, T. & Cavanagh, P. (1996). Texture laciness, *Perception*, in press.

Watanabe, T., & Cole, R. (1995). Constraint propagation of apparent motion. *Vision Research*, 2853-2861.

Welch, L. (1989). The perception of moving plaids reveals two motion- processing stages. *Nature*, *337,* 734-736.

Wolfe, J. M., & Held, R. (1981). A purely binocular mechanism in human vision. *Vision Research*, *21*, 1755-1759.

Wolfe, J. M. (1996). Personal communication.

Wurtz, R. H., Goldberg, M. E., & Robinson, D. L. (1980). Behavioral modulation of visual responses in the monkey: stimulus selection for attention and movement. In J. M. Sprague & A. N. Epstein (Eds.), *Progress in Psychobiology and Physiological Psychology*. (pp. 43-83). New York: Academic Press.

Yo, C. & Wilson, H. R. (1992). Perceived direction of moving two-dimensional patterns depends on duration, contrast and eccentricity. *Vision Research*, *32*, 135-147.

Yuille, A. L., & Grzywacz, N. M. (1988). A computational theory for the perception coherent visual motion. *Nature, 333,* 71-74.

Yuile, A. L. and Grzywacz, N. M. (1997). A Theoretical Framework for Visual Motion. In T. Watanabe (Ed), *High-level Motion Processing,* Cambridge: MIT Press.