

Orienting of spatial attention – its reflexive, compensatory, and voluntary mechanisms

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Abstract

Attention is a mechanism to select sensory information. It is a modulatory process which normally cannot be observed as overt responses. We have studied spatial attention using a new visual illusion of motion – line-motion effect: a line, which was presented physically at once, was perceived to be drawn from one side when attention was captured to that side of the line by a preceding visual cue stimulus. This effect was due to acceleration of visual information processing at the locus of attention. The motion illusion was produced by both stimulus-induced (bottom-up) and voluntary (top-down) attention, which suggested that the two kinds of attention act on relatively early stages of visual processing. The objective of this study was to examine how various modes of spatial attention might be represented and reorganized in the brain. Using the induction of illusory line motion as a measure we found that: (1) once attention is captured by a moving object, it follows the object as it moves; and (2) attention moves with a saccade in the retinal coordinates such that its focus remains fixed in space. We then asked whether attention acts across different sensory modalities. We found that both auditory and somatosensory cues induced focal visual attention in space where the cue was presented. Based on these findings we propose a model which would allow (1) matching of visual spatial information obtained across saccades, and (2) matching of spatial information obtained in different sensory modalities.

Keywords: Spatial attention; Visual illusion

1. Introduction

Suppose you open a book in total darkness which is then to be illuminated briefly. Before the illumination you can decide to read letters, say, on the right of where you fixate. Consequently, you in fact can read letters on the right side, but not letters on the left side, even those that were close to the point of fixation.

This demonstrates that sensory information can be selected in our brain depending on our intention, and this process can be called attention. It is possible, however, that the selection occurs after perception but before memory encoding [23]. According to this idea, all of these letters are in fact perceived and then encoded into memory one by one based on the attentional priority. Because the memory-encoding procedure is quite demanding, the percepts of letters in lower priorities would eventually be eliminated.

On the other hand, there is a well-known situation in which attention appears unnecessary. Suppose, on a sheet of paper, there are many letters, all of which are 'S' except for one 'X'. You can immediately see the 'X'; or 'X' pops out. This process is very fast and does not depend on how many elements are present, as Treisman and Gelade [27] demonstrated. Information from the whole visual field appears to be processed in parallel. This process is therefore frequently called 'pre-attentive'.

According to this idea, our perceptual-cognitive processes would be composed of two stages, parallel/pre-attentive process and serial/attentive process. Information would be selected when it is stored into memory or when it is used for motor actions [18,22]. Before perception, every bit of sensory information would be passed through all at once.

On the other hand, many people have suggested that attention also acts on early stages of sensory information processing [2,5,10]. Our psychophysical experiments supported this early selection hypothesis. Thus, sensory information is selected, or biased, by attention before percep-

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tion, perhaps in addition to the late selection. But how can we demonstrate it?

2. Temporal asynchrony of sensory information produced by attention

Previous psychophysical studies showed that attention affects the speed of sensory information processing [25]. According to our interpretation, the signals from the attended location are accelerated compared with the signals from the unattended locations. The accelerated signals may well suppress the late-coming, unattended signals, presumably using surround inhibitory mechanisms. Selection is therefore a natural outcome.

This conclusion was based on the temporal order judgment task [7,13,24]. Typically, two visual stimuli are presented with a short time interval and the subject is asked to judge which came on first. If the interval between the two stimuli is long, the answer is easy, close to 100%. If the asynchrony is short, the answer would become closer to the chance level.

This is not true, however, if another visual stimulus (cue stimulus) appears at the location of one of the two target stimuli. Suppose the cue stimulus appears on the right, the target stimulus on the right side is judged to appear earlier than the left target stimulus, even if the two targets appear simultaneously. For the two target stimuli to be judged to be simultaneous, the left target must appear before the right target by about 50 ms. In other words, the spot of light facilitates the local visual information processing so that it reaches perception 50 ms earlier than the uncued signal.

However, judgment in this task is difficult. Many task trials are needed before drawing any conclusion. It is difficult to reveal the spatio-temporal characteristics of attention. Our new technique – *line motion method* – can overcome these difficulties [7].

3. Attention can be detected by an illusion of motion

The principle of the line motion method is shown in Fig. 1. Here a small spot of light, which we called a cue

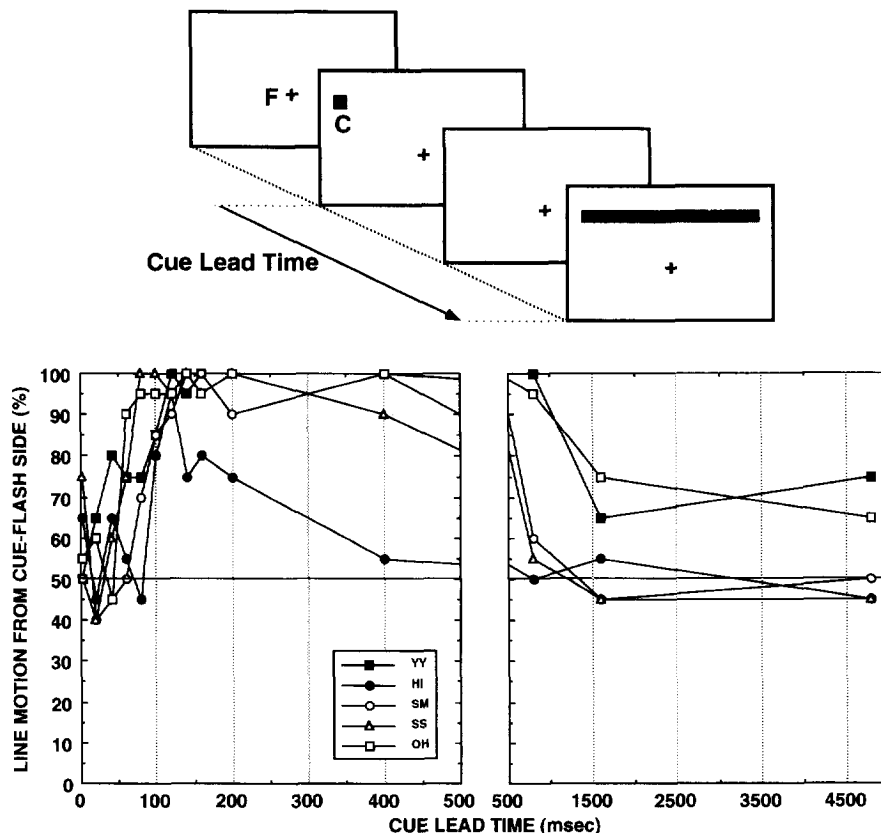


Fig. 1. Stimulus onset induces illusory motion sensation in a line. Top: while the subject was fixating a central spot (F), another spot of light (C) was flashed briefly (2 ms) at either one of two possible sites (right and left) in the upper visual field. After a randomized time interval (cue lead time) a line was presented at once between the two cue locations. The subject had to judge in which direction the line appeared to be drawn (two alternative forced choice paradigm). Bottom: the percentage of trials in which the line appeared to be drawn from the cued side (ordinate) was plotted against the cue lead time (abscissa). The graph is interrupted at 500 ms to see both the transient and sustained components. Data from five subjects are shown with different symbols. Twenty trials were obtained for each cue lead time in each subject. The chance level is 50%.

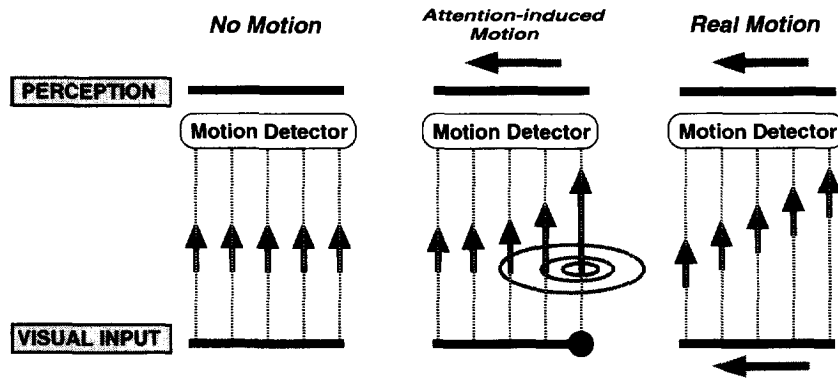


Fig. 2. Hypothetical information processing underlying perception of a line. Focal attention accelerates visual processing locally, so that visual signals reach the motion detector sequentially, as in the case of real motion.

stimulus (C), was used to attract attention of the subject. While the subject kept fixating a center spot (F), the cue stimulus was presented either to the right or to the left. After a random time interval (cue lead time) a probe line was presented connecting the two possible cue locations. A striking motion illusion was perceived such that the line appeared to grow in length over time emanating from the cue stimulus, even though the line was presented physically all at once. The line motion effect was strongest when the cue lead time was between 100–200 ms, weaker with longer or shorter cue lead times, and virtually absent with zero lead time.

We also found that any local change in visual environment induced illusory line motion, such as the offset of a stimulus, a change in color, orientation, shape, texture, and depth.

4. Hypothetical mechanism of the illusory line motion

Why do we think that this is related to attention? Let us consider the process in which the visual information from a line is fed into a central motion detector (Fig. 2). The motion detector can be regarded as a very sensitive mecha-

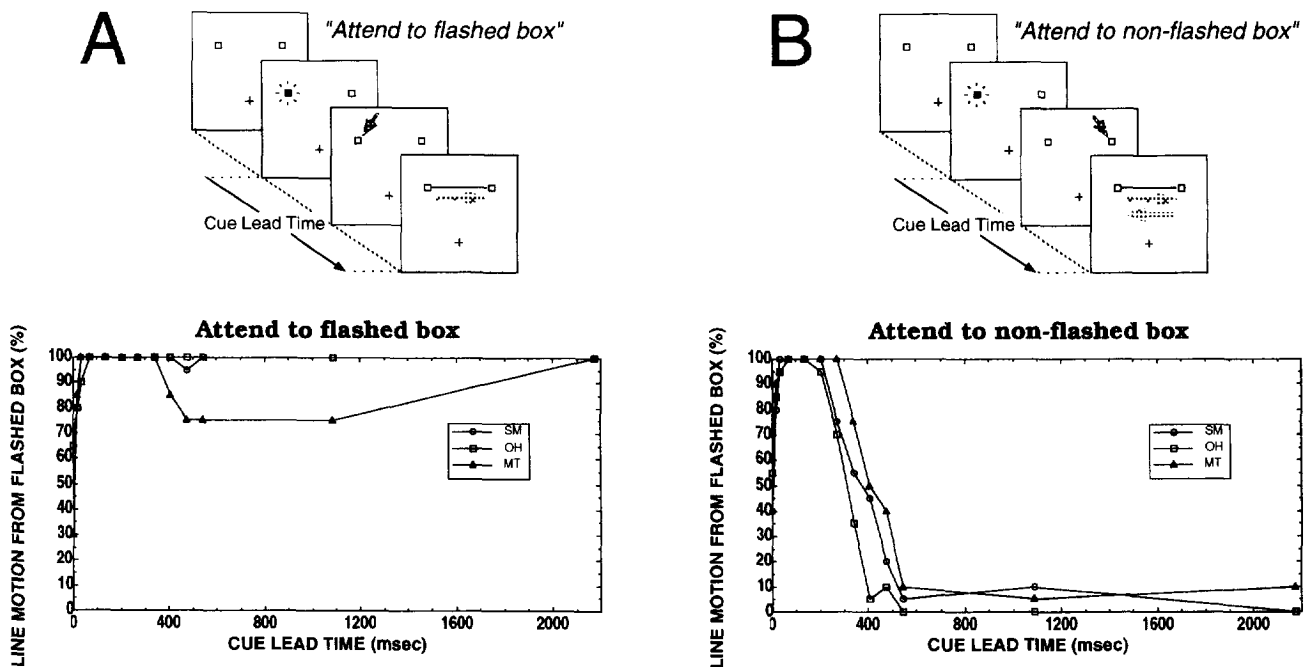


Fig. 3. Voluntary attention also produces a similar motion sensation in the line. A: line motion induced by pro-stimulus attention. While the subject fixated a center spot, one of two boxes was flashed. The subject was required to direct attention to the flashed box as soon as possible. After a randomized time delay (cue lead time), a probe line was presented between the two boxes. The shaded arrow indicates the perceived direction of motion. The percentage of trials in which the line was perceived to be drawn from the flashed side is plotted against cue lead time at the bottom. Data from three subjects are superimposed. The chance level is 50%. B: line motion induced by anti-stimulus attention. The subject was required to direct attention to the non-flashed box.

nism for temporal order judgment [15]. A line can be regarded as a linear aggregate of spots of light. If the spots come on sequentially from right to left (Fig. 2, right), the corresponding visual signals reach the motion detector sequentially, which will activate the motion detector. If the spots turn on simultaneously (Fig. 2, left), the visual signals reach the motion detector simultaneously, so that no movement will be detected. Suppose attention is directed to one end of the line (Fig. 2, center), the attention will increase the speed of visual processing locally. If we assume that the effect of attention decays outward from its locus, the visual signals will reach the motion detector sequentially from the attended side. The motion detector will be deceived to tell that a motion has occurred.

Our data suggest the presence of early selection, at least before the motion detecting mechanism. In other words, early visual information is not completely parallel but undergoes selection or biasing by attention.

In the example we have shown so far, attention was induced passively by a change in the visual environment, like a reflex. The striking feature of attention is its voluntary nature, however. Does the same early selection mechanism work for the voluntary attention? Or does voluntary attention act on the late selection mechanism? The next experiment addressed this issue.

5. Voluntary attention also produces illusory line motion

While the subject was fixating, two squares appeared and then one of them was flashed (Fig. 3) [8]. Unlike the previous experiment, we asked the subject to direct atten-

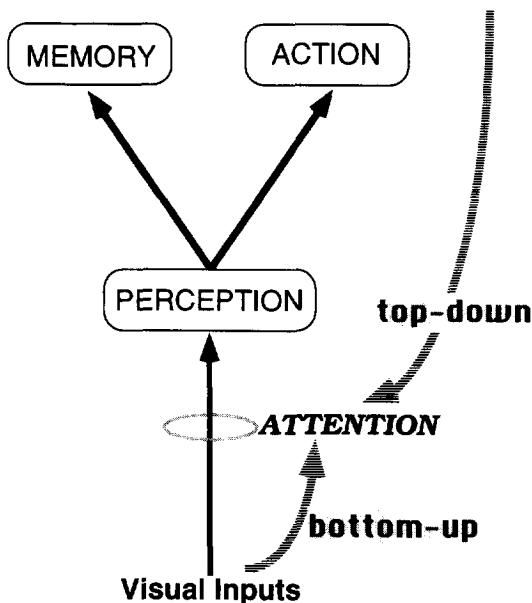


Fig. 4. Two modes of attention (bottom-up and top-down) share common action sites in early visual processing.

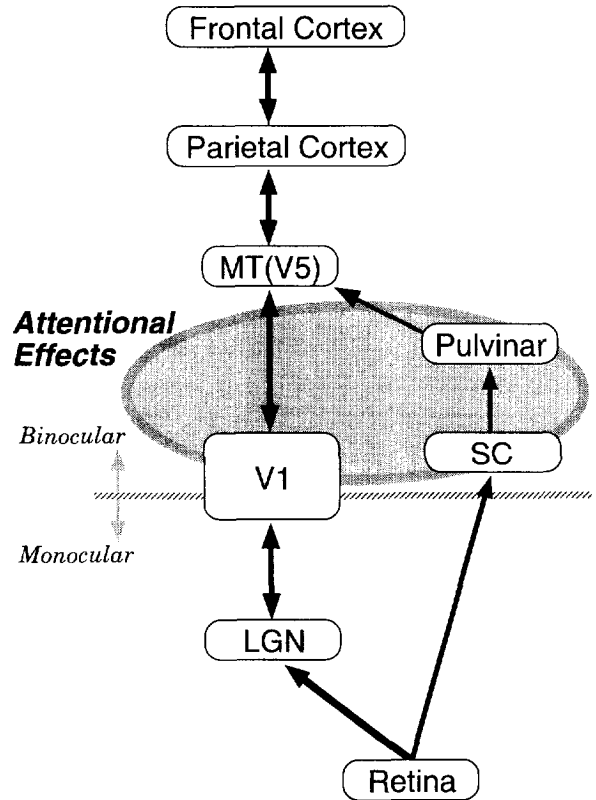


Fig. 5. Where attention might work? Our experiments suggest that attention may modulate early stages of visual information processing (indicated by the shaded region), possibly in addition to selections in later stages of information.

tion voluntarily: in the first experiment to the flashed square (Fig. 3A), and in the second experiment to the non-flashed square (Fig. 3B). The probe line was presented at a different interval after the flash to see which side attention was focused.

Immediately after the flash, the motion sensation was perceived almost always from the flashed side regardless of the intention of the subject, suggesting that attention was attracted by the light flash passively.

Voluntary attention came into work after 200 ms. The direction of the motion did not change when the subject continued to attend to the flashed square (Fig. 3A). In contrast, when the subject paid attention to the opposite side (Fig. 3B), the direction of the motion gradually changed accordingly, and the reversal was completed in 400 ms. Note that the stimuli were physically identical between these experiments.

Attention can also be directed voluntarily to an object that has a particular feature [8]. Two squares, one red and the other green, were presented simultaneously. The subject was asked to direct attention, for example, to the green square ignoring the red one. After a random time delay a probe line was presented. When the interval was long enough, the illusory motion was perceived from the green square. In the next block of experiment, the subject was

asked to attend to the red square, and the motion was perceived from the red square, although the stimuli were identical between these cases.

To summarize the above results, voluntary attention produces illusory motion sensation, as does reflexive attention, and its direction is from the attended object to the unattended object. This suggests that active (top-down) attention, as well as passive (bottom-up) attention, locally accelerates early visual processing (Fig. 4). This, of course, does not preclude the possibility that attentional effects are exerted at stages later than perception.

6. Both reflexive and voluntary attention acts on early visual processing

For the illusory line motion to occur, attention must act at a level (or levels) before the motion detector. If we

assume that the motion detector is in the area MT, as recent physiology suggests [16,17,29,32], the site of attentional effect should be before MT (Fig. 5). How much before is the site of attentional effect? Is it before or after binocular convergence?

To answer this question we presented the cue stimulus and the probe line to different eyes (dichoptic condition shown in Fig. 6, bottom) [12]. If the attentional interaction occurs within monocular pathways, we would not expect illusory motion sensation, because, in the examples shown in Fig. 6, left eye-sensitive neurons that carry the cue signal could not influence right eye-sensitive neurons that carry the line signal. The results indicated that virtually the same line motion was perceived as when the cue and line were presented to the same eye (to be compared with monoptic condition shown in Fig. 6, top). This suggests that the effect of attention acts at the level after binocular convergence - perhaps in or after the primary visual cortex (V1) [11].

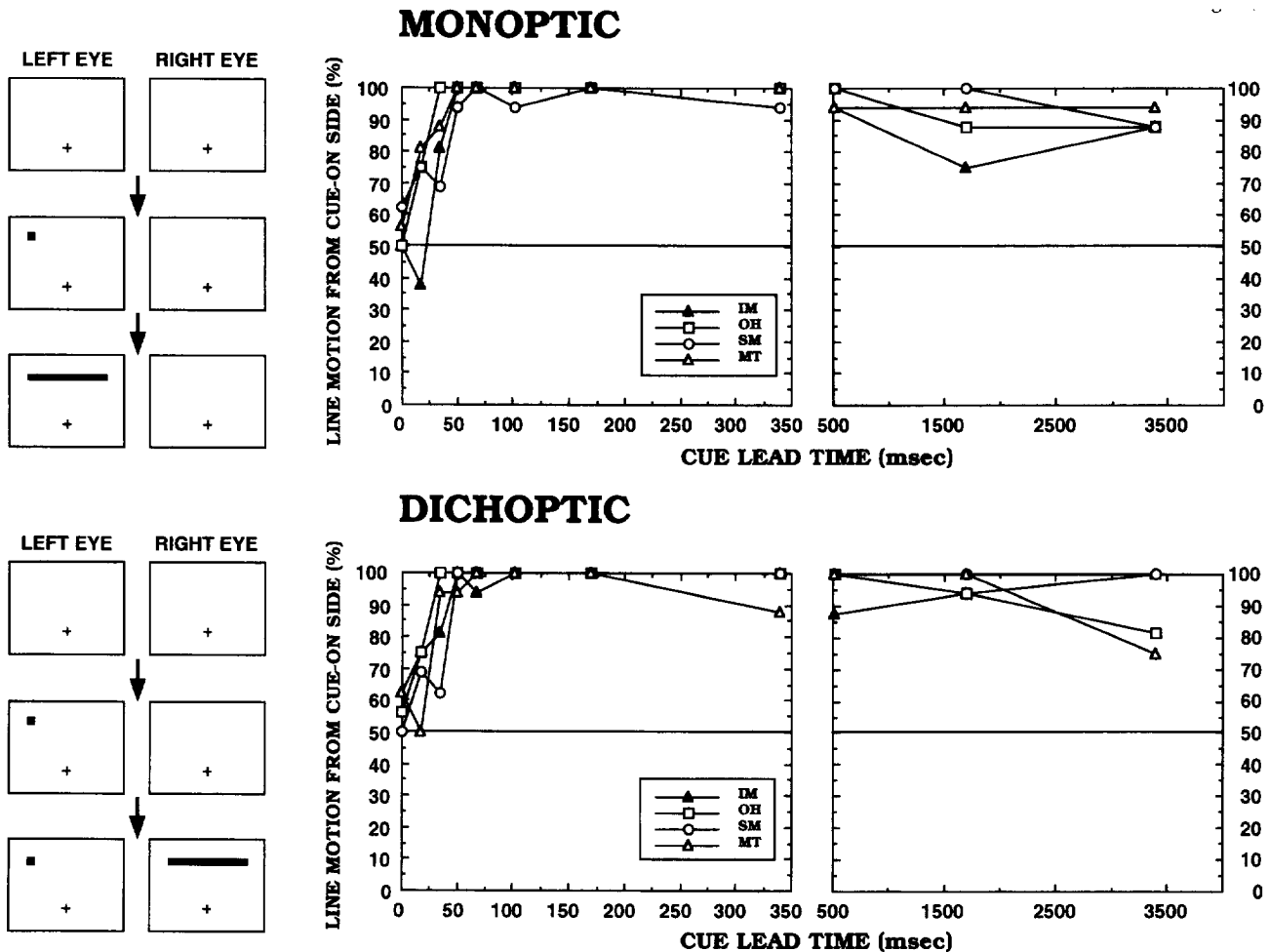


Fig. 6. Illusory motion sensation is induced by visual inputs from the contralateral eye. This experiment was the same as the one in Fig. 1, except that stimuli were presented under the monoptic and dichoptic conditions. The cue stimulus and the probe line were presented to the same eye (top) or to the different eyes (bottom), while the fixation point was always presented binocularly. The percentage of trials in which the line appeared to be drawn from the cued side (ordinate) was plotted against the cue lead time (abscissa). The side of the cue stimulus (right or left in the visual field) as well as the side of the eye receiving the cue stimulus input was randomized (2 x 2); so was the cue lead time. Data from four subjects are shown with different symbols. Twenty trials were obtained for each cue lead time in each subject. The chance level is 50%.

These results led to the hypothesis that attention acts on some visual cortical areas between V1 and MT (Fig. 5). But there are multiple routes from V1 to MT [28]. Subcortical areas such as the superior colliculus and pulvinar may well contribute to this process [19–21]. However, it is still unknown whether the illusory motion perception actually occurred in area MT. There are other brain areas that are quite sensitive to visual motion, such as area VIP [4].

As an attempt to resolve this issue, we performed functional MRI experiments. The motion-sensitive area, MT/V5, was identified and extensively studied in macaque monkeys. Recent studies using PET or functional MRI confirmed the presence of a motion-sensitive area in the human brain [3,26,31]. We asked whether the illusory line motion also activates the human homologue of MT/V5.

Our functional MRI study was composed of three experimental sessions. In Expt. 1, which was designed to identify the human MT/V5, the subject viewed many color balls moving around. Expts. 2 and 3 were designed to reveal the neural activities correlated with the line motion; real motion in Expt. 2 and illusory motion in Expt. 3. In Expt. 2, five horizontal lines were drawn physically from the left or right. In Expt. 3, the same five lines came on at once, but 200 ms after cue stimuli were presented at either one end of the lines, so that robust motion was perceived.

Our preliminary results suggested that, in four subjects so far tested, the illusory line motion was associated with a few active loci in or very close to the MT/V5. Expt. 1

revealed strong bilateral activation at the level connecting the anterior commissure and the posterior commissure and slightly posterior to the superior temporal sulcus. This was similar to the previous reports suggesting the human homologue of the MT/V5 [31]. In Expts. 2 and 3, we found similar but smaller activation. Typically, the active loci associated with the illusory line motion were fairly small but were, at least partly, coextensive with the active loci associated with the real line motion. The active loci associated with the illusory or real line motion were either included in or very close to the active loci associated with moving balls which were presumably within the MT/V5.

The results suggest that our perception of the illusory line motion is dependent on, or correlated with, the activation of MT/V5. This in turn supports the idea that visual spatial attention acts at the level before or within MT/V5. These are still preliminary data, however. We do not know, for example, whether different kinds of ‘motion’ stimuli activate slightly different regions in or around MT.

7. Spatial coordinates of attention – retinotopic, environmental, object-centered?

We have characterized attention as if it were a local attractor in the retinotopic map somewhere along the pathway from V1 to MT. Using a cancellation method, we and other investigators were actually able to visualize such an attractor which was set up by a visual onset and decayed

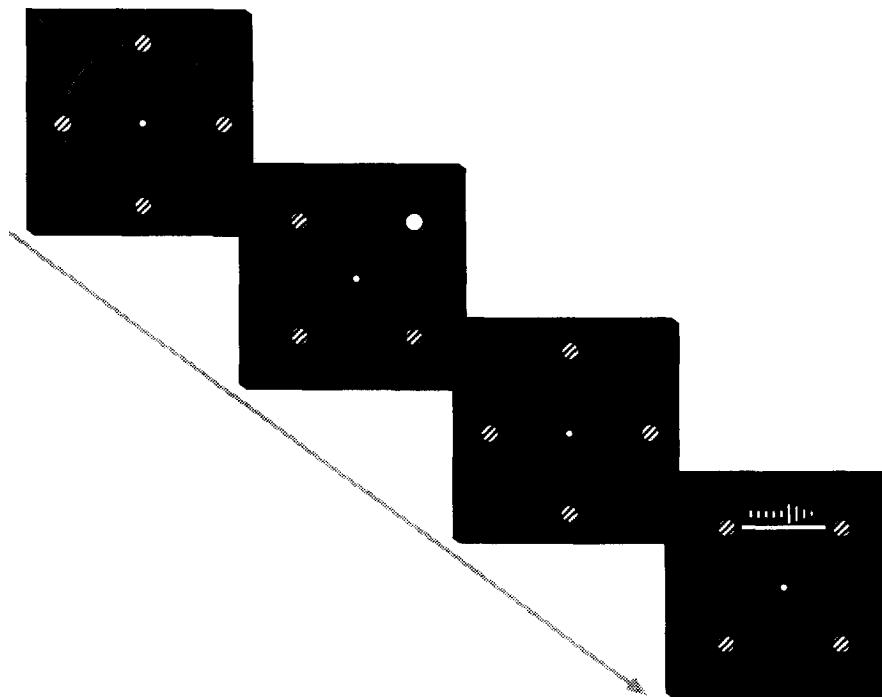


Fig. 7. An object, once attended, carries attention as it moves. Four blue spots appeared and rotated around the fixation point (frame 1). One of them was flashed (frame 2) and the four spots continued to rotate (frame 3). The probe line was presented between the location where the spot had been flashed (right-up) and the current location of the flashed spot (left-up) (frame 4). A motion was perceived from the flashed spot (from left to right).

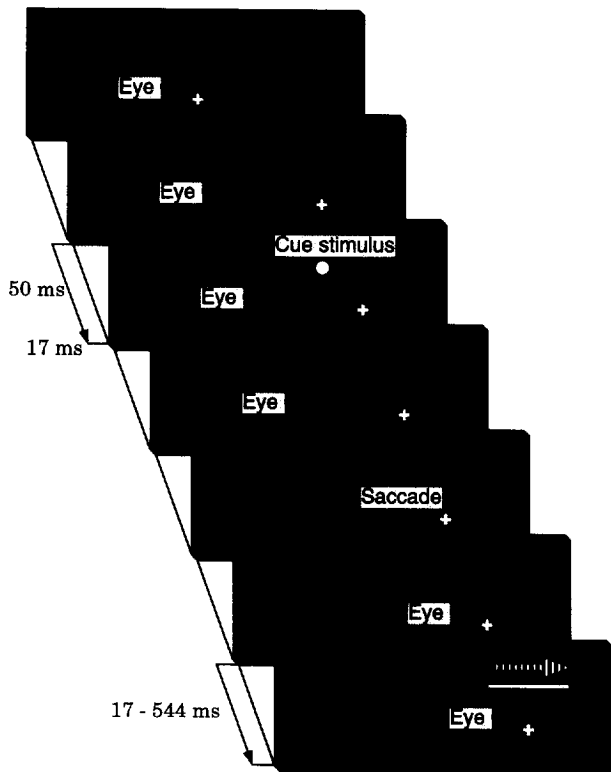


Fig. 8. Attention remains in space across a saccade. A fixation point stepped from the center to the right or left (frames 1 to 2), and 50 ms later a cue stimulus was briefly presented (17 ms), halfway to the location of the peripheral fixation point (frame 3). A saccade then occurred to the new fixation point (frame 5). At a random interval after the end of the saccade (17–544 ms) a probe line was presented directly above the new fixation point (frame 7). The subjects perceived motion in the line from the environmental location (from left in this case), not retinal location, of the cue stimulus in most of the trials.

with time [14,30]. However, the retinotopic representation is a local phenomenon that is specifically dependent on the direction of gaze.

In other words, the retinotopic signal processing can be violated by object's movement or by our own movements. In the experiments so far described, everything was fixed and therefore in register; the cue stimulus stayed still or just disappeared, and the direction of gaze was fixed. We could not tell whether attention might follow other rules, such as the object-centered and environmental rules. In addition, non-visual information should naturally not follow the retinotopic coordinates.

We thought at first that it is unlikely that such non-retinotopic rules are valid because our data have suggested that attention, at least partly, acts on the early visual processing where the retinotopic rule is thought to dominate [1]. However, we found that this idea was wrong, as shown in the following experiments in which there were conflicts between the retinotopic and non-retinotopic coordinates.

8. Attention follows a moving object once attached

In the experiment shown in Fig. 1, the onset of a spot of light drew our attention. Was attention directed to the location of the spot? Or was it directed to the spot itself? In that situation, the location and the object were not differentiated.

Fig. 7 shows the experiment to answer this question [8]. While the subject is fixating a central spot, four blue spots appear and rotated around the fixation point. One of the four spots is flashed briefly, and then all the four spots continue to rotate.

Now the question is: where is the focus of attention? Is it at the location where the spot was flashed? Or is it at the location of the spot that was flashed?

We examined this question by presenting a probe line between the two locations, and found that motion was perceived almost always from the flashed spot, not flashed location. This was so irrespective of the amount of rotation up to 360°.

To summarize this experiment, once attention is drawn to a moving object, the attention does not stay at the initial location but follows the object as it moves.

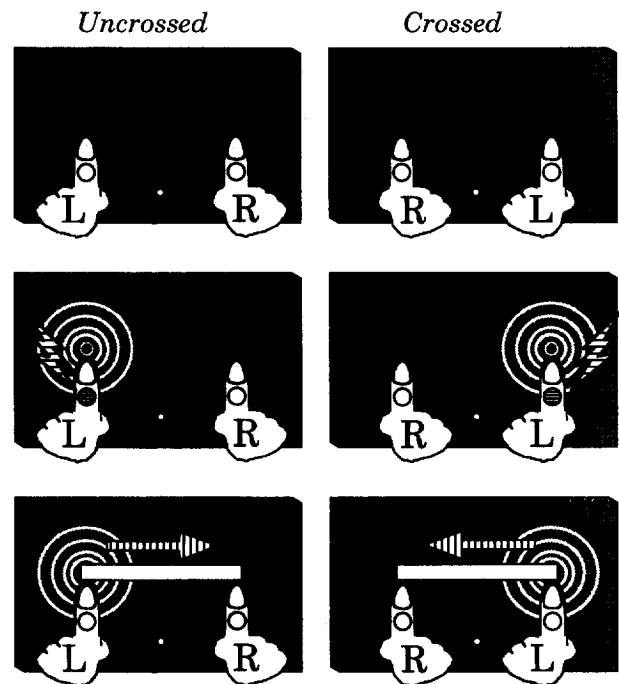


Fig. 9. Cross-modal spatial attention: the somatosensory-to-visual effect is bound to space, not to the hemisphere. Stimulating electrodes were attached to the tips of the right and left index fingers, which were placed at the locations between which the probe line would appear. The somatosensory cue (a short train of electric pulses) was applied to one of the index fingers and then the line was presented. The experiments were performed in two conditions: when the subjects did not cross (left) and crossed (right) their hands. The subjects perceived motion in the line from the location where the cue stimulus was applied, regardless of the side of the hand stimulated.

9. Attention remains stationary in the environment, not with respect to the retina, across a saccade

Another factor that might violate the retinotopic rule is our own movements, especially eye movements. If we shift our gaze by making a saccadic eye movement, what happens to the focus of attention. Does it remain stationary with respect to the retina? Or does it remain stationary in space?

To answer this question we performed the following experiment [9]. The subject first fixated at the central spot. The fixation point then stepped to the right or left and the subject had to follow the step by making a saccade. After 50 ms following the step of the fixation point (before the saccade started), the cue stimulus was presented briefly. Some time after the end of the saccade, the probe line was presented directly above the new fixation point location.

In this condition, the retinal position of the cue stimulus was aligned at the right end of the line, while the environmental position of the cue stimulus was at the left end. All subjects reported that they perceived motion sensation usually from the environmental location (Fig. 8).

This experiment showed that attention is kept stationary in the environment. There must be some mechanism that would compensate for the saccade. We assume that the focus of attention is represented somewhere in the retinotopic map. An important point is that the focus of attention shifts simultaneously with every saccade so as to align itself with the environmental location of the object of interest. This may well correspond to the striking observation on LIP parietal cortex neurons ([6]; Colby, this volume).

This is a kind of compensatory mechanisms that should operate together with our voluntary behavior but probably without invoking our conscious experience.

10. Cross-modal spatial attention – visual attention can be evoked by somatosensory or auditory stimuli

The third factor that may violate the retinotopic rule is non-visual information. The concept of space is constructed also from somatosensory and auditory information and from body movements. Spatial attention should thus be extended to the non-visual sensory modalities.

To test this hypothesis we performed the line motion experiment using non-visual cue stimuli [9]. Auditory cues (beep sounds) were elicited from audio speakers located beside the CRT screen. Somatosensory cues (electric pulses) were applied to the tips of the index fingers of both hands which were placed beneath the ends of the probe line (Fig. 9).

We found that a similar illusory motion was evoked by these non-visual cues: the line motion sensation was perceived from the side on which the auditory or somatosensory cues were applied.

Now the hand is quite mobile and therefore the spatial information from the hand should critically depend on its position. We thus repeated the same experiment while the subject crossed their hands. When electrical stimulation was applied, say, to the left hand (which was placed on the right side), the subjects perceived line motion sensation from the right side most of the time.

This feature is purposeful (or obligatory), but would require complex mechanisms of remapping. It is now clear that somatosensory information must somehow reach the visual areas while preserving its positional information, finally enhancing local visual processing. An inevitable feature of this process is that somatosensory information must be redirected or remapped each time the hand moves. When the left hand is placed on the left side, for example, its somatosensory information would be sent to the right

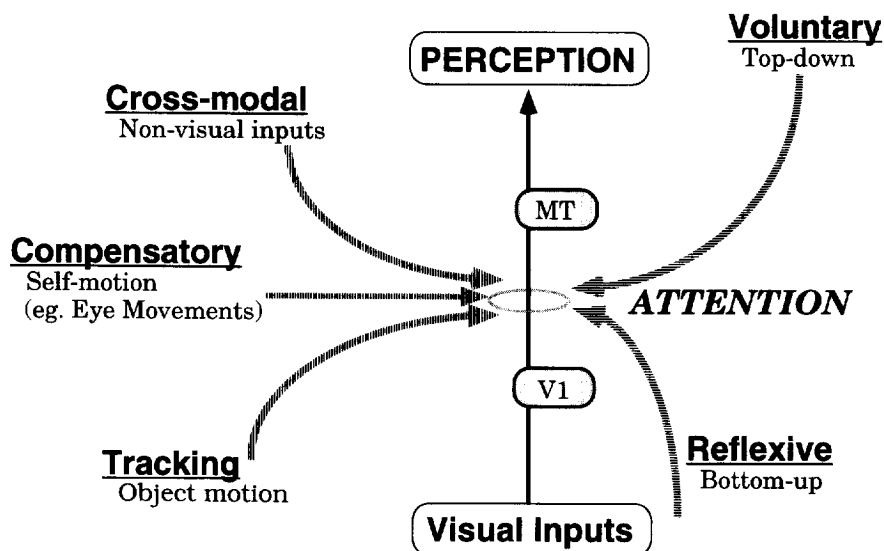


Fig. 10. Different modes of spatial attention. Spatial attention may be induced and manipulated in different behavioral contexts.

somatosensory cortical areas and then to the visual retinotopic map on the same (right) side. When the left hand is now placed on the right side, the neural process would be the same until the somatotopic map, but the information would be redirected to the visual map on the opposite (left) side.

11. Spatial attention can be reflexive, voluntary, compensatory, object-bound, or cross-modal

In summary, our experiments, together with preceding studies, suggest that there are several different modes in which attention operates (Fig. 10). Attention is not just what we control voluntarily. Attention is not just caused passively by external sensory events. Attention can go across the boundaries of sensory modalities while preserving its environmental positional information. Once attention is attached to an object, it tracks the object nearly automatically. Attention compensates for the subject's movements, particularly eye movements. These operations require shift, remapping or redirection of information processing between different brain regions.

In terms of spatial attention, these various complex operations lead to a common outcome, that is, acceleration of the early visual information processing between V1 and MT, as shown by the line motion method.

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