

Complementary Cognitive and Motor Image Processing

BRUCE BRIDGEMAN

PHYSIOLOGICAL INTRODUCTION

Everyone shares the irresistible conception that vision is one sense. We experience one coherent visual world and produce visually guided behavior to interact with that world. Extensive laboratory work, however, has shown this introspection to be in error: visual processing has several representations of space, coding different aspects of the information available from vision. The representations operate simultaneously, in parallel, in performing various visual functions.

One approach to the multiple-representations phenomenon is physiological and begins with the observation that over a dozen topographic maps represent the visual world in the cortex (Van Essen *et al.*, 1982). This observation raises a question of the relationship between physiology and function: do all of these maps work together in a single visual representation, or are they functionally distinct? And if they are distinct, how many functional maps are there, and how do they communicate with one another? These questions can be answered with psychophysical techniques, reinforcing the evidence for separate visual representations obtained in physiological studies.

The many visual representations might conceivably support an equal number of distinguishable visual information-processing systems, running quasi-independently in parallel. Physiological evidence, however, indicates that the topographic maps are organized into groups of serially organized representations spreading out from a common starting point on the retinas.

The number of such functionally separable sys-

tems is not known, but there is good evidence for at least two modes of visual processing. A primary distinction, with experimental support from a number of directions, is between visual perception on one hand and control of visually guided behavior on the other. The thesis of this chapter is that a common thread from physiological, anatomic, and psychophysical directions distinguishes these two separable functional systems. Other subdivisions may exist, and other kinds of distinctions (such as the magnocellular-parvocellular pathways) may cut across the perception-behavior distinction.

The organizations are parallel and independent in that perception can suffer spatial illusions that are not shared in spatial behavior, and visually guided behavioral orientation can be modified without affecting perception. Psychophysical studies have revealed that subjects are unaware of sizable displacements of the visual world if they occur during saccadic eye movements, implying that information about spatial location is degraded during saccades (Ditchburn, 1955; Wallach and Lewis, 1965; Brune and Lücking, 1969; Mack, 1970; Bridgeman *et al.*, 1975). Yet people do not become disoriented after saccades, implying that spatial information is maintained.

Experimental evidence supports this conclusion. For instance, the eyes can saccade accurately to a target that is flashed (and mislocalized) during an earlier saccade (Hallett and Lightstone, 1976b), and hand-eye coordination remains fairly accurate following saccades (Festinger and Cannon, 1965). How can the loss of perceptual information and the maintenance of visually guided behavior exist side by side?

In an attempt to resolve this paradox, we noted that the two conflicting observations use different response measures. The experiments on saccadic

suppression of displacement require a nonspatial verbal report or button press, both symbolic responses. Successful orienting of the eye or hand, in contrast, requires quantitative spatial information with a 1:1 correspondence between stimulus position and motor output. This distinction produces a functional, as opposed to anatomic, distinction between the two proposed systems. By definition, then, perceptual tasks with a symbolic output address the cognitive system, whereas isomorphic motor responses address the motor system. The remainder of this chapter examines the validity of the cognitive-motor dichotomy.

HISTORY OF THE SEPARATION OF FUNCTIONS

Interest in the distinction between pathways for spatial and object vision crystallized with a symposium and a series of articles in *Psychologische Forschung* (now *Psychological Research*). In that series, Trevarthen (1968) named the two systems focal and ambient; the focal system was supposed to reside in the geniculostriate pathway and to specialize in pattern recognition. The ambient system, in the superior colliculus and related brainstem structures, handled visually guided behavior. This may be the case in the hamster (Schneider, 1967), but we now realize that both systems have important cortical components in primates (Mishkin *et al.*, 1983). The successor to the ambient system includes occipitoparietal pathways as well as superior colliculus, and the focal system uses an occipitotemporal pathway.

The two visual systems are not equal in size, for relatively little information is required to drive visually guided behaviors. Perception, in contrast, requires sensitivity to fine detail, which requires a large processing capacity for high-spatial-frequency information. For this reason, processing in the focal (cognitive) system is concentrated in the foveal projection, where high-spatial-frequency information is available, although the remainder of the visual field is available to this system as well. Ambient (motor) vision, in contrast, requires a large field of vision, the larger the better, and consequently the fovea plays only a relatively minor role because of its small angular size. Because of the asymmetry in function and the resulting differences in locations of projections, the terms "focal" and "ambient" have

been widely misunderstood by others to be related to foveal and peripheral vision, respectively, though the originators of the distinction did not intend this interpretation.

Since the 1960s several workers, using different methods and approaches, have converged on a general distinction between spatial and object vision. They have generated slightly different definitions and a chaotic nomenclature that makes a complete search of this literature difficult: the terms and their principal proponents are given in Table 19-1.

More recently, Post and Leibowitz (1982, 1985) have used a distinction between two types of eye movements, one voluntary and corresponding to the focal system and the other reflexive and corresponding to ambient vision, to interpret several motion illusions. Key to the interpretation is that innervations of the voluntary "pursuit" system are perceived as object motions, whereas reflex "optokinetic" innervations are not perceived. The latter are interpreted indirectly as self-motions.

Thus, induced motion results from the pursuit system, tracking a target, having to counter the effects of a reflexive system that is stimulated by a background frame. Motion of the frame is misattributed to target motion because the extra pursuit effort, required to maintain fixation on the target despite reflex innervation from background tracking, is perceived while the reflex innervations are not. The pursuit-optokinetic distinction maps onto the cognitive-motor distinction reviewed above. As a result, concomitant changes in apparent straight ahead, not predicted by other theories, can be explained (Post and Heckman, 1986). The theory has also been applied to the oculogyral illusion (Post, 1986) and to changes in perceived movement with changes in gain of the VOR.

TABLE 19-1
Nomenclature Used for Components of Vision

Terms		Originator
1. Focal	Ambient	C. Trevarthen
2. Experiential	Action	M. Goodale
3. Cognitive	Motor	B. Bridgeman
4. Cognitive	Sensorimotor	J. Paillard
5. Explicit	Implicit	L. Weiskrantz
6. Object	Spatial	M. Mishkin
7. Overt	Covert	K. Rayner
8. Exocentric	Egocentric	I. Howard

PSYCHOPHYSICAL CHARACTERIZATION OF THE COGNITIVE-MOTOR DISTINCTION

Most of the early work in this field was done in lesioned animals and in neurological patients. Recent work shows that the dissociations are not disconnection syndromes or compensations for deficits induced by lesions but, also exist in normal humans. Both pathways retain a topographic representation of space, but the representations follow different rules, reflecting their differing functions.

In our first experiment on this question (Bridgeman *et al.*, 1979), subjects pointed to the position of a target that had been displaced and then extinguished. Subjects were also asked whether the target had been displaced or not. Pointing accuracy was similar whether the displacement was detected or went undetected because of a simultaneous saccadic eye movement. This implied that quantitative motor control was unaffected by the perceived target position. But it is possible (if a bit strained) to interpret the result in terms of signal detection theory as a higher response criterion for the report of displacement. The first control for this possibility was a two-alternative forced-choice measure of saccadic suppression of displacement. This criterion-free measure showed no information about displacement to be available to the cognitive system under conditions where pointing was affected (Bridgeman and Stark, 1979).

A more rigorous way to separate the two systems is with a double-dissociation paradigm, introducing a signal only into the motor system in one condition and only into the cognitive system in another. We know that induced motion affects the cognitive system, because we experience the effect. But the above experiments implied that the information used for pointing might come from sources unavailable to perception.

We inserted a signal selectively into the cognitive system with stroboscopic induced motion (Bridgeman *et al.*, 1981). A surrounding frame was displaced, creating the illusion that a target had jumped. Target and frame were then extinguished, and the subject pointed open-loop to the last position of the target. Trials where the target had seemed to be on the left were compared with trials where it had seemed to be on the right. Pointing was not significantly different in the two kinds of trials, showing that induced motion did not affect pointing.

Information was inserted selectively into the motor system by asking each subject to adjust a real motion of the target, jumped in phase with the frame, until the target seemed stationary. Thus, the cognitive system specified a stable target. Nevertheless, subjects pointed in significantly different directions when the target was extinguished in the left or the right positions. Thus, a double dissociation was obtained: in the first condition apparent target displacement affected only perception; in the second, real displacement affected only motor behavior.

Dissociation of cognitive and motor function has also been demonstrated by giving cognitive and motor systems opposite signals at the same time. A target jumped in the same direction as a frame but not far enough to cancel an induced motion. Immediate saccadic eye movements followed the true direction even though subjects perceived motion in the opposite direction (Wong and Mack, 1981). If a delay in responding was required, however, eye movements followed the perceptual illusion, implying that the motor system has no memory and must rely on information from the cognitive system when the motor map no longer contains the needed information.

A NEW METHOD FOR DISSOCIATING THE SYSTEMS

All of these experiments involve motion or displacement, leaving open the possibility that the dissociations are related in some way to motion systems rather than with representation of visual space *per se*. A new method, however, can test dissociations of cognitive and motor function without motion of the eye or the stimuli at any time during a trial. The dissociation is based on the Roelofs effect (Roelofs, 1935), a tendency to misperceive the position of an edge of a large target presented in an unstructured field. The effect has also been observed as a tendency to perceive the locations of light flashes as closer to the line of sight than their true positions (Mateeff and Gourevich, 1983).

This method takes the Roelofs effect one step further and measures the misperception of target position in the presence of a surrounding frame presented asymmetrically in the field; this is an "induced Roelofs effect" but is called a Roelofs effect below. Positions of targets within the frame are misperceived in the direction opposite the offset of the

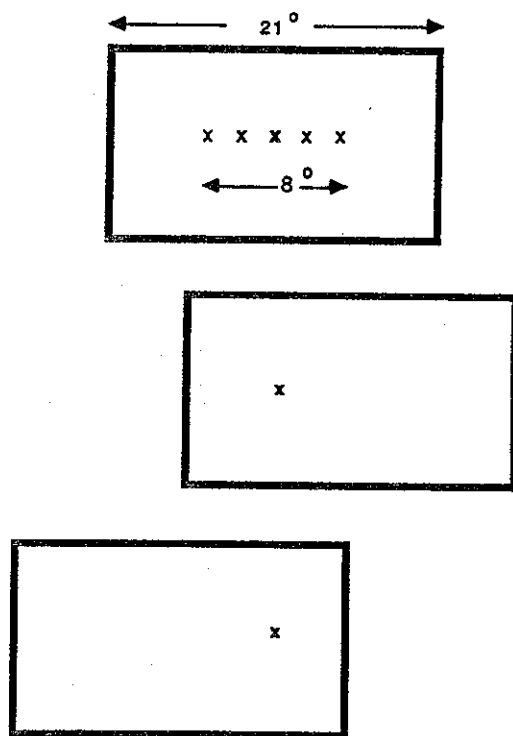


FIGURE 19-1. Stimulus array used in experiments on the Roelofs effect. The frame could be centered (top), offset 5° right (middle), or offset 5° left (bottom). A target appeared in one of the five positions indicated within the top frame. Targets always appeared in the same positions, regardless of frame position, and only one target was visible at a time. The center target (shown in boldface in the top frame) is shown in the frames offset left and right. Only one target and frame were shown in a given trial.

frame. The effect is similar to a stroboscopic induced motion in which only the final positions of the target and frame are presented (Bridgeman and Klassen, 1983). After reviewing some new experiments using this effect, implications for the two-visual-systems theory are discussed.

An Experiment

Subjects sat with stabilized heads before a hemicylindrical screen. A rectangular frame was projected, via a galvanic mirror, either centered on the subject's midline or 5° left or 5° right of center. Inside the frame, an "x" could be projected via a second galvanic mirror (Fig. 19-1).

A pointer with its tip near the screen gave an analogue voltage indicating its position. Perceived target position was recorded on a keyboard. For each trial, one of the five targets and one of the three frames were presented with simultaneous onset, exposed for 1 sec, and simultaneously extinguished. Subjects could not respond until stimulus offset, so that at the time of the response they were looking at a blank field. Thus, the task was a response to an internally stored representation of the stimulus, not a perceptual task.

For judging trials, all subjects showed a Roelofs effect (Fig. 19-2). The mean magnitude of the effect was a difference of 2.0° between judgments with the frame on the left and judgments with the frame on the right. Though small, this effect is reliable; it is present in all subjects under all condi-

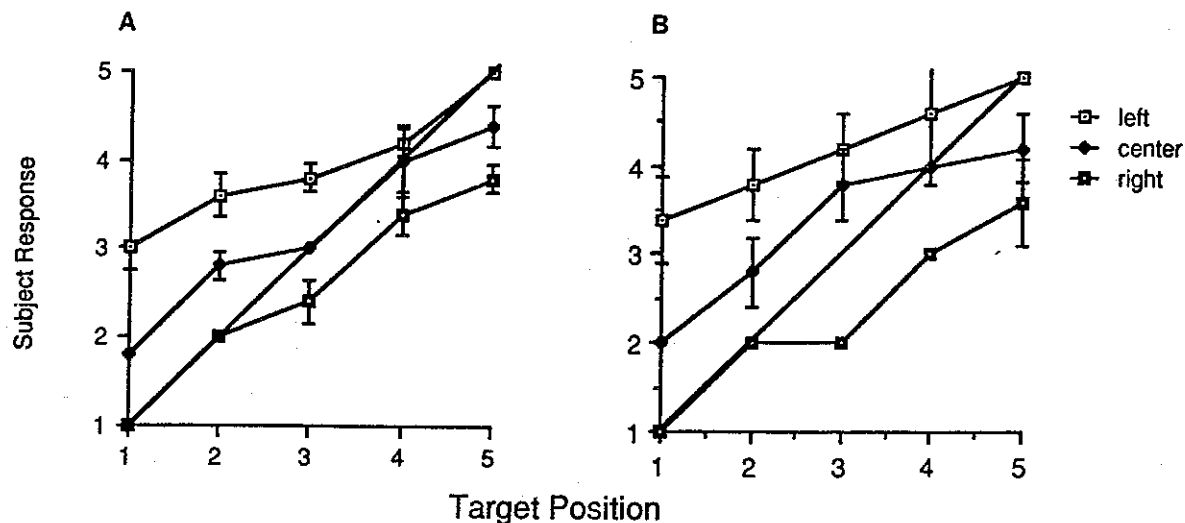


FIGURE 19-2. Judging of target position immediately after stimulus offset. Data illustrated here are from two subjects, though statistical analyses in the text are from all subjects. Lack of error bars indicates that the standard deviation was less than the width of the symbol. A: subject A. B: subject B.

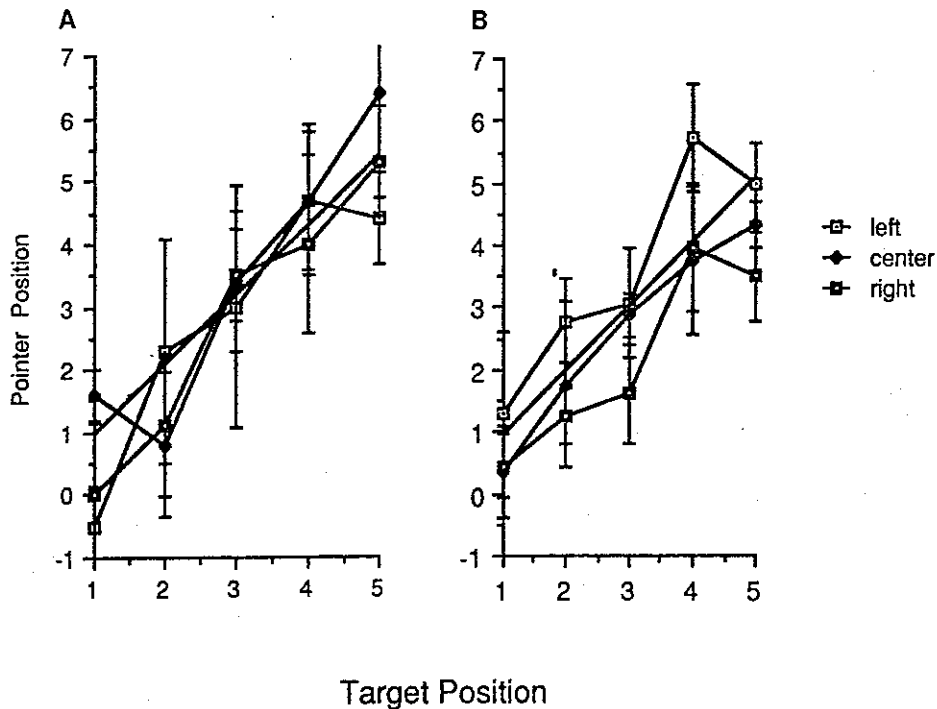


FIGURE 19-3. Pointing to targets under the same perceptual conditions as in Fig. 19-2 in trials randomly intermingled with the judging trials. Subjects A and B correspond to the two subjects in Fig. 19-2. Overlap of the three curves in subject A indicates lack of influence of frame position on pointing behavior. Separation of the curves in subject B indicates a continuing influence of the frame. All subjects showed either the type A or the type B pattern.

tions and is statistically reliable in each one using within-subject statistical analyses.

Pointing trials (Fig. 19-3) yielded a sharp division of the subjects into two groups: five of the ten subjects showed a highly significant Roelofs effect ($P < 0.005$), while the other five showed no sign of an effect ($P > 0.18$). The bimodal distribution (Fig. 19-4) reveals two qualitatively different results; the distribution of significances between subjects is not related to a small, normally distributed effect reaching significance in some subjects and not in others. A given subject showed either a large, robust effect or no sign of influence of the frame. Thus, pointing was qualitatively different from judging for half of the subjects; these subjects showed a Roelofs effect only for judging.

Nine of the ten subjects were also run with a 4-sec delay interposed between display offset and tone. Eight of the nine showed a significant Roelofs effect for the judging task ($P < 0.01$), with a mean difference of 2.12° between pointing when the frame was on the left and when it was on the right.

The major difference between the results in this condition and the no-delay condition was that seven

of the nine subjects showed a significant Roelofs effect for the pointing task ($P < 0.05$ for 2 Ss, $P < 0.01$ for 7 Ss).

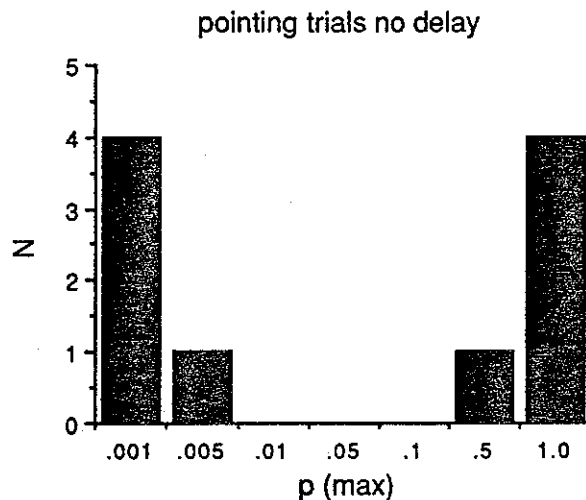


FIGURE 19-4. Statistical significance of within-subjects two-way ANOVA frame (Roelofs) effects. Each bin contains subjects with results at least as significant as the probability indicated on the abscissa but not as significant as the next probability to the left. The bimodal distribution shows two different types of subjects, widely spaced, with no intermediate cases.

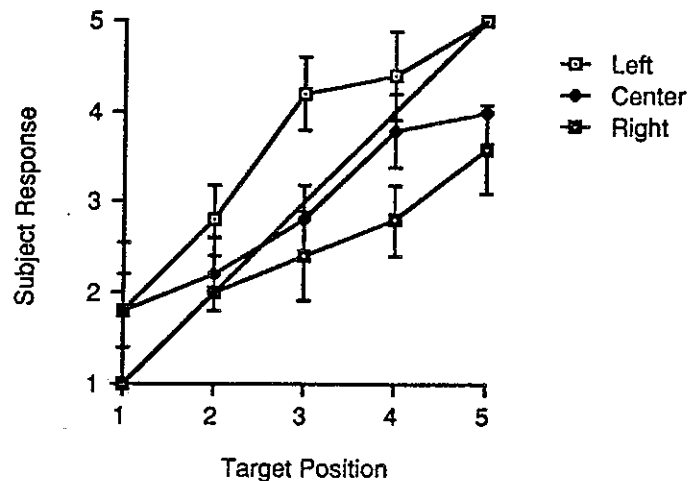


FIGURE 19-5. Judging of target position after an 8-sec delay in subject A. Results are similar to those in Fig. 19-3 (no delay), showing a stable representation of visual positions in the system controlling target position judgments. Display format as in Fig. 19-2.

One of the two remaining subjects showed no significant effect of frame position for either pointing or judging. The other subject whose pointing still showed no effect of the frame was retested with an 8-sec delay between display offset and tone. A

Roelofs effect was found both for judging ($P < 0.001$) (Fig. 19-5) and pointing ($P < 0.001$) (Fig. 19-6).

The experiment was repeated with a continuous centimeter-estimation judging measure, so that

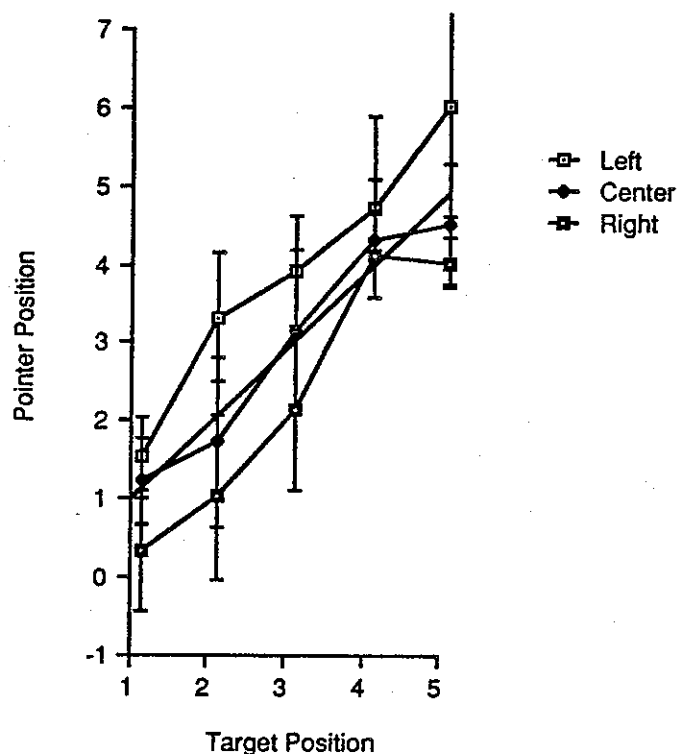


FIGURE 19-6. Pointing to targets after an 8-sec delay in subject A, from trials intermingled with those shown in Fig. 19-5. A Roelofs effect for pointing has appeared, indicating that frame position affects pointing just as it affects judging at this latency, though the effects of a separate spatial representation are still evident: slopes of the lines here are more than 1, in contrast to slopes of less than 1 at all latencies for judging. Display format as in Fig. 19-3.

subjects would not be forced to remain within the 8° range of the target stimuli. Results were similar, though variability in judging was somewhat greater with the centimeter estimation method, resulting in less significant Roelofs effects.

Interpretation of the Results

Interposing a long enough delay before the response forced all subjects to use pointing information that is biased by frame position, even though half of the subjects were not vulnerable to this bias when responding immediately. Differences between pointing and judging to the same target in the same trial block could amount to more than 5°.

These experiments show that perception of a Roelofs effect is robust, being seen by all subjects under all delays. The Roelofs effect in visually guided behavior, though, depends much more strongly on the subjects and conditions. Half of the subjects showed a strong effect of a surrounding frame on pointing behavior, while the other half showed no effect. The bimodality of this distribution suggests that subjects went about the task in two different ways. Since all responses were made in a blank field after the stimuli had been extinguished, the contrast may be related to differing strategies of the subjects; some responded in a motor mode, whereas others switched almost immediately to a cognitive mode, which brought the illusion along with it. The difference between the modes explains the bimodal nature of the distribution in Fig. 19-4, with subjects showing either a large Roelofs effect or none at all.

One need not assume that the two groups of subjects followed different psychological laws, only that they switched from motor to cognitive modes at differing delays after stimulus offset. Discussion in terms of differential accuracy and decay rates of cognitive versus motor responses would redescribe the data but would not explain their source.

Further, all of the subjects showed a Roelofs effect in pointing when a long enough delay was interposed between target presentation and response; a closer titration of delay times would probably show a unique critical delay for obtaining a pointing Roelofs effect in each subject.

The appearance of the Roelofs effect with a delay between stimulus and motor response is reminiscent of the results of Wong and Mack (1981) that saccadic eye movements followed a veridical motion with a short delay but followed a perceived

motion in the opposite direction after a long delay. Though the delays used here were longer than those of Wong and Mack, the pattern of results is similar. Thus, it appears that if the motor representation of space possesses a memory for the positions of stimuli no longer present, the memory begins to degrade after no more than a few hundred milliseconds. The duration of this memory and the conditions under which it is degraded are subjects for future research.

Conclusions

In addition to differences in the Roelofs effect, the results have shown a differential decay rate of perceptual responses and pointing responses along with greater variability for pointing than for perceptual measures; how are these to be interpreted? An interpretation that is consistent with cortical neurophysiology as well as with the literature cited above is that the two measures access information from different maps of visual space. The motor map is accessed by a pointing measure that requires a 1:1 relationship between stimulus position and behavior; stimulus and response map isomorphically onto one another. The cognitive map, in contrast, requires a categorization in which the relationship between target position and behavior is arbitrary.

Our conclusion is that the normal human possesses two maps of visual space. One of them holds information used in perception: if a subject is asked what he sees, the information in this "cognitive" map is accessed. This map can obtain great sensitivity to small motions or translations of objects in the visual world by using relative motion or position as a cue. The price that the cognitive system pays for gaining this sensitivity is that it loses absolute egocentric calibration of visual space. In calculating dx/dt by differentiation, the constant term (the spatial calibration) drops out.

The other visual map drives visually guided behavior, but its contents are not necessarily available to perception. This map does not have the resolution and sensitivity that the cognitive map has, but it is not required to: a small error in pointing, grasping, or looking is of little consequence. The advantage of this map is its robustness; the "motor" map is not subject to illusions such as induced motion and the Roelofs effect. In this sense it is more robust, but as a result it is less sensitive to small motions or fine-grained spatial relationships. It also has only a short memory, being concerned mainly with the here-and-now correspondence between visual information

and motor behavior. If a subject must make motor responses to stimuli no longer present, this system must take its spatial information from the cognitive representation and brings any cognitively based illusions along with it. This is not to say that the sequence cannot be stored in memory and used to improve motor performance in the future; the current egocentric spatial values are lost, however. The relationships of information flow in the two systems are schematized in Fig. 19-7.

Another way of interpreting the relationship between the cognitive and the motor representations of visual space is in terms of the subject's ability to

integrate information from the map with other information. The cognitive map's contents can be described and compared with other spatial or non-spatial information, whereas the motor map is generally inaccessible to integration with information from other sources.

An example of this dichotomy between overt and covert aspects of visual processing is seen in experiments in which a monocularly viewing eye is pressed to separate efference copy from eye position. When the eye is pressed and held, it does not undergo a passive rotation—quite the reverse, it actively resists rotation, for fixation on a target can be maintained while the eye is pressed. As a result, the efferent commands to the eye change, and the efference along with it, while position of the retinal image remains constant. One can easily demonstrate this active resistance by closing one eye and slowly pressing on the other; a fixated object will remain fixated even while apparent motion is seen. Monitoring the movements of the occluded eye provides an objective record of the change in the efference to the eye.

Cognitive components of vision can be measured under these conditions by asking a subject to set a target to appear straight ahead while the eye is pressed. Motor components are measured by open-loop pointing to a target. The cognitive measure is affected by visual context; in a normally illuminated environment, eye-press has little effect on straight-ahead settings, but the same settings correspond to the offset of the efference copy if the judgment is made in darkness with only the target visible. Pointing, in contrast, is determined by the change in efference copy regardless of the illumination conditions, and is always offset by eye-press (Bridgeman and Stark, 1981; Stark and Bridgeman, 1983). Again, the subject is unaware that the cognitive settings and the pointing directions do not correspond.

The difference between cognitive and motor representations in this context is comparable to the distinction between explicit and implicit modes of memory, respectively. The explicit mode is accessible to language and to experiential memory, whereas the implicit mode may hold information that the subject is unaware of or even that is contradictory to the contents of explicit memory (Roediger *et al.*, 1988). Similarly, subjects can hold one position of a stimulus in the cognitive mode and simultaneously hold a different position for the same stimulus in the motor mode.

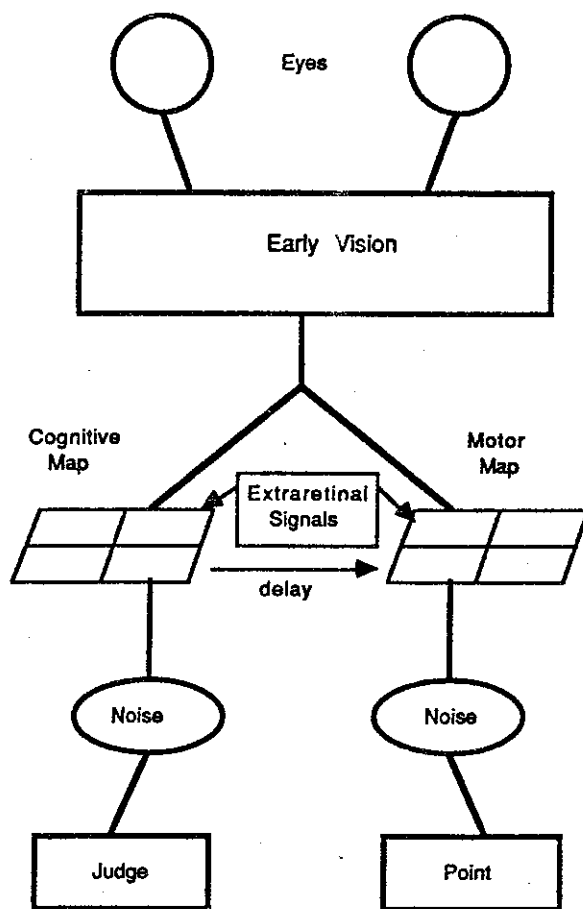


FIGURE 19-7. A proposed information flow scheme for perceptual judgments and visually guided behavior. After a common input stage, spatial information maps into both a cognitive representation (left center) and a motor representation (right center). Extraretinal information does not affect early vision, because receptive fields at the striate cortex and below have retinotopic rather than spatiotopic receptive field organization. The extraretinal information is supplied to the two maps separately because it may affect them differently. If the motor map has no spatial information, it can receive information from the cognitive map. The two maps influence behavior through independent noise sources.

REMAINING PROBLEMS

The two-visual-systems idea needs further development both in laboratory experimental work and in theory. The theoretical problems must be addressed before empirical work can make further contributions. First, the definitions of the two systems must be clarified and standardized. Some workers have defined the two systems anatomically, some physiologically (in terms of receptive field properties), and still others functionally. The approach taken here is functional, distinguishing the two systems in terms of the task required of an observer. This, I argue, is the primary mode of definition, because anatomic or physiological distinctions make sense only when weighed against behavioral and perceptual criteria. Lesions in monkeys are interpreted with perceptual-motor experiments, and receptive fields are compared to behaviors. The variety of modes of definition has led to some inconsistency and to the possibility that different workers are distinguishing different systems. There may be more than two separable streams of visual information, for example, or different groups may be defining a stream at different points.

It is likely that the two modes are not independent but that limited information exchange occurs even at the most central levels. This is an area that needs further investigation.

SUMMARY

Two distinct modes of visual image processing have been identified in normal humans: first, a cognitive system, serving perception and assessed with perceptual measures; and second, a motor-oriented system, serving visually guided behavior and assessed with open-loop pointing or looking. Experiments in my laboratory and others have identified some of the properties of each system. The cognitive system requires fine-grained, high-spatial-frequency signals for optimal function; because of limitations of retinal sampling, such signals are available only on and near the fovea. Moderate amounts of high-pass filtering have little effect on this system. The motor system, in contrast, requires only lower spatial frequency signals and cannot make use of information at the highest spatial frequencies. This grosser information must be gathered from a large area of the retina, however, ideally including both the fovea

and a large region of the retinal periphery. Thus, one can conceive the retinal image as containing two spatially overlapping, complementary images: a high spatial frequency, primarily foveal image used in perception, and a larger, low-spatial-frequency image used to guide visual-motor coordination. Because most of the information in the image is in the high frequencies, the perceptual branch of the system dominates the geniculostriate pathway and has received the most attention from neurophysiologists.

The implication for lens design is that if compromises must be made between image quality and spatial distortion off the center of vision, it is preferable to sacrifice image quality in the high spatial frequencies to preserve spatial relationships.

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