A THEORY OF VISUAL STABILITY ACROSS SACCADIC EYE MOVEMENTS

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Keywords

Abstract

We identify two aspects of the problem of how there is perceptual stability despite an observer's eye movements. The first, visual direction constancy, is the (egocentric) stability of apparent positions of objects in the visual world relative to the perceiver. The second, visual position constancy, is the (exocentric) stability of positions of objects relative to each other. We analyze the constancy of visual direction despite saccadic eye movements.

Three information sources have been proposed to enable the visual system to achieve stability: the structure of the visual field, proprioceptive inflow, and a copy of neural efference or outflow to the extraocular muscles. None of these sources by itself provides adequate information to achieve visual direction constancy; present evidence indicates that all three are used.

Our final question concerns the information processing operations that result in a stable world. The three traditional solutions involve elimination, translation, and evaluation. All are rejected. From a review of the physiological and psychological evidence we conclude that no subtraction, compensation or evaluation need take place. The problem for which these solutions were developed turns out to be a false one. We propose a "calibration" solution: correct spatiotopic positions are calculated anew for each fixation. Inflow, outflow, and retinal sources are used in this calculation: saccadic suppression of displacement bridges the errors between these sources and the actual extent of movement.

I. Introduction

Our eyes are almost constantly moving. Body and head movements change the position of the eyes relative to the world. Subjects trying to remain as steady as possible, while using normal postural supports to keep the head in place, still show appreciable head movements (Steinman and Collewijn 1980). Even during steady fixation with the head immobilized, a variety of small eye movements, e.g., micro-saccades, drifts and tremors, constantly change the position of the eyes relative to the world. Moreover, a variety of larger eye movements, e.g., saccades, pursuits and vergence movements, change the position of the eyes relative to the world (Collewijn, Steinman, and van der Steen 1985).

When the eyes move relative to a stable world, the projection of the stationary world on the retina, i.e., the pattern of light containing information about the outside structure of extrapersonal space, changes position. Some of these changes in projection resemble the signals that would be generated if the eyes were stationary and the visual world had moved. An example is the quick movement of an object against a homogeneous background. Nevertheless, a stable and nonmoving world is perceived. Of course, this state of affairs immediately raises the question how this is brought about. How can continually changing retinal projections be the basis of the perception of a stable visual world?

This article is concerned with a part of the problem of perceptual stability. Only part of the problem is dealt with because the total problem of perceptual stability is a large one; several subsystems and a great number of cues are involved (see, e.g., Shebilske 1977). We address the problem of how visual direction constancy is maintained despite saccadic eye movements. This is a major part of the total problem. In fact, saccadic eye movements, unaccompanied by other behaviours, form the vast majority of all our behavioural acts (Bridgeman 1990), and a solution to the saccadic problem would be a large step toward solving the problem of perceptual stability in general. We explicitly exclude the third (z- axis) dimension from our analysis, considering only saccades of roughly equal amplitude in the two eyes and neglecting vergence movements. We also exclude visual-motor coordination and concentrate on perception, because visual-motor coordination may take place in systems separate from perception (Hansen & Skavenski 1985; Bridgeman 1983). Physiological evidence relating to this distinction will be reviewed below.

Two Constancies

At least two "perceptual stabilities" or "constancies" must be distinguished. The first is visual direction constancy; when only the eyes move, the apparent position of objects in the world remains constant relative to the head and/or body. In this form of constancy, two frames of reference that remain stable with respect to one another (the world and the head/body) are unaffected by changes in a frame of reference at an intermediate level (the eyes).

The second form of constancy is visual position constancy; when the eyes, head and/or body change position, visual direction relative to the observer changes but the apparent position of objects in the visual field remains constant. Here the world and the eye, head or body frames of reference change orientation with respect to one another, but the change is attributed to motion of the organism rather than to motion of the world.

Saccadic eye movements are very fast, ballistic, eye movements, separated by fixation periods during which the eyes are relatively still. In fact, the movements are time optimal: the eyes move as fast as physiologically possible (Clark and Stark 1975). Speeds of up to about 1000 degrees per second are possible. Saccades are ballistic in the sense that, once initiated, they cannot be stopped or modified. The duration of the neural impulse determines the size of the movement.

Visual sensitivity is reduced during and just before a saccadic eye movement, a phenomenon called saccadic suppression (see, e.g., Volkman, Schick and Riggs 1978). Suppression of flashed targets amounts to less than 0.7 log units, and even that applies only to targets already near threshold. But sensitivity to displacement of targets decreases by more than 4 log units during saccades (Bridgeman 1983), so that motion and position information are severely degraded. Visual information is taken in during the fixational pauses between movements. Therefore a sequence of fixational pauses provides a sequence of discrete retinal images, a sequence of glimpses or samples separated in time. Despite the difference in retinal projections, a stable world is perceived.

Figure 1 illustrates the geometry of what is happening according to this analysis. For ease of exposition a one-dimensional map (-4 to 4) is used as the representing space. For the moment we assume that this map is capable of calculating -- in one way or another -- the spatiotopic coordinates of objects. The outcomes of these calculations are the codes for the represented space. In panel a) spatiotopic information appropriate to fixation N is coded in the retinotopic map. World position -3 is fixated, i. e. the code for world position -3 is in map position 0. The other retinotopic positions contain corresponding spatiotopic codes. After a saccadic eye movement that brings world position -1 into the middle of the fovea, the situation shown in panel b) results. In fixation N+1 the world position -1 is coded in map position 0, and the other spatiotopic codes have changed position accordingly.

< Figure 1 near here >

In the next section we look briefly at solutions for our problem that have been proposed in the past. In section III we review some neurophysiological findings that are important for the solution of the problem of perceptual stability, and in section IV we develop a new conception that makes use of these findings. In the final section we note some further implications of our view.

II Past solutions for the problem of perceptual stability

The problem how a stable world is perceived despite body, head, and eye movements has aroused much interest in the past. Eminent scientists such as Helmholtz, Hering, Mach and Sherrington have been concerned with aspects of the problem. Shebilske (1977) argues convincingly that none of the proposals for a solution these and other scientists arrived at is fully adequate and complete. In this section we sketch the main relevant issues proposed and elaborated in the recent past. As guides in this endeavour we use two key studies: Bischof and Kramer (1968) and MacKay (1973).

To appreciate the solutions proposed in the traditional approaches, it is worthwile to distinguish two independent problems. The first problem is: What kind(s) of information can be used to differentiate between changes of the retinal projection as a result of motion in or of the visual world and changes due to movement of the eyes or body of the observer? What kind of information can be used to achieve perceptual stability? The second problem is: What use does the system make of the available information to arrive at perceptual stability? What are the information processing operations that result in a stable perceptual world?

Three Kinds of Spatial Information

With regard to the first problem -- the kind of information used -- at least three proposals can be distinguished: - aspects of the structure of the visual world, or of the movement of the retinal projection, i.e., "structural cues", provide the information needed (see, e.g., Gibson 1950; 1966; 1979; Haber 1983). - proprioceptive messages from the extraocular muscles and/or from other receptors, i.e., "neural inflow", provide the information (see, e.g., Sherrington 1918; Matin 1972; 1976). - neural commands to the extraocular muscles and/or to other motor systems, i.e., "neural outflow", provide the information on which the stable visual world is based (see, e.g., Helmholtz 1867; Sperry 1950; Von Holst and Mittelstaedt 1950; 1971). Inflow and outflow together constitute the "extraretinal signal" (Matin 1972). Let us look at these three proposals in turn.

Retinal Information

Gibson has pointed out convincingly and shown with various demonstrations that the retinal projection -- or the "ambient optic array" -- contains appreciably more information about the visual world, and about the position and activities of the observer in the visual world, than traditionally has been assumed. Saccadic eye movements are activities of the observer in the visual world, and there is information in a sequence of retinal projections that unambiguously specifies that a saccadic eye movement was made. The sorts of image transformations experienced in video or motion picture sequences, for instance, can inform a subject about motion of the camera without benefit of any extraretinal signals about camera behavior. This sort of information is limited, however -- abrupt image movements, such as those introduced by hand-held cameras, do disrupt constancy, and large image displacements (simulating what happens on the retina during saccades) are both noticeable and disorienting. Motion picture camera technique emphasizes smooth motions and transitions. The rigid displacement of the whole retinal image, or something like "higher- order" relational cues that are invariant over a succession of fixations, are good candidates for image-based information that could specify eye movement (see Gibson 1950; 1966). Gibson (1966, p. 256) simply denies that there is a problem of perceptual stability because the world is stable ecologically, and any motion of the image as a whole must be due to eye movement rather than world movement.

However, the fact that there is information in the optic array at the retina is not enough. We need to know not what information can be used, but what information is actually used. A simple experiment shows that the information does not consist solely in retinal cues. Tapping lightly on the canthus of the eye displaces the whole retinal image, comparable to the rapid displacement produced with a saccadic eye movement. Under these conditions an illusory displacement of the whole visual scene (against the direction of the passive eye movement) is obtained. This observation was made by Purkinje and has been replicated by Helmholtz (1867) and a host of others since.

With saccadic eye movements no such displacement is observed. So, retinal cues cannot prevent a perception of destabilisation of the visual world (and because the world is stable during tapping the eye, there is a problem of perceptual stability). The exact dynamics of the eyepress maneuver are not important here -- minor changes in focus, center of rotation of the eye, and mechanical deformation are secondary, as long as the retina is made to shift relative to the retinal image. The quality of the retinal image is poor during saccades in any case, because of the high slew rate

of the image.

The tap is too quick for the heavily damped oculomotor fixation system to follow, so that a passive eye movement occurs (Ilg, Bridgeman and Hoffman 1989) just as Helmholtz would have predicted. Thus the tapping experiment is consistent with the fact that a sustained press on the eye normally induces a compensatory change in innervation to the eye without a change in fixation position, because automatic fixation systems maintain eye posture despite the eyepress (Stark and Bridgeman 1983). The converse experiment, eliciting an eye movement without a shift of the image on the retina, is accomplished with an afterimage in darkness. Even an extended, meaningful afterimage of a naturalistic visual world will seem to jump with each saccade, showing again that structure of the optic array alone is not adequate to stabilize perception. Again, this observation was made by both Purkinje and Helmholtz, and can be repeated easily.

Other examples also demonstrate the extreme vulnerability of space constancy across saccades, despite the seemingly perfect constancy achieved under normal conditions (Bridgeman 1983). Drugs such as alcohol can disrupt normal functioning, causing breakdown in constancy, and eye paresis causes both breakdown in constancy and errors in visual- motor coordination. Repeated large saccades lead to apparent displacements with each saccade, and even a single large saccade from one point to another, if both points are at the edge of the oculomotor range, can interfere with perceptual space constancy, as Helmholtz (1867) realized. Saccadic suppression of displacement masks jumps of the retinal image due to saccadic eye movements, so that perception of the sensory results of saccades is very different from the perception in a similar sensory situation caused by artificially imposed jumps of the visual world (Bridgeman 1983).

Proprioceptive Information

Sherrington demonstrated the existence of stretch receptors in the extraocular muscles and defended the view that the visual system uses proprioceptive information provided by these receptors during an eye movement, i.e., the neural inflow, to achieve perceptual stability (see, e.g., Sherrington 1898; 1918). There are, however, theoretical and empirical reasons to doubt the correctness of this proposal. Theoretically, it is not clear whether this information is available early enough. As noted above, saccadic suppression begins even before the eye begins to move, at a time when proprioception can play no role. The earliest possible influence of proprioceptive input from extraocular muscles is about 20 msec after the start of the actual movement, but saccadic suppression can begin more than 50 msec before saccade onset. Thus proprioceptive signals arrive at the CNS too late to affect the initial stages of perceptual change preceding saccades, even allowing for a 30 msec transmission delay of the retinal signal to the cortex. Thus, though proprioception might play some role later in a saccade, it cannot be responsible for the initial events, and it cannot be the sole extraretinal influence on visual space perception.

Empirically, the simple experiment described in the foregoing section suffices to undermine the plausibility of the inflow hypothesis. That is, when the eye is moved passively by tapping on the canthus, the stretch receptors are activated and will discharge. Nevertheless, under these conditions a clear impression of displacement of the whole visual field is obtained. So, the stretch receptors in the extraocular muscles by themselves cannot prevent the destabilisation of the visual world. While some researchers grant proprioceptive information a function in stabilising the visual world (see, e.g., Matin 1976; Breitmeyer, Kropfl and Julesz 1982; Steinbach 1987), it is now generally assumed that neural inflow is not the only kind of information used.

There is now evidence, however, that proprioceptive inflow contributes to space constancy under some conditions. Gauthier, Nommay and Vercher (1988) have described a high-threshold, low-gain effect of inflow obtained during static fixation. Gain is defined as the output of a system divided by its input; in this case it is the ratio of pointing error to passively induced eye deviation, and is a useful measure for comparing effects from disparate sources. Gauthier et al. changed inflow by passively moving one eye with a suction contact lens, and measured small deviations in pointing at targets seen with the other eye.

The existence of Gauthier's effect was confirmed by Bridgeman and Stark (1991) using an eyepress method, with both outflow and inflow being measured quantitatively in the same experiment. Measuring perceptual deviation under these 2 conditions, Bridgeman and Stark found inflow to contribute about one-quarter of the total extraretinal signal. (This updates the conclusion of Stark and Bridgeman (1983) emphasizing outflow.)

There are several reasons to expect that under saccadic conditions the contributions of both inflow and outflow are smaller than they are during fixation. First, previous estimates of the gains of outflow (which in most cases, in our interpretation, measure outflow and inflow together) find the signal to be smaller when the eye is moving than it is during fixation. Gr_ sser, Krizic and Weiss (1987) found the gain of the extraretinal signal to be 0.70 during saccades, and to be reduced further when saccades were repeated in rapid succession. Inflow is expected to be less important during saccades than during fixation or slower movements, because of physiological delays. Indeed, during small

saccades the movement should be finished before an inflow signal reaches the CNS. This may explain why inflow has no measurable effect below a threshold of several degrees. For larger saccades, inflow could begin to reach the CNS before the completion of the movement.

Efference Copy

Helmholtz (1867) argued that the command signal from the brain to the eye muscles, the "Willensanstrengung" (effort of will), constitutes the information used to achieve perceptual stability. And indeed, because the motion of the eye is determined by the neural command, this kind of information can be the basis of the perception of a stable visual world.

There are theoretical and empirical reasons that make attractive the view that neural outflow or a branch of the neural outflow such as a "corollary discharge" (Sperry 1950) or an "efference copy" (Von Holst and Mittelstaedt 1950; 1971) is the information used. First, there is no timing problem. Even with very small saccadic eye movements neural outflow is available in time to serve a function in stabilising the visual world. Inflow cannot be transduced, however, until after the eye begins to move, so that initial parts of a saccade could not be compensated. Second, the neural outflow hypothesis is consistent with empirical results. In the tapping experiment referred to in the two foregoing sections there is a change in the retinal projection but there is no neural outflow to the extraocular muscles.

In a more complicated, converse, experiment, in which attempts are made to move a partly paralysed eye, there is little change in the retinal projection but there is neural outflow. Subjects experience apparent motion of the entire visual field when attempting to make eye movements (Mach 1885; Stevens, Emerson, Gerstein, Kallos, Neufield, Nichols and Rosenquist 1976). Incidentally, the Gibson eclogical school would hold this sort of experience to be impossible, such shifts of the optic array always being assigned to the results of eye movement.

During complete paralysis, however, no jump seems to occur. Stevens et al. (1976) observed that at the time of an attempted saccade by a paralyzed subject, the world seemed to be in a different position when sustained eccentric gaze was unsuccessfully attempted. This would be expected if outflow provides information about position of the visual world. In the presence of even a small motion transient under conditions of incomplete paralysis, the perceptual system accepts the retinally given transient as marking the time of a location change that is specified by outflow and static retinal position. With complete paralysis there is no retinal motion transient, and no time at which the changed outflow can contribute to replacing previous spatial values. Hence the ambiguity of the perception and the difficulty of reporting it accurately.

The sustained eyepress technique, with similar innervation and retinal conditions, yields a similar result (Bridgeman and Stark 1981; Stark and Bridgeman 1983). In both the paralysis and the eyepress cases a strong impression of movement is obtained. Only when retinal change and neural outflow correspond, as is the case during normal saccadic exploration, is a stable visual world perceived. This all makes it highly likely that neural outflow contributes in one way or another to a stable visual world.

How the Information is Used

With regard to the second problem -- how the information is used to create a stable world -- it is also the case that at least three solutions can be distinguished. We call them the elimination, the translation and the evaluation solutions. In the remainder of this section we discuss these three proposals in turn.

The Elimination Solution

A major background assumption of what we call the elimination solution is that the varying retinal information should be perceived. However, no illusory displacement of the visual world is perceived. Therefore according to this theory information about eye movements, usually consisting mainly of the efference copy (neural outflow), must be used to "eliminate", "cancel out", "subtract" or "compensate for" the effects of eye movements (see, e.g., Sperry 1950; Von Holst and Mittelstaedt 1950; 1971).

Let us imagine an active CNS sending out orders, or "commands" in our terminology, to the effectors and receiving signals from its sensory organs. Signals that predictably come when nothing occurs in the environment are necessarily a result of its own activity, i.e., are reafferences. All signals that come when no commands are given are exafferences and signify changes in the environment or in the state of the organism caused by external forces. In general, one could say this: The difference between that which is to be expected as the result of a command and the totality of what is reported by the sensory organs is the proportion of exafference. In the former example it is zero, in the latter 100 percent. When there is overlap the proportion is between these two values. It is only this difference to which there are compensatory reflexes; only this difference determines, for example during a moving glance at movable objects, the

actually perceived direction of visual objects. This, then, is the solution that we propose, which we have termed the "reafference principle": Distinction of reafference and exafference by a comparison of the total afference with the system's state -- the "command". (Mittelstaedt 1971; Translated from German by the authors).

MacKay (1973, p. 308) explains that "the proposed subtractive mechanism... is quite analogous to that by which the map of the coastline on a ship's radar screen is prevented from rotating when the ship's head turns, by using signals indicative of ship-rotation to subtract an equal and opposite rotation from the input to the display" (Figure 2, top).

< Figure 2 near here >

MacKay (1973) argues that this elimination solution cannot be the solution selected by nature. Subtraction would work only if the motion of the eye were precisely determined by the neural outflow to the effectors. In physiological reality, this required precision is never reached. The spatial precision of the motor system is appreciably lower than the spatial resolution of the retina. Therefore, the low accuracy of the motor system, if elimination were the solution, would cause perception of spurious world displacement on innumerable occasions (MacKay 1973, p. 317).

The elimination solution might be salvaged if the visual system interpreted mismatches between the retinal image displacement and the extraretinal signals as errors in the motor system (Skavenski, 1990). Quick adaptation of saccadic dysmetria is evidence that the oculomotor system is designed to adjust for errors. The empirical evidence, though, is that subjects are quite sensitive even to small displacements of the entire visual world, simulating the retinal conditions during a saccade. To test this, Bridgeman (1983) displaced an extended pattern target by 18 degrees in one jump and by slightly more or less than that in another jump. The subject's task was to determine which jump was larger. Performance remained good even down to differences between the jumps of 0.25 degrees. During saccades, in contrast, a 2-alternative forced-choice measure showed that performance was at chance even with a 2-degree displacement superimposed on an 18- degree saccade. So the rules of perception change during saccades, with a decrease in sensitivity to image jumps that cannot be attributed to criterion shifts, retinal stimulation conditions or oculomotor errors.

The Translation Solution

The basic assumption of what we call the translation solution is that a memory, containing a stable representation of the world, is at the basis of our visual experience. Information about eye movements, the neural outflow, is needed to map the limited momentary retinal representation -- a representation in retinal coordinates or retinotopic coordinates -- into the more enduring higher order representation, in world coordinates or spatiotopic coordinates. To achieve this mapping a coordinate translation is needed (Figure 2, bottom). Several authors have proposed variants of this solution (see, e.g., Bischof and Kramer 1968; Breitmeyer et al. 1982; Breitmeyer 1984; Feldman 1985). This solution not only explains why we see a stable visual world but also why we experience a continuous and detailed visual world, and therefore can be put forward very convincingly.

In fact: when we are reflecting upon the "retinal image" while looking rigidly at a certain point in our environment (e.g. a letter in the present text), asking ourselves what it is that we are actually seeing and how we are seeing it, we suddenly realize that, in comparison to that retinal image, the normal and naive perceived world is so much richer, so much more differentiated and comprehensive. Our perception would be sorely inadequate if, in content and structure, it remained limited at any given moment to that which the retina actually reports. But nothing could be further from the truth: What surrounds us in the form of concrete, perceived reality, i.e., in the phenomenal mode of what is encountered, and not merely imagined or thought (cf. Metzger 1954), is constructed for the most part out of information that is remembered: The physiological base of our perceived world is a store. A store, though, that is kept up to date by a continuous "servicing". (Bischof and Kramer 1968, p. 209; Translated from German by the authors.)

The problem with this solution, however, is that extensive research has not revealed such a higher-order spatiotopic visual memory under conditions where it should have appeared. Davidson, Fox and Dick (1973) reported that subjects could integrate information across saccades, keeping targets in space-constant spatial registration, but later studies have failed to replicate this effect (Irwin, Zacks and Brown 1990). The original Davidson et al. study has also been called into question on theoretical grounds, for internal inconsistencies and conclusions that are not justified by the data (Van der Heijden, Bridgeman and Mewhort 1986). Another early report of precise spatiotopic registration across saccades (Jonides, Irwin & Yantis, 1982) turned out to be based on a phosphor persistence artifact, as later empirical work demonstrated (Bridgeman and Mayer, 1983; Irwin et al., 1983; Rayner and Pollatsek, 1983).

Recent work has revealed that integration of information between saccades is based more on objects than on spatial locations (Pollatsek, Rayner & Henderson, 1990). Irwin (1990) concludes that "transsaccadic memory is an undetailed, limited-capacity, long lasting memory that is similar to, and perhaps identical with, visual short-term memory".

Further, known visual maps in the brain are retinotopic, not spatiotopic. Some exceptions to this retinotopic rule have been reported: in a polysensory parietal area of the cat, Pigarev and Rodionova (1988) found that nearly half of the visually responsive neurons had space-constant receptive fields with respect to the head. The fields were 10 to 40 degrees in extent, however, making it unlikely that these neurons support normal perception. Their receptive field size and anatomical location make it more likely that they are involved in visual-motor coordination, a process distinct from the perceptual problem (Paillard 1987). This evidence is equally damaging to the elimination solution.

Vision certainly involves long-term memories (see, e.g., Hebb 1949; Hochberg 1968; 1970) and short-term memories capable of integrating information over a series of fixations (see e.g., Neisser 1967; Coltheart 1980). The translation solution requires a spatiotopic map to support visual perception of space constancy, however, and this probably does not exist (see Irwin et al. 1990).

The Evaluation Solution

A major assumption in the evaluation solution is that perceived space constancy depends on a neural map with representations of the locations of objects in the world. The "null hypothesis" of the information processing system is that this map is correct and needs no revision. Only with sufficient evidence to the contrary is a change made in the map (see Figure 3). Information about eye movements, the neural outflow, is used to assess whether a change in the map is called for (see, e.g., MacKay 1962; 1973). MacKay argues

The location of (the fixed contents of the world) could be permanently represented in some suitable internal form .... The physiological details of this internal representation or "map" are not important for the present argument. The point is that once it had been built up, in whatever form, there would be no further need for any coupling to it from the sensory input, as long as the world was stable. It would be pointless to allow the input to play constantly upon the "map", having to be corrected by means of elaborate "compensations" for the changing sensory effects of locomotion and eye movements, yet contributing to it only 100% redundant information...To take an analogy from the tactile domain..., we may think of a blind man finding his way around a room full of stationary objects. He uses a variety of muscles to move a sensory surface (his palm or finger-tip) over the sensory field (the surfaces of objects). The result is a constantly changing stream of "rubbing sensations" ... once he has become familiar with the objects around him these changing signals ... have no selective- information-content ... requiring any changes in the blind man's internal "map" of the objects he explores. (MacKay 1973, p.313).

< Figure 3 near here >

This proposal has problematic, but also highly attractive features. Problematic, for instance, is how the position of the organism (its body, limbs, eyes, etc.) with respect to the visual world, or possibly better, the position of the objects in the world with respect to the organism, is represented. If perception is for action (see e. g. Allport 1987, for this view), then a spatial map must specify what actions the visual world affords and how the actions are to be executed. Mere specification of the location of objects in a metric not related to action is useless. A more radical view is that perception is for making decisions about actions with the details of coordination being performed elsewhere (Bridgeman 1986). MacKay (1973) indeed suggests that the problem of sensory- motor coordination can be solved in visual subsystems different from the centres involved in the perception of the visual world.

This solution also runs into trouble in the details of its execution. MacKay's (1973, p. 315) conception asserts that the system assumes the map to be "correct until sufficient evidence is received to the contrary" (italics in the original). How much evidence is sufficient, and how does the system decide? Will individually insufficient errors accumulate?

An attractive feature of the proposal is that it makes use of neurophysiological evidence indicating that the (human) visual system is modular, with different functions for its distinguishable parts. For MacKay the advantage of modularity consists mainly in ensuring economy of information processing. This feature of the system makes it possible for "... the location attributed to a moving object to be changed appropriately ..., with the minimum of disruption of its other attributed features (e.g. shape) or those of its neighbours" (MacKay 1973, p.314). But modularity has other important consequences. To these consequences we turn below.

Taking all of the evidence together, it is likely that neural outflow is the principal kind of information used to achieve perceptual stability despite eye movements. With regard to the problem of how stability is achieved, i.e. how the visual system uses the neural outflow, there is no agreement. Moreover, as indicated at the conclusions of the sections on each of the three existing proposals, all have their drawbacks, conditions under which they fail to account for known data or make unreasonable demands on physiology. In our view, from among these proposals MacKay's is the most attractive as a starting point because it uses the relevant neurophysiological evidence. We now turn to this evidence.

III Separate neurophysiological processing for spatial localization and object recognition

An important distinction emerging in contemporary neurophysiology of vision is that of localization and object recognition. Introduced by a series of articles in Psychologische Forschung (Held 1968; Trevarthen 1968), this distinction was initially conceived as connected with differences between cortical and subcortical structures: the focal (form perception and recognition) system was supposed to reside in the geniculostriate pathway and the ambient (that is, spatial) one in the superior colliculus and related brainstem structures. Later, Mishkin, Ungerleider and Macko (1983) provided data on differential effects of cortical lesions in primates which favour a similar separation but in cortical pathways. What those authors call "object vision" follows a ventral inferior temporal cortex route, while their "spatial vision" follows a dorsal parietal cortex route. It is possible that in the course of evolution (cf. the so-called "encephalization" hypothesis) some subcortical functions, such as spatial processing, became in part cortically localized.

The picture has become more complicated, however, than was supposed in the original theory, and the exact anatomical relationships among all these levels and subsystems of the visual brain have not yet been defined. At one time the object vision and spatial vision functions were proposed to be served by parvocellular and magnocellular afferent systems respectively (Hubel and Livingstone 1987; Livingstone and Hubel 1988), but more recent work has called into question the degree of segregation of these two systems at more central levels (i. e. Maunsell and Gibson, 1992). An index of transience was unimodal for neurons in striate cortex, and lesions of magnocellular or parvocellular layers of the lateral geniculate yielded only minor changes in this measure. Regarding geometric isomorphism, neurophysiological research in sensory coding has shown that ".. any candidate code can represent any perceptual dimension; there is no need for an isomorphic relation between the neural and psychophysical data. Space can represent time, time can represent space, place can represent quality, and certainly, nonlinear neural functions can represent linear or nonlinear psychophysical functions equally well" (Uttal 1979, p. 286). From the genetical and functional perspectives the two modes of processing are asymmetrically related: while egocentric evaluation of "where" need not take into account the identity of objects, the perception of "what" usually proceeds through an intermediate stage in which objects are dynamically localized (Velichkovsky 1982).

Sokolov (1980) and Shebilske (1990) have hypothesized that there could be many visual systems, that is, more than two anatomically and functionally distinct representations of the visual field - a kind of brain's projective maps. In addition to the retina itself, such projective or retinotopic maps of the visual field have been discovered in the midbrain, the LGN, the striate (V1) and extrastriate (V2, V3, V4) occipital, temporal (MT and medial superior temporal area, MST), and posterior parietal (lateral interparietal area, LEA and area 7b) cortex. The maps code a variety of elementary features such as position, orientation of edges, color, disparity and direction of retinotopic motion. For each location in these maps, neighborhood relations of the corresponding features are preserved (Kaas 1988). There is also the possibility of a selective mapping from the early retinotopic representations into more central non-topographic representations (Koch and Ullman 1985).

If one disregards finer subdivisions within the domain of spatial vision, a case can be made for two spatial processing pathways, one residing in the midbrain and another in the parietal cortex. These two "spatial visual systems" probably underlie the control of visually guided behavior rather than the processing needed for the perceptual stability of the visual world. Sensorimotor coordination, unlike perception, requires a continuous quantitative correlation between object position in the world and motor response. Within the spatial system, current evidence suggests at least two different modes of spatial coding in different parietal regions of the monkey. Receptive fields of neurons in the lateral intraparietal area are spatially corrected before each saccade, so that they respond to stimuli that will be in their retinotopic receptive fields following a planned saccade (Duhamel, Colby and Goldberg 1992). Andersen, Essick and Siegel (1985) have discovered that neurons in parietal area 7a provide information that is sufficient for a reconstruction of spatial position in head-centered coordinates. The responses of these neurons depend on both eye position in the orbit and retinal location of a target, in a multiplicative interaction. No single neuron gives a space-constant response, but within the retinotopic map of the area information is available about the head-centered location of a target. Later simulations showed that information sufficient to derive spatiotopic output exists in such a network of cells (Zipser & Andersen, 1988). Both of these areas are small and their reveptive fields are large, however, so that they are unlikely to support high-acuity perceptual function.

The informational bandwidth of any single neuron is too limited to provide adequate information about any stimulus dimension. Further, several stimulus dimensions are confounded in the response of any single neuron. So the brain must code aspects of the visual world, and therefore also movement and location, as activity patterns in large ensembles of neurons, each neuron contributing only a tiny fraction of the needed information (Bridgeman, 1992; Fetz, 1992).

Spatial stability, however, may be too basic a function to be limited to the parietal cortex, which is a relatively high-order structure well differentiated only in primates. Some features of the midbrain mechanisms, such as their

broad intermodal integration, are consistent with their possible role in ambient vision. Stone (1983) proposed that ambient vision mainly depends on the low-level W- pathway leading to the superior colliculus.

In parallel with these distinctions between perceptual and motor- oriented systems, there is also behavioral evidence that extraretinal signals are used differently for movement discrimination and egocentric localizations: during pursuit tracking, Honda (1990) found systematic errors in perceptually judged distance of target movement, even while egocentric localization was not affected by the mode of eye movements.

Though the discussion of neuroanatomical mechanisms is ongoing, we will assume the relative autonomy of localization processes from the rest of visual function. We can use the idea of modularity of vision to take another look at the problem of perceptual stability, a problem that now breaks down into different problems for the various input modules, possibly with different solutions for each.

IV A new solution for the problem of perceptual stability with

saccadic eye movements

For a real insight into the problem of perceptual stability with saccadic eye movements, one distinction is vital: the distinction between where in the brain position and movement are coded anatomically (the position of representing) and by what code the position and movement of an object in the world are represented (the mode of representing).

In the foregoing section we saw that in all branches of the visual system information about the visual world is coded in layers of neurons that wholly or partially preserve the spatial relationships in the retina. So, movement and spatial location are probably coded in anatomical positions corresponding to retinal positions at several levels of the visual system. For our arguments it does not matter where these maps are located, but only how they are organized.

Past solutions for the problem of perceptual stability across saccadic eye movements all share one assumption; that with a saccadic eye movement there is a change in where in the brain aspects of the visual world are coded. All solutions then assume that this change in the where of encoding introduces a problem for perception. If no special measures -- elimination, translation, or evaluation -- are taken to eliminate the effects of this change, spurious movement or spurious displacement will be perceived.

It will now be clear why the distinction between anatomical position of representing and mode of representing is vital. A unique position in the world need not be coded by a unique position in a neural map, and movement in the world need not be coded by "movement" in such a map. Analogously, anatomical position in a map need not be the code for position of an object in the world, just as "movement" in the maps need not be the code for movement in the visual world. Assuming that it is, is to confuse the position of representing an object in the brain's map on one hand with the representation of the object's position in the world on the other (see Dennett and Kinsbourne, 1992, for a similar argument).

A perceptual consequence of this property of neurological coding is the existence of perceptions of motion without accompanying perceptions that an object has changed its location, as in classical motion aftereffects. The two are linked intuitively, but motion seems to be coded separately in neurons specifically sensitive to motion as opposed to position.

There are good mathematical and physiological reasons for this. The task of motion-sensitive receptive fields is to detect a differential of position with respect to time, dx/dt, and presumably they accomplish this by the equivalent of differentiating a position signal with respect to time. But in calculus the process of differentiation results in constant terms (i. e. the position x) dropping out of the differentiated expression. One cannot code both position and motion optimally at the same time. This is the source of the aperture problem in visual physiology and psychophysics (Shimojo, Silverman & Nakayama, 1989; Watanabe & Cavanagh, 1991). The distinction has recently been demonstrated empirically by cortical microstimulation. Discrete electrical stimulation can result in changes in judgements of motion, even though the electrode-elicited stimulus itself does not move (Salzman, Britten & Newsome, 1990).

Let us now use the distinction between the where and the how of encoding to elucidate in greater detail the problem of the stable visual world despite saccadic eye movements. First we examine the problem of why no spurious movement of the world is seen during saccades.

Many investigators have emphasized that the problem of a stable position of the visual world despite eye movements and the problem of why no movement is seen with saccadic eye movements must be distinguished (see, e.g., Bischof and Kramer 1968, p. 216, and MacKay 1973, p. 310). Nevertheless, there is an irresistable tendency in handbooks and textbooks to combine the two problems under "Movement" (see,e.g., Gregory 1966; Goldstein 1984). This is very

likely a mistake. The problem of why there is no movement perception differs from the problem of why there is no displacement perception with saccadic eye movements.

The idea that there is a movement perception problem when the eyes saccade arises from thinking about what happens during a saccade, and from confusing the position of representing an object in the brain with the position of the object that is represented in the world. Indeed, during a saccade the image flashes over the retina, too fast to be transduced faithfully, and the neural replicas of the image "flash" over the retinotopic maps higher up in the visual system. We know of these events from anatomy and neurophysiology. Most receptive fields in the monkey striate cortex respond differently to slow and to saccade-speed motions (Wurtz 1969), though many do respond to the fast motions. But these transient responses need not be the system's code for movement. For movement detection, specialised movement detectors have to be activated that ultimately code their detection in one or another activity pattern in the brain. But saccades are very fast movements (see section I), too fast to be detected (see, e.g., MacKay 1973). Intermediate locations of the image are not visible. We conclude that during a saccade, the displacement of the image from one location to another is more important than its motion per se.

Moreover, saccadic suppression (see section I) makes it unlikely that movement detectors can detect a retinal image displacement as a movement, and it is likely that no code for movement is activated in the brain. But then there is neither spurious movement perception nor a movement perception problem which a space constancy theory has to deal with. Displacement of the entire visual field can certainly be perceived, as the eye tap experiments reviewed in section I revealed, but the stimulus is distinct from normal perception of the movements of objects in the world, and the physiological mechanism is distinct also. So, while seen from the outside something "moves" in the neural maps during saccades, there need not be any movement perception.

There is a similar paradox in the perception of movement in the perceptual world. It seems obvious that movement should be perceived if an object's projection is moving on the retina, and most physiological studies of visual movement have assumed this to be the case (reviewed by Gruesser and Gruesser-Cornehls, 1973). But the most common and general case of movement perception concerns a target object moving against a stable background, with the observer tracking the moving object with pursuit eye movements. The eye movements reverse the movement conditions on the retina: the tracked object sweeps across the retina very little, while the background undergoes a brisk motion. Yet we perceive just the opposite -- the train seems to be moving and the track seems to be standing still, even though the reverse is true on the (moving) retina. The important thing is the relationship between background and target motion, and not the amount of sweep of either across the retina.

Application to Visual Stability

Let us now return to our main problem: how is it that after a saccadic eye movement we see the objects in the world at the same position as before, and not displaced? This spurious displacement perception problem differs from the spurious movement perception problem because during fixation, position can be perceived clearly. Also, for this problem the distinction between where something is coded and how something is coded is essential. And again it appears that, at least under some formulations, there is not very much of a problem. Below we present such a formulation. It relies on the idea that retinotopic position, i.e. the where of encoding, is not used as a code for the positions of objects in the world.

As a result of a saccadic eye movement, the pattern of activation changes its position, "moves", or is displaced in several retinotopic maps -- in the retina, the LGN, V1, V2, etc. But in most of these maps that change is simply irrelevant. They do not code position and position is not their code. They therefore neither detect a stable nor an unstable visual world. One or a few maps, however, may be in that business (see section III). They code spatial position in their retinotopic maps, and their patterns of activation on the various retinotopic positions may be the code for the positions of objects in the visual world (see Figure 4).

These patterns of activation also change their retinotopic position, or are displaced, as a result of saccadic eye movements. But again, this change of position is irrelevant. While these maps code position, it is not the cortical position that codes the spatial position in the visual world. Rather, the activation pattern of the retinotopic positions codes the position in space. While the codes may change in retinotopic position, the codes themselves, i. e. the activation patterns, can remain the same. The correct spatiotopic positions, then, are available both in fixation N and in fixation N+1 (recall the physical layout in figure 1), and there is no illusory displacement. There is a stable visual world.

If this interpretation, which is a prerequisite to our theory, is correct, then it should be possible to code positions of objects in the visual world without a space-constant map. Indeed, such a coding scheme exists for sensorimotor processing in area 7a of monkey parietal cortex (Andersen, Essick & Siegel 1985), reviewed above.

< Figure 4 near here >

The Calibration Solution

During a given fixation, retinal and extraretinal sources combine to produce a perceived position of the visual world. During the next fixation, the same sources again produce a perceived position. To the degree that the process is reasonably accurate, the world will be perceived in the same location during both fixations. There need be no corrections or translations from the previous fixation, because spatial orientation is achieved anew with each fixation.

The problem of stabilization of the visual world during saccades, then, reduces to a series of calibrations of retinotopic maps during successive fixations. What is needed for space constancy is not a correction, but a correctionless calibration of current retinal and extraretinal information. In the language of Strong and Whitehead (1989), the problem is related to tag assignment rather than space-constant maps. The calibration is accomplished by different mechanisms, and with various sources of information participating to a different extent, for varying perceptual conditions and behavioral requirements.

It remains only to consider perceptually unusual situations where this process begins to break down. We will consider the case of perceptual stabilization in an unstructured visual field, where only extraretinal information is available, such as a single point in darkness.

Psychophysical Evidence

Because in our conception the important extraretinal signals occur not during saccades but during fixation, this section will review the contributions of extraretinal signals during steady fixation. While fixating a point in an unstructured field, Bridgeman and Stark (1991) found oculomotor outflow to have a gain of 0.612 and inflow to have a gain of 0.256, averaged across subjects. The sum of these values is only 0.868, suggesting that during fixation subjects should underestimate the eccentricity of their own gaze. This is indeed the case, as Morgan (1978) found; during eccentric gaze, subjects estimate the straight ahead direction to have deviated in the same direction as their eyes. The gain of this illusion can be calculated from Morgan's data; in an unstructured visual field, it amounts to 0.126. The inflow, outflow, and illusion components together add up to 0.994, increasing our confidence that these experimentally obtained values are close to those present under normal perceptual conditions. The three components should add linearly because each is constrained by the linearity of geometric optics, and each is measured in geometric coordinates. The inadequacy of the extraretinal gain creates a problem for all three of the existing solutions for the space constancy problem, and thus provides evidence that is consistent only with our conception.

These outlfow and inflow values were measured with a static eye and can be generalized to dynamic situations only with limitations. At the beginning of a saccade, however, the gain values must be roughly as reported above because the system could change them only after a delay. Presence of a visual context tends to reduce the influence of extraretinal signals, however: Bridgeman and Stark (1991) review evidence that efference copy gains are reduced in dynamic situations. A conservative conclusion would be that visual context and saccadic suppression are even more important in the saccadic context of space constancy than the static Bridgeman and Stark data suggest.

In an unstructured visual field, the missing gain of the extraretinal signals should lead to small perceived jumps of the world after saccadic eye movements. The perception is prevented by saccadic suppression of image displacement (see section I). The magnitude of the suppression can be expressed as a gain, amounting to about 0.2 in an unstructured field (Mack 1970) and about 0.3 in a richer visual environment (Bridgeman, Hendry and Stark 1975). This gain is not enough to account for the entire image displacement that takes place during a saccade, so that an afterimage continues to appear to jump during a saccade. Thus during sustained eccentric fixation, low gain of the extraretinal signal results in illusions of localization, while across saccades the low gain is masked by saccadic suppression. Sensory adaptation, like the adaptation to any other repeated sensory event, may also play a role (Bridgeman 1983).

For perceptual localization in structured fields, extraretinal signals are less important because the visual image can provide information about localization. In the train on the tracks case, for example, the decision about what is moving and what is not can be made without regard to extraretinal signals. Reflecting this situation, the effects of deviated extraretinal signals are smaller in structured fields (Matin, Picoult, Stevens, Edwards, Young and MacArthur 1982; Stark and Bridgeman 1983), though they are still measurable (Bridgeman & Graziano 1989). Figure 5 summarizes how outflow, inflow, and perceptual factors might combine in achieving visual stability. Temporal delays in availability of the three sources of information could be the basis of the dislocation phenomena discovered during saccadic eye movements by Bischof & Kramer (1968; see also Wuermle 1983).

< Figure 5 near here >

In the context of other theories of space constancy, ours is a taking-into- account theory, as opposed to a higher order stimulus theory in Rock's (1977) terminology. That is, we invoke both retinal and extraretinal sources of information to solve the space constancy problem, and we require some combining of these sources in a process classically identified as unconscious inference (Helmholtz, 1867). We do not deny the importance of visual experience in this process, however; height of a lamp on a desk can be perceived as eye-height on the basis of familiar visual information alone, without extraretinal influences. The perception of a floor's position in an unfamiliar setting might be based on more general retinally-based information, while position of a light in an unstructured environment requires extraretinal information with little contribution of visual experience. At any moment, the relative weight given to the various potential information sources depends on their quality.

Our theory makes some predictions which, if falsified, would disprove it. The calibration theory requires no space-constant coding in the cortex, with neurons shifting their receptive fields for each new fixation. If a space-constant topographic map were found, and if removing it in animals prevented the animal from showing space constancy, our theory would be disproved. Alternatively, if a homologous field in a human patient were damaged neurologically, and the patient lost space constancy, the theory would also be disproved.

Conclusions

Our 'calibration' solution to the problem of visual stability differs from the a) elimination, b) translation, and c) evaluation solutions. In contrast to a), there is nothing "eliminated, cancelled, or subtracted". The correct spatiotopic positions are calculated anew with each fixation, using the currently available retinal and extraretinal information. Unlike b), we require no "more enduring higher order visual memory" into which retinal representations must be mapped. Position and identity are calculated separately. If this is done correctly, then there is no problem remaining because the currently avaliable information is used to perform the needed calibrations without reference to past information. And unlike c), there need be no "fixed map plus evaluation mechanism". The map changes from fixation to fixation, and positions are calibrated, but nothing is evaluated. Further, the necessary calibrations differ from one visual subsystem to another. The stability of the visual world despite eye movements, and other constancies, are consequences of correct space perception.

Our theory is the only one which does not require a space- constant representation of the visual world somewhere in the brain to support space- constant perception. Specialized space-constancy modules and extra neural machinery are unnecessary. The data of Irwin et al. (1990) provide direct psychophysical evidence that is consistent with our theory but not with any of the three other solutions. We can also explain how a person becomes oriented upon first opening the eyes in the morning, or opening the eyes in a new visual environment. Older theories, based on corrections between the previous fixation and the current one, never addressed this problem.

Seen in this light, the problem of perceptual stabilization across saccades is analogous to the old problem of why the world appears upright even though the retinal image is inverted. The inversion problem was never solved; rather, it was determined that the structure of the image, and not its retinal orientation, was crucial for accurate perception. A similar argument can be made for the location of the image in our case, with the addition that extraretinal as well as retinal signals contribute to location. Intermodal interaction as well as visual-motor coordination can be interpreted in this way. Eye-hand calibration for instance is performed on the basis of currently available information, without regard to previous saccades or other behaviors. The problem is even simpler because the appearance of retinal displacement is not relevant. In fact, for intermodal coordinations in perception there is probably no cross-modal integrating area (Hoerster, Rivers, Shuster, Ettlinger, Skreczek & Hesse 1989). The system needs no memory because only the current conditions are important. As Kinsbourne (1987) put it in another context, "It would be the pattern as a whole, rather than some bystanding area that observes it, that generates the experience and initiates the decisions" (p. 425).

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Figure Captions

Figure 1. Retinotopic and spatiotopic codes a) before and b) after a saccadic eye movement. At fixation N + 1 the image has shifted by 2 units to the right relative to the retina. The figure represents only one dimension of space.

Figure 2. Top: A summary of the "elimination" solution to the problem of visual direction constancy. In this and subsequent figures, a shift occurs from retinal location a to retinal location c. The box contains a retinal image abc; to maintain constancy following an eye movement (solid arrow), the elimination theory requires an efference copy (dashed arrow) equal and opposite to the retinal shift. In addition to efference copy, it is logically possible that muscle proprioception or other extraretinal sources of information could contribute to the dashed arrow.

Bottom: A summary of the "translation" solution. The image information is corrected at an intermediate stage by a composite signal consisting of efference copy and proprioception (dashed arrows) before being added to a space-constant store.

Figure 3. A summary of the unique aspects of the "evaluation" solution. Information is assigned to the correct location by its content, rather than by extraretinal signal corrections alone. The process is successful as long as the error in the overlap b is small.

Figure 4. An alternative, 'calibration' conception of the mechanism of visual direction constancy. The current fixation position is known by those levels of the system concerned with fixation control (solid arrows), but the information coded in successive fixations is related only by the correlation of the images themselves.

Figure 5. A 3-fold conception of visual stabilization from one fixation to the next, across a saccadic eye movement. Top: Outflow (efference copy), inflow (extraocular muscle proprioception), and saccadic suppression of image displacement (SSID) contribute to perceptual stabilization. Bottom: Timing of the contributions of the three components. These components serve principally to prevent perception of a jump of the visual world during the saccade; recalibration of direction is accomplished anew at the start of each fixation. Duration along the horizontal axis is 100 msec.