

Oxford Handbook on Eye Movements

Visual Stability

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Abstract

Space constancy, the perception that the visual world remains stable despite the fact that all visual information arrives through retinas that are in continuous motion, has historically been explained by an ‘efference copy’ of eye innervation that is subtracted from retinal image shifts. Quantitative work has found the efference copy to be too small and too slow to offer full compensation. A newer conception is that little is carried over from one fixation to the next; we do not build a visual world by pasting together samples calibrated with efference copy, but use what is currently available, plus a gist and a few previously attended objects. The stable, rich visual world of our perception is more promise than physiological reality.

Keywords

efference copy
corollary discharge
proprioception
space constancy
saccade

Everyone takes visual stability for granted – the idea that the visual world should seem to jump or jiggle with each movement of the eyes or of the head seems bizarre. Yet all visual information arrives in the brain through the retinas, and the images projected on the retinas are in nearly continuous motion. They are displaced with each saccadic (jumping) eye movement, and the images of the visual background sweep across the retinas when we track visual targets.

How does the brain accomplish the stabilization? This problem defines one of the fundamental accomplishments of visual perception: space constancy, the perception that the world remains stable and in a fixed position even as the eyes scan across it. The perception seems paradoxical. Yet perceiving a stable visual world establishes the platform on which all other visual functions rest, making possible judgements about the positions and motions of the self and of other objects.

Historically the problem of visual stability has been simplified to address only the mechanisms involved in perceiving a fixed visual world despite saccadic eye movements with a fixed head. More recently considerations of stability have expanded to include situations of locomotion, of tracking eye movements, and of tiny eye movements that occur during normal visual fixation. The problem of space constancy across saccades will be considered first.

History

By the mid-20th century it seemed that the problem of space constancy had been solved; the basic mechanism was known, and it remained only to find the physical substrate and clean up the details. The solution was a signal emanating from motor areas of the brain to inform the visual system about when and where the eyes had moved. At the time of an eye movement this signal could be subtracted from the resulting shift of the retinal image, achieving visual space constancy. Because the idea requires that the visual centers receive a copy of the neural efference to the eye muscles, it was named efference copy. It is also called ‘outflow’, because a signal flows out from the oculomotor centers to compensate for retinal image motion (Teuber, 1960). An extraretinal signal (Matin, 1972), it affects vision but does not originate from the retina.

The solution was a long time in coming, for ideas about something coming out of the brain, complementing what was coming in, go back to the ancient Greeks (Grüsser, 1986). Their idea was very different, though; for Aristotle, some sort of energy emanated from the eyes to allow vision to take place. Thinking that the eyes of animals seeming to glow in the dark were visible manifestations of such emanations, they concluded that the emanations interacted with objects in the world to mediate vision. This was evidence enough for the Greeks, though we know now that the glow of animal eyes in the dark is actually a reflection from a highly reflective layer behind the retinas of nocturnal creatures. Arab scholars followed the Greeks’ interpretation. Needless to say, such ideas did little to advance vision science. The first formal description of efference copy originated with the physiologist Charles Bell (1823/1974), who was already one of the era’s leading authorities on neuroscience. At about the same time Jan Purkinje (1825) also described the idea, apparently independently.

Both descriptions are based in part on perceptions that occur when the side of an eye is pressed with a finger. If the eye is pressed in darkness with an afterimage on the retina, the afterimage does not appear to move. An active eye movement, though, will result in apparent movement of the afterimage. Experience with a real image is just the reverse – it appears to move when the eye is pressed, but does not move with a voluntary eye movement. The experiments are so simple that the reader can verify the results personally. These four observations could be explained if an active eye movement elicited an extraretinal signal to compensate for the eye movement, but the eye press did not.

The explanation of these effects was taken as evidence for the efference copy. Failure of afterimage movement with the eye press in darkness would be inevitable, for the afterimage would remain fixed on the retina while the eye press did not elicit an extraretinal signal. The movement of the afterimage with an eye movement in otherwise dark surroundings could be explained only by an efference copy, for only the efference copy is changing in this condition. A normal eye movement in a normal environment would not elicit apparent motion because the efference copy would be matched by an equal and opposite retinal image motion. But the eye press in a normal environment would elicit apparent motion because the resulting retinal image motion would not be compensated by an extraretinal signal. The four conditions and their results are summarized in Table 1. The conditions in bold type result in space constancy, either with both efference copy and active eye movement, or with neither efference copy nor active eye movement. The other two conditions represent failure of space constancy because of a mismatch between efference copy and image movement.

	Retinal image motion	No retinal image motion
Efference copy	Normal eye movement	Afterimage with saccade
No efference copy	Eye press in normal field	Eye press in darkness

Table 1. Physical and perceptual conditions in eye press and eye movement.

The evidence seemed so convincing that for more than a century after this, efference copy was the major mechanism assumed to mediate space constancy. Both Bell and Purkinje went further to conclude that gaze movement signals cancelled retinal image displacements to achieve space constancy. Somewhere in the brain, signals representing change in position of a retinal image were subtracted from signals representing change in oculomotor innervation. Ewald Hering (1861/1990) further asserted that one should obtain compensation for voluntary eye movements but not for involuntary movements such as those generated during dizziness. These are the involuntary eye movements induced by continuing vestibular activity following sustained head rotation, accompanied by feelings of vertigo and perceived motion of the visual world. The breakdown in space constancy occurs because the eye movements are driven directly by the vestibular system, in a 3-neuron arc that does not activate the normal efference copy.

Hermann von Helmholtz assured the dominance of outflow mechanisms in explaining space constancy in his monumental *Physiological Optics* (1866/1962), then and now the most influential work in the field. He expanded the empirical base for outflow theories with observations of neurological patients collected by Albrecht von Graefe. These patients had damage to one or more eye muscles, so that they could not use part of their oculomotor

fields. When they attempted to look into the paralyzed field, the world seemed to jump in the direction of the intended movement, and pointing to a target in that direction went too far in the direction of the intended movement. In analyzing these observations Helmholtz extended the efference copy idea to include sensorimotor coordination as well as perception. The patient has two facts to evaluate, for example in pointing with a gaze that is paralyzed for movements to the right:

- 1) I am looking toward the right.
- 2) There is an image on my fovea (the fixational area of the retina).

The reasonable conclusion is that there is an image to the patient's right, though (due to the failure of the eyes to move) the patient's gaze has actually remained straight ahead. Helmholtz called this reasoning an 'unconscious inference', analogous to the processes of formal logic but executed effortlessly and without training. Pointing too far in the direction of the paretic field ('past pointing'), to the right in this case, shows that the patient has no information from eye muscle proprioception or any other source that might inform him of the actual gaze position. It is only the intended gaze position that affects perception and action. Helmholtz called the intention to change gaze position a 'Willensanstrengung', an effort of will, pointedly avoiding a mathematical or physiological interpretation of the signal.

The explanation is similar for the perception of a jump of the world in the direction of an intended eye movement. Before the intended jump there is an image on the fovea and a Willensanstrengung straight ahead. After the intended jump the eyes have not moved because of the paralysis, but the Willensanstrengung is now directed toward the right, and the same image is still on the fovea. The patient's quite reasonable conclusion is that the image has now jumped to the right, because eye position (as reported by Willensanstrengung) has changed but the retinal image position has not.

Helmholtz also gave four observations in normal subjects supporting his outflow theory: First, moving the eye passively results in apparent motion; second, moving the eye passively does not result in apparent motion of an afterimage; third, image displacement is compensated in normal saccades (space constancy); and fourth, that adaptation to displacing prisms transfers intermanually.

Perhaps because Helmholtz saw his eye movement signal as related to the will, he did not analyze it mathematically. Ernst Mach (1906), another physicist-physiologist, made that step by hypothesizing that a neuronal copy of eye muscle innervation sums algebraically with the retinal signal to yield a position of viewed objects relative to the head.

In 1950 two papers appeared that defined efference copy theory for the next generation. In fact the term 'efference copy' first appeared in a paper in German by Erich von Holst and Horst Mittelstaedt (1950) as 'Efferenzkopie'. This paper describes the results of an experiment inverting the head of the blowfly *Eristalis* by rotating its neck 180 deg and holding it there with a bit of wax (the blowfly has a very flexible neck).

Von Holst and Mittelstaedt observed that the fly would circle continually. When the fly was in darkness, though, its locomotion seemed normal. With light restored, the fly would circle either in the original direction or in the opposite direction at random. These results were explained with the assumption that the fly monitored the output of its locomotor system and compared that output with the retinal flow field (since the *Eristalis* eye is fixed to the head, and in the experiment also fixed to the body, the locomotor system is also the oculomotor system). The copy of locomotor efference, the 'Efferenzkopie,' would normally be subtracted from the retinal signal to stabilize locomotion by negative feedback. Inverting

the head converted the negative feedback to a positive feedback – a random nudge in one direction would feed back a signal to ‘correct’ in the same direction. That would result in a further deviation in the same direction, and continuous circling would result.

Von Holst and Mittelstaedt also contributed an engineering flow diagram and algebraic analysis, with the efference copy exactly cancelling the afferent retinal signal. This seminal paper also introduced the terms exafference, a retinal motion signal resulting from motion of objects in the world, and reafference, a retinal motion signal resulting from the organism’s movements.

Roger Sperry (1950) independently made similar observations in a fish whose eye he inverted surgically. He concluded that his fish’s normal swimming in the dark excluded the possibility of brain or nerve damage from the eye operation, and he introduced the term ‘corollary discharge’ to identify the efferent signal. These papers formalized the quantitative compensation idea that had dominated physiology and psychology for more than a century. The new evidence offered for the idea was motor rather than sensory in nature, an emphasis that would prove important in the coming decades, though some speculations about perception were made.

Visual Stability Across Saccadic Eye Movements

Though compensation theories completely dominated thinking about space constancy up to this point, there had always been some problems with them. Considerations from control theory, which had made rapid progress during World War II, made these problems clear. First, the efference copy is feedforward, a signal that informs the brain of where the eyes ought to be rather than where they actually are. As such it cannot be exact – it should drift with time, and could not be corrected when it is in error. Yet the perception of space constancy is perfect – the world does not appear to jump in the slightest when the eyes move. To the average person, the idea that the world should jump with each saccade seems bizarre at best. If perception is rock solid, but the efference copy is not, something else must be supplementing the feedforward signal. That something else might be all that is necessary to do the job, making the efference copy redundant for perception.

Ethyl Matin (1974), recognizing these arguments, proposed that saccadic suppression could mask the inevitable errors. It was known then that displacements of the entire visual world would not be detected perceptually if they occurred during saccadic eye movements (Wallach, 1965; Mack, 1970); if the imprecision of efference copy was less than the displacement thresholds during saccades, space constancy could be maintained despite small mismatches of efference copy and retinal displacement.

Though it was the best idea available at the time, Matin’s solution didn’t last long. The first parametric evaluation of saccadic suppression of displacement showed that at the optimal synchronization of image displacement and saccade, the perceptual threshold was nearly 1/3 as large as the saccade itself (Bridgeman, Hendry & Stark, 1975). Clearly, any visual orientation mechanism that tolerated an error of one part in three had no idea where the visual world was, and could support neither perceptual space constancy nor any reasonable visual-motor calibration. This result along with similar observations should have led to a capitulation of the efference copy theory, but it did not. The reason why is that a theory cannot be abandoned because of evidence; it can only be replaced by another theory,

and none was at hand. There was a realization, though, that efference copy would not be the answer to the space constancy question.

Other problems with the efference copy theory soon began to surface. One of them emerged from the technique of reverse modeling, applying an output (behavior) to a linear model and running the equations backward to read the input (nerve signals to the muscles) that must have been necessary to drive the behavior. Applied to the oculomotor system, reverse modeling was able to clarify the motor signals that drive ‘voluntary nystagmus’, a rapid oscillation of the eyes that can be performed by a small proportion of otherwise normal people. The oscillations are small in size, usually 3 deg. or less, but high in frequency, up to 20 alternations of eye motion per second. The resulting rotatory accelerations of the eye are so great that the oculomotor driving signals can be generated only by the brain’s saccadic controller. Even though the movements have a nearly sine-wave profile, they must be elicited by the pulse-step mechanism of saccades; the sinusoidal appearance is a result of temporal filtering by the eye itself and its motor apparatus.

All of this is relevant to the space constancy question because subjects experience oscillopsia, a back-and-forth fluttering of the visual world, during voluntary nystagmus. In short, space constancy breaks down. But normally, space constancy survives saccades, which are accompanied by saccadic suppression. What is going on? The possibility that small saccades do not elicit saccadic suppression was disproved by comparing suppression during voluntary nystagmus to suppression during single voluntary saccades matching the amplitude of nystagmus in the same observer (Nagle, Bridgeman & Stark, 1980). The suppression was virtually identical in both cases, demonstrating that space constancy does not necessarily accompany saccadic suppression. Further, an afterimage remained motionless during voluntary nystagmus (Table 2), showing that the changes of eye position failed to elicit changes in apparent position of a visible target fixed on the retina. Space constancy must use some other mechanism.

	Retinal image motion	No retinal image motion
Space constancy	Normal saccade	Nystagmus with afterimage
No space constancy	Nystagmus in normal field	Saccade with afterimage

Table 2. Physical and perceptual conditions in voluntary nystagmus.

The voluntary nystagmus experiment showed that single isolated saccades were accompanied by space constancy, while rapidly alternating saccades of the same size were not. Perhaps the space constancy mechanism was still operating, but could not keep up with the rapidly alternating saccades of voluntary nystagmus. Grüsser, Krizic & Weiss (1987) achieved a better temporal resolution of the constancy/frequency relationship in studies of the apparent movement of an afterimage with saccadic eye movements in darkness. They asked subjects to look from one loudspeaker to another, cued by tones from each speaker. After a bright light gave a lasting afterimage, eye movements were performed in darkness. The experimenters measured the subjects’ estimates of the spatial separation of the afterimages when the eye was aimed at the left speaker versus the right speaker. As saccades became more frequent, the subjective separation of the afterimages decreased until at the highest eye movement frequency (about 3.8 saccades/sec) the afterimage appeared to remain fixed in front of the subject. Space constancy had failed completely. The result showed that

the voluntary nystagmus frequency was far higher than space constancy could handle, and that perceptual compensation is quite slow. Even for inter-saccade intervals well within the temporal range of eye movements accompanying normal perception, the compensation was smaller than the saccade amplitudes.

A few years later, temporal properties of space constancy were linked directly with efference copy in experiments exploiting the deceptively simple maneuver of pressing with a finger on the outer canthus of the eye. Explaining the method in these experiments requires a brief diversion into methodology. The consequences of a gentle press on the outer edge of the eyelid have been misunderstood for centuries, since Purkinje's 1825 assumption that the press resulted in a passive eye movement. Helmholtz (1866) made the same assumption, that pressing on the eye moves it passively, and that the resulting experience of apparent motion originates from retinal image movement without an efference copy.

Two observations support this interpretation: First, the entire visual world appears to move in the direction opposite the eye press; and second, the eye of another person appears to move when it is observed during their eye press. The two observations are consistent with one another, but both are misinterpretations. The apparent motion is based on the assumption that there is motion on the retina, but the two kinds of motion are not necessarily linked. The real situation is easily demonstrated – simply pick a fixation target, then close one eye while slowly pressing on the outer canthus of the other. You will be able to hold your gaze on your fixation target, even while the entire visual world, fixation target and all, appears to move. This means that the retina is not moving with respect to the visual world.

Since motion is experienced despite lack of motion of the target on the retina, the motion must come from another source. That source originates with the activation of oculomotor tracking mechanisms, which cannot be turned off, keeping the eye on the fixation target despite the eye press. The effort requires oculomotor innervation, and with it a change in efference copy. Thus, far from demonstrating the effect of passive eye movement, the eye press actually demonstrates the effects of active compensation for oculomotor disturbance, and shows that efference copy alone can drive motion perception.

The observation that the eye of another person performing an eye press appears to move is also misinterpreted. What the observer sees in another person is not an eye rotation but a lateral translation of the eye in the orbit. The eye is influenced by two rotational forces in opposite directions; one originates from the pressing finger producing a nasalward rotational force; the other is an equal and opposite force generated by the eye muscle that normally rotates the eye away from the nose. The oculomotor innervation is driven by a small retinal motion initiated from the finger but compensated by the involuntary object tracking system. Thus the two rotatory forces cancel, and the eye does not rotate.

But each of these forces also moves the eye sideways in the medial direction, the finger pushing the front part of the eye nasalward and the eye muscle pulling the back part of the eye nasalward. The translational forces sum to move the eye several millimeters in the orbit, as measured in the laboratory (Stark & Bridgeman, 1983). Because the cue that humans use to perceive movements of the eyes of others is the amount of sclera visible on the two sides of the iris, the translational motion is misinterpreted by observers as a rotation. The rotation of the covered fellow eye, whose rotation is not cancelled by the eye press, provides an objective measure of the forces applied. We could now exploit the eye press technique, which changes the efference copy without changing the position of the image on the retina, to

measure the temporal aspects of efference copy. First, though, we needed some additional methods.

Normally eye movements are monitored by finding the position of the eye's pupil relative to the head, because the center of rotation of the eye remains constant. These methods cannot be used for measuring eye movements during an eye-press, however, because the whole eye is translating in the orbit. The alternative method uses tiny coils of fine wire embedded in a contact lens that fits tightly over the border between the iris of the eye and the white sclera. It was possible to use scleral 'search coils' in both eyes simultaneously, and also to press on the eye without popping out the contact lens (the experiment is not for the faint-hearted). Again the non-pressed eye is covered, so that its movements are measured in darkness. In this experiment we pressed repeatedly on the viewing eye in a roughly sine-wave pattern (Ilg, Bridgeman & Hoffmann, 1989), using a force transducer on the fingertip to provide an objective record of the frequency and timing of the eye-presses.

At low temporal frequencies the viewing eye did not rotate, replicating Stark & Bridgeman (1983). Only the covered eye rotated, under its occluder, revealing the compensatory eye muscle innervation; according to Hering's law (Hering, 1868), that innervation affects both eyes equally.

When we began pressing more rapidly on the eye, however, the compensation was no longer complete. At a rate of less than one eye-press per second the covered eye still rotated, but in addition the viewing eye rotated passively as it was repeatedly pressed and released. At the surprisingly low rate of two presses per second the covered eye ceased its rotation completely, and only the viewing eye rotated, in the passive manner that Purkinje and Helmholtz would have predicted.

These data implied that the motor compensation system ceases to function somewhere between these two rates. Thus any efference-copy based system that normally contributes to space constancy must cease to function at these rates, well within the temporal range of normal perception.

By 1989, then, evidence from a number of directions was converging on the idea that efference copy could not be responsible for space constancy. Its action was too slow, and its gain too low to support a perceptual compensation for eye movements. The theory continued to dominate, however, because no theory was available to replace it. Evidence of a more qualitative sort should also have eliminated efference-based theories from consideration, but did not, again because of the lack of an alternative theory.

One bit of evidence came from an experiment by Brune & Lücking (1969), who fed an eye movement signal into a mirror that moved an image with the eyes, but at variable gain (output/input). At low gains, when the image was moving one-tenth as far as the eye, the image appeared always to be stable, demonstrating saccadic suppression. But at a slightly higher gain, 'prominent objects' would seem to jump or jiggle with each saccade even while the world as a whole continued to appear stable. The efference copy theories, however, do not allow this possibility – the visual world is conceived as a monolithic object. The observation would seem to eliminate all efference copy and related theories in a single stroke. There are technical reasons, however, why this experiment might have resulted in dissociations for uninteresting reasons. The prominent objects might have been brighter than the background, for example, and therefore signals coding them would move through the visual system faster than the signals from dimmer parts of the image. In a continuously

moving environment, prominent objects would then be perceived in different locations than the background.

These possibilities were eliminated in an extension of the study that used images by the Dutch artist Maurits Escher as the stimulus materials. Escher used two repeated shapes that interlocked to completely cover a surface. For instance, devils and angels might cover a plane. Some subjects could selectively concentrate on just the angels, or just the devils, at will. All of those subjects saw slight movement of the attended figure while the 'background' figure remained stable, at a near-threshold feedback gain from eye movement to image movement (Bridgeman, 1981). Because this perception occurred for either figure, without any change in the stimulus, all image variables were controlled. Something was very wrong with compensation theories – none of them could account for this result.

Another method stems from an illusory motion. Normally the visual world remains quite stable, but observing a small bright dot in darkness results in the dot beginning to appear to wander slowly through the dark field. Space constancy in the efference copy theory, however, requires an extraretinal signal that is compared to whatever comes in through the retina, regardless of its structure or extent. This 'autokinetic' motion is thought to originate from noise in the vestibular system affecting eye movements through a vestibulo-ocular reflex that is not registered in perception (Leibowitz, Shupert, Post & Dichganz, 1983). The noise drives the eye away from a target, and pursuit eye movements, which are registered in perception, are required to cancel the eye drifts. In a full field, however, another motor reflex, which is also not registered in perception, stabilizes the eye relative to the visual field.

The observations can be made consistent with efference copy theory only if one assumes that some kinds of eye movements are accompanied by an efference copy while others are not. It then becomes impossible for any brain mechanism comparing efference copy and retinal input to know what head-centered position to assign to the retinal input (Bridgeman, 1995).

If the extraretinal signal theories have so many problems, what use are they? An answer came from quantitative work on the gains of the efference copy and of proprioceptive signals, coming from sensors in the eye muscles that report muscle length to the brain. The work again exploited the static eyepress technique, but with an additional twist. Pressing on the side of the viewing eye changed efference without changing gaze position, but pressing on the covered eye should change only proprioception. The argument is that the covered eye when pressed will rotate under the eyelid, because the press does not result in any corrective signal from error feedback. Since the proprioceptive signals from the two eyes are summed in the brain, the resulting binocular gaze signal would equal half of the deviation of the covered eye.

As infrared techniques had already been developed to monitor this eye position in darkness, the proprioception could be measured, and its effect on behavior could be assessed simultaneously by having subjects point to targets while eyepress deviates the covered eye. The situation in pressing the viewing eye is now more complicated, because the perceptual changes will result from a combination of two signals working in opposite directions. Proprioceptive signals will come from the deviated, covered eye, and altered efference copy will be driven by the active compensation for the press of the viewing eye (this analysis was suggested by Wenshun Li). With these improvements in the eyepress technique it became possible to quantify gains of both efference copy and proprioception. The internal signals could be recovered by algebraic rearrangement of the measured signals.

Careful measurements of perceptual deviations with various magnitudes of eye press on the viewing or the covered eye (Bridgeman & Stark, 1991) resulted in magnitudes of deviations that could be used to recover the internal proprioception and outflow signals. The resulting gains were 0.61 for efference copy and 0.26 for proprioception, a disturbing result because even with perfect summation of the two gains, the brain would underestimate how far the eye really moved. The efference copy gain is in general agreement with earlier estimates made with indirect methods.

There was still a 'missing' gain of 0.13. Where did it go? The answer came from data on perception of the deviation of an eccentric target from an observer's midline. Targets are perceived as more eccentric if their position is judged while looking at them through peripheral vision, with the eyes straight ahead, than if they are fixated with eccentric gaze (Morgan, 1978). This implies that eye deviations are registered as being smaller than the actual eccentricity of gaze. It was a simple matter to calculate the gain from her graph, and the result was 0.13, precisely the 'missing' gain from the eye press experiments. Efference copy, proprioception and illusion gains sum to 1.00, closing the circle on the signals used in registering eye gaze position and the resulting perceptions.

We can draw two conclusions from this work. First, proprioception and outflow gains are summed in the brain's calculation of eye eccentricity. Two centuries of work on efference copy and proprioception had led to the conclusion that efference copy dominates; we can now see that the reason for the apparent domination is that the efference copy gain is about 2.4 times greater than the proprioceptive gain. Thus efference copy explains a wide range of results and clinical observations better than proprioceptive input. Second, proprioceptive deviations are not compensated in eye posture. Presses on the covered eye are passive, resulting in no oculomotor compensation. The role of efference copy and of extraretinal signals generally, then, appears to be to inform the brain about static eye position during visual fixation, the time between saccades when the retina is transducing the visual world reliably. It does not support space constancy.

The efference copy was finally discarded only recently as a mechanism for space constancy, with a new theory reanalyzing the information that is carried over from one fixation to the next. The break came in 1992 when Kevin O'Regan asserted that it is not necessary to link successive images together – there need be no memory of the content of previous fixations, because the information remains in the world and can be re-acquired whenever the observer wants it. What the brain possesses is the presently available retinal information, and nothing more. This idea that memory across saccadic eye movements is in the world rather than in the brain turned out to be too radical, but not by much.

Two years later another reanalysis appeared, along with a critique of previous theories (Bridgeman, van der Heijden & Velichkovsky, 1994). According to this analysis three information sources are traditionally used to achieve space constancy: proprioception from eye muscles, efference copy, and retinal information. The work reviewed above, in addition to other physiological studies, converges on the conclusion that none of these sources by itself provides adequate information. Physiologically, we were already certain by then that no brain area contained a panoramic, high-acuity representation that corresponds to our perceptual experience. The experience had to come from something else, something not coded in a topographic visual map in the brain. The alternative was a 'calibration' solution: correct spatiotopic positions are calculated anew from proprioception, outflow and retinal sources for each fixation. There is no need to take previous fixational positions into account;

the world appears to be in the same place because nothing tells the brain that it isn't. The role of extraretinal signals during saccades, if any, is not to compensate the previous retinal position but to destroy it. Perception can then begin anew during the next fixation interval.

In a more specific elaboration of this idea, attention shifts to a reference object at the saccade target before a saccade is executed (Deubel, Bridgeman & Schneider, 2004). Due to the attention shift, location and visual attributes of the reference object and of surrounding objects are stored in transsaccadic memory. After the saccade, the visual system searches for the reference object within a restricted spatiotemporal "constancy window" which is about 50 ms in duration, and is confined to a few degrees around the saccade target. If the object is found, the world is assumed to be stable. Spatial information from the previous fixation is discarded or ignored, and localization proceeds using the currently available information. If no other prominent objects are in the region of the saccade landing point, even an object quite dissimilar to the original saccadic goal object will be accepted as the target if it is in the right position. Other objects in the visual field are then localized in terms of the position of the reference object. Only if the object is not found do outflow and other information sources come to bear. Extraretinal signals are used in static conditions, though, especially for controlling motor behavior (Bridgeman & Stark, 1991).

Evidence for this new position comes from a number of sources, the most dramatic being the demonstrations of change blindness, the inability of observers to identify changes in naturalistic scenes if the change in images is masked by a brief blank of 100 msec or even less, a 'flicker' paradigm (Simons, 1996; Rensink, O'Regan & Clark, 1997). The interruption need not blank the entire image; if a few 'mud splashes' provide visual transients simultaneous with the image change, the change becomes equally invisible (O'Regan, Rensink & Clark, 1999). Even the abrupt transient has been shown not to be necessary (Turatto, Betella, Umiltà & Bridgeman, 2003); an image can be ramped down from normal contrast to zero contrast in 1 sec, changed at the instant of zero contrast, and immediately ramped up again, the pattern repeating as in the flicker paradigm. Change blindness is just as strong as in the flicker paradigm, suggesting that it is the diversion of attention rather than abrupt image transients that underlie the effect.

The importance of change blindness for this review, then, is that a willful inattention to previous images prevents their interfering with present perception. This reanalysis posits that little is carried over from one fixation to the next; we do not build a visual world by pasting together samples calibrated with efference copy, but simply use what is currently available, plus a gist and a few previously attended objects. The stable, rich visual world of our perception is more promise than physiological reality.

Visual Stability Across Pursuit Eye Movements and Locomotion

The achievement of apparent visual stability of the world is fundamentally different during self-motion, and during the continuous tracking of moving objects, from the achievement of stability across saccadic eye movements, because saccadic suppression of vision cannot aid the process. Further, stabilizing mechanisms must operate continuously, rather than in short bursts as in the case of saccadic eye movements with a fixed head. As a result, qualitatively different mechanisms are involved in the continuous case than in the saccadic case.

Several characteristics of physiological optics, however, make the problem easier than it seems at first. Unlike the saccade case, where abrupt translation of the visual field is the only consequence of eye movement, a rich variety of transformations provides information about self-motion and motions of objects in the world. The process of differentiating shifts of retinal images from object motions begins in the retinal ganglion cells, some of which respond to differences between motion in the receptive field center and periphery (Ovliczky, Baccus & Meister, 2003). An example at higher levels is looming of the visual image, where all points in the image undergo a retinal motion away from a single point, which is the point toward which the observer is moving. Looming always specifies movement of the observer, never of the environment, and therefore is always interpreted by the brain as an indication of self-motion (Gibson, 1966). If the observer is fixating in the direction of locomotion, distance of objects in the world can also be inferred from looming because the sweep of objects across the retina is faster as they grow nearer. For a given retinal eccentricity of a target, the sweep speed on the retina also specifies the distance of that target once the distance to any point in the field (such as the distance to the feet) is known (Nakayama, 1990).

The looming situation becomes more complicated if the observer is tracking a target that is offset from the direction of motion. In that case the tracked target does not sweep across the retina (because of pursuit eye movements), but looming will occur for all other parts of the retinal array. The geometry of the looming pattern is slightly different from the case of looming from the direction of motion, but the differences are subtle if the target is not far from the direction of motion. In the extreme case of fixating sideways from the direction of motion the pattern of retinal sweep becomes a horizontal sweeping pattern rather than a diverging one, with objects nearer than the fixated target moving faster on the retina, and more distant objects moving more slowly. This sort of pattern is seen for instance when looking out a train window. There is a controversy about whether an efference copy signal is necessary or is used to disambiguate the direction of motion for fixation on slightly eccentric targets.

The family of continuous image transformations that takes place does not specify whether motion belongs to the observer, the world, or some combination of the two. Looming, for instance, might originate from self-motion or from the entire visual world moving toward the observer. Because the latter condition occurs only in the laboratory, however, looming of the entire visual field is invariably interpreted by the visual brain as self-motion. This interpretation is the source of illusions of self-motion, for instance in films, video games or amusement parks.

Similar illusions of motion occur for continuous unidirectional motion of the entire visual field, interpreted by the brain as translation of the body with respect to the visual texture. Using the algorithms reviewed here, the visual system is continually distinguishing motion of objects in the world from motion of the self. Space constancy is an achievement of the visual brain, not simply a lack of perception of motion of the world.

References

- Bell, C. (1823) Idea of a new anatomy of the brain. In *Francois Magendie, Charles Bell and the Course of the spinal Nerves*, P. Cranefield, Ed. Mt. Kisco, NY: Futura, 1974.
- Bridgeman, B. (1981) Cognitive Factors in Subjective Stabilization of the Visual World. *Acta Psychologica*, 48, 111-121.
- Bridgeman, B. (1995) Extraretinal signals in visual orientation. In W. Prinz and B. Bridgeman (Eds.), *Handbook of Perception and Action Vol. 1: Perception*. London: Academic Press.
- Bridgeman, B. (1981) Cognitive Factors in Subjective Stabilization of the Visual World. *Acta Psychologica*, 48, 111-121.
- Bridgeman, B., Hendry, D., and Stark, L. (1975) Failure to detect displacement of the visual world during saccadic eye movements. *Vision Research*, 15, 719-722.
- Bridgeman, B., van der Heijden, A.H.C., and Velichkovsky, B. (1994) Visual stability and saccadic eye movements. *Behavioral and Brain Sciences*, 17, 247-258.
- Bridgeman, B. and Stark, L. (1991) Ocular proprioception and efference copy in registering visual direction. *Vision Research*, 31, 1903-1913.
- Brune, F. and Lücking, C. (1969) Okulomotorik, Bewegungswahrnehmung und Raumkonstanz der Sehdinge. *Der Nervenarzt*, 240, 692-700.
- Deubel, H. Bridgeman, B. & Schneider W. X. (2004) Different effects of eyelid blinks and target blanking on saccadic suppression of displacement. *Perception & Psychophysics*, 66, 772-778.
- Gibson, J. J. (1966) *The Senses Considered as Perceptual Systems*. Boston: Houghton-Mifflin.
- Grüsser, O.-J. (1986) Interaction of efferent and afferent signals in visual perception. A history of ideas and experimental paradigms. *Acta Psychologica*, 63, 3-21.
- Grüsser, O.-J., Krizic, A. and Weiss, L.-R. (1984) Afterimage movement during saccades in the dark. *Vision Research*, 27, 215-226.
- Helmholtz, H. von (1866) *Handbuch der physiologischen Optik*. Leipzig, Voss.
- Ilg, U., Bridgeman, B., and Hoffman, K.-P. (1989) Influence of mechanical disturbance on oculomotor behavior. *Vision Research*, 29, 545-551.
- Leibowitz, H. W., Shupert, C. L., Post, R. B. & Dichgans, J. (1983) Autokinetic drifts and gaze deviation. *Perception & Psychophysics*, 33, 455-459.
- Mach, E. (1906) *Die Analyse der Empfindungen und das Verhältnis des Physischen zum Psychischen*, 5th edition. Jena, Fischer.
- Mack, A. (1970) An investigation of the relationship between eye and retinal image movement in the perception of movement. *Perception & Psychophysics*, 8, 291-298.
- Matin, E. (1974) Saccadic suppression: A review and an analysis. *Psychological Bulletin*, 81, 899-917.
- Matin, L. (1972) Eye movements and perceived visual direction. In *Handbook of Sensory Physiology*, vol. 7 part 3, D. Jameson and L. Hurvich, Eds. New York: Springer, pp. 331-380.
- Morgan, C. L. (1978) Constancy of egocentric visual direction. *Perception and Psychophysics*, 23, 61-68.

- Nagle, M., Bridgeman, B., and Stark, L. (1980) Voluntary nystagmus, saccadic suppression, and stabilization of the visual world. *Vision Research*, 20, 1195-1198.
- Nakayama, K. Properties of early motion processing: Implications for the sensing of ego motion. In R. Warren and A. H. Wertheim (Eds.), *The Perception and Control of Self Motion*. Lawrence Erlbaum, Hillsdale, NJ pp. 69-80 1990.
- Olveczky, B., Baccus, S. and Meister, M. (2003) Segregation of object and background motion in the retina. *Nature*, 423, 401-408.
- O'Regan, J. K., Rensink, R. A., & Clark, J. J. (1999) Change-blindness as a result of "mud-splashes". *Nature*, 398, 34.
- Purkinje, J. (1825) Über die Scheinbewegungen, welche im subjectiven Umfang des Gesichtsinnes vorkommen. *Bulletin der naturwissenschaftlichen Sektion der Schlesischen Gesellschaft*, 4, 9-10.
- Rensink, R. A., O'Regan, J. K., & Clark, J. J. (1997). To see or not see: The need for attention to perceive changes in scene. *Psychological Science*, 8, 368-373.
- Simons, D. J. (1996). In sight, out of mind: when object representation fails. *Psychological Science*, 7, 301-305.
- Sperry, R. (1950) Neural basis of the spontaneous optokinetic response produced by visual inversion. *Journal of Comparative and Physiological Psychology*, 43, 482-489.
- Stark, L. and Bridgeman, B. (1983) Role of corollary discharge in space constancy. *Perception and Psychophysics*, 34, 371-380.
- Teuber, H.-L. (1960) Perception. In *Handbook of Physiology*, sect. 1; *Neurophysiology*, vol. 3, J. Field and H. Magoun, Eds. Washington, DC: American Physiological Society, , pp. 1595-1668.
- Turatto, M., Betella, S., Umiltà, C. and Bridgeman, B. (2003) Perceptual conditions necessary to induce change blindness. *Visual Cognition*, 10, 233-255.
- von Holst, E., and Mittelstaedt, H. (1950) Das Reafferenzprinzip. Wechselwirkungen zwischen Zentralsystem und Peripherie. *Naturwissenschaften*, 27, 464-476.
- Wallach, H., and Lewis, C. (1965) The effect of abnormal displacement of the retinal image during eye movements. *Perception & Psychophysics*, 81, 25-29.

