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## Space constancy: the rise and fall of perceptual compensation

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### Summary

Information about eye position comes from efference copy, a record of the innervation to the extraocular muscles that move the eye and proprioceptive signals from sensors in the extraocular muscles. Together they define extraretinal signals and indicate the position of the eye. By pressing on the eyelid of a viewing eye, the extraocular muscles can be activated to maintain a steady gaze position without rotation of the eye. This procedure decouples efference copy from gaze position, making it possible to measure the gain of the efference copy signal. The gain is 0.61; the gain of oculomotor proprioception, measured by a similar eye press technique, is 0.26. The two signals together sum to only 0.87, leading to the conclusion that humans underestimate the deviations of their own eyes and that extraretinal signals cannot be the mechanisms underlying space constancy (the perception that the world remains stable despite eye movements). The underregistration of eye deviation accounts quantitatively for a previously unexplained illusion of visual direction. Extraretinal signals are used in static conditions, especially for controlling motor behavior. The role of extraretinal signals during a saccade, if any, is not to compensate the previous retinal position but to destroy it. Then perception can begin with a clean slate during the next fixation interval.

### 7.1 Introduction

All visual information arrives in the brain through the retinas, whose images are displaced with each eye movement. Yet we perceive a stable visual world. 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 fixed even as the eyes scan across it. Perceiving a stable visual world establishes the platform on which all other visual function rests, making possible judgments about the positions and motions of the self and of other objects. The perception seems paradoxical.

A half-century ago, it seemed that the problem of space constancy had been solved; the basic mechanism was known, and it remained only to find the physiological 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 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 is now called efference copy. The efference copy is an extraretinal signal (Matin 1972) affecting vision but not originating from the retina. It is also called “outflow” because a signal flows out from the oculomotor centers to compensate for retinal image motion (Teuber 1960).

The solution was a long time coming; ideas about something coming out of the brain, complementing what was coming in, go back to the ancient Greeks (Grüsser 1986a). 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 was a visible manifestation of such emanations, they concluded that the emanations interacted with objects in the world to mediate vision. Arab scholars followed this interpretation. Needless to say, such ideas did little to advance vision science.

## 7.2 Early formulations

The efference copy idea originated with the physiologist Charles Bell (1823/1974), who had already discovered the Bell/Magendie law of separated afferents and efferents in the spinal cord. At about the same time 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, no motion of the afterimage is perceived. 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. These four observations could be explained if an active eye movement elicited an extraretinal signal to compensate for eye movement, but the eye press did not.

The 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 changes in this condition. A normal eye movement in a normal environment would not elicit apparent motion because the retinal image motion would be matched by the efference copy. But the eye press in a normal environment would elicit apparent motion because the resulting retinal image motion would not be compensated by the extraretinal signal.

The four conditions are neatly explained with a single theory summarized in Table 7.1. 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.

Both Bell and Purkinje went further to conclude that gaze movement signals canceled retinal image displacements to achieve space constancy. Somewhere in the brain, signals

Table 7.1

	Retinal Image Motion	No Retinal Image Motion
Efference copy	<b>Normal eye movement</b>	Afterimage with saccade
No efference copy	Eye press in normal field	<b>Eye press in darkness</b>

representing change in position of a retinal image were subtracted from signals representing change in oculomotor innervation.

### 7.2.1 *The founding of physiological optics*

For more than a century after this, efference copy was the major mechanism assumed to mediate space constancy. Hering (1861/1990) further asserted that one should obtain compensation for voluntary eye movements but not for involuntary movements such as vestibular afternystagmus. These are the involuntary eye movements induced by continuing vestibular activity following sustained head rotation, accompanied by feelings of dizziness 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 three-neuron arc that does not activate the normal outflow signal.

The dominance of outflow mechanisms in explaining space constancy was assured by von Helmholtz in his *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 muscle pareses so that they could not use part of their oculomotor fields. When they attempted to look into the parietic 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 von 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, although due to failure of the eyes to move, the gaze has actually remained straight ahead. Von 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 parietic 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. Von

Helmholtz called the intention to change gaze position a “Willensanstrengung,” an effort of will.

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 paresis, but the Willensanstrengung is now directed toward the right, and the same image is still on the fovea. The 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.

Von 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); fourth, adaptation to displacing prisms transfers intermanually. However, perhaps because von Helmholtz saw his eye movement signal as related to the will, he did not analyze it mathematically. Mach (1906), another physicist–physiologist, made that step by hypothesizing that a neuronal copy of oculomotor efference sums algebraically with the retinal signal to yield a position of viewed objects relative to the head. The first flow diagrams to define the concept came from von Uexküll (1920, 1928), who foreshadowed later mathematical analyses by differentiating efference copy from eye muscle proprioception and describing the consequences of each.

### 7.2.2 *Mathematical theories and the modern era*

Two papers appeared independently in 1950 that defined efference copy theory for the next generation. In fact the phrase “efference copy” first appeared in an article in German by Erich von Holst and Horst Mittelstaedt (1950) as “Efferenzkopie.” This was an empirical article, describing the results of 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. The results compared that output with the retinal flow field (because the *Eristalis* eye is fixed to the head, the locomotor system is also the oculomotor system). The copy of locomotor efference, the “Efferenzkopie,” would be subtracted from the retinal signal to stabilize locomotion by negative feedback. Inverting the head converted the negative feedback to 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 canceling the afferent retinal signal (Fig. 7.1). This seminal article also introduced the terms exafference, a retinal motion signal resulting

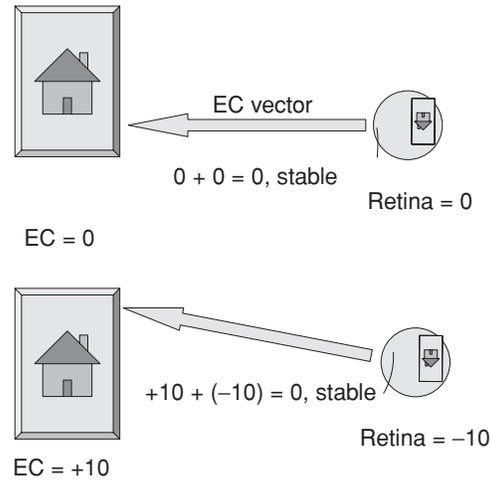


Fig. 7.1 Perceptual compensation by efference copy (EC). The EC, expressed as innervations to the six extraocular muscles controlling each eye, can be conceived as a vector along the line of sight. Top: The eye in primary position receives an image of the world. Bottom: The eye moves up 10 deg. As it does so, the EC indicates a 10-deg upward deviation and the retinal image shifts by 10 deg. The two signals of equal magnitude cancel, resulting in constant apparent position.

from motion of objects in the world, and reafference, a retinal motion signal resulting from the organism's movements.

Sperry (1950) 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 and introduced the term "corollary discharge" to identify the efferent signal.

These articles 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.

### 7.3 Problems with compensation theories

Though compensation theories completely dominated thinking about space constancy to this point, there had always been problems with them. Considerations from control theory, which had made rapid progress during World War II, made these problems clear.

#### 7.3.1 Spatial problems

First, the efference copy is a 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 it is not 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

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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, and that something else might be all that is necessary to do the job.

Recognizing that efference copy could not be perfect, E. Matin (1974) 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 & Lewis 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.

Matin's solution was the best idea available at the time, but it didn't last long. The first parametric description of saccadic suppression of displacement showed that at the optimal timing of image displacement and saccade, the perceptual threshold was about one-third as large as the saccade itself (Bridgeman et al. 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 a 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.

### 7.3.2 *Temporal problems*

Before long, other problems with the efference copy theory began to surface. One of them began with 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) 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 amplitude, usually 3 deg or less, but high in frequency, up to 20 Hz in most cases. The resulting rotational accelerations of the eye are so great that the oculomotor driving signals can be generated only by the saccadic controller. Even though the movements have a nearly sinusoidal profile, they must be elicited by the pulse-step mechanism of saccades; the sinusoidal appearance is a result of temporal filtering by the oculomotor plant. 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 Nagle et al. (1980), who compared suppression during

Table 7.2

	Retinal Image Motion	No Retinal Image Motion
Space constancy	<b>Normal saccade</b>	<b>Nystagmus with afterimage</b>
No space constancy	Nystagmus in normal field	<b>Saccade with afterimage</b>

voluntary nystagmus to suppression during single voluntary saccades matching the amplitude of nystagmus in the corresponding subject. The suppression was virtually identical in both cases, demonstrating that saccadic suppression does not necessarily accompany space constancy. Further, an afterimage remained motionless during voluntary nystagmus (Table 7.2), showing that the changes of eye position failed to elicit changes in apparent position. Space constancy must use some other mechanism.

The voluntary nystagmus experiment showed that single isolated saccades were accompanied by space constancy, whereas rapidly alternating saccades of the same size were not. Perhaps the space constancy mechanism was still operating but could not keep up with rapidly alternating saccades of voluntary nystagmus. Grüsser et al. (1984) achieved a better temporal resolution of the constancy/frequency relationship in studies of the apparent movement of an afterimage with saccades in darkness. They asked subjects to make saccades from one loudspeaker to another, cued by tones from each speaker. After a bright light gave a lasting afterimage, saccades were performed in darkness. Grüsser et al. 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 became smaller and smaller, until at the highest saccade 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 voluntary nystagmus frequency was far higher than space constancy could handle and that perceptual compensation is quite slow. Even for intersaccade intervals well within the temporal range of saccades accompanying normal perception, the compensation was much smaller than the saccade amplitudes.

The temporal properties of space constancy were linked directly with efference copy a few years later in experiments exploiting the deceptively simple maneuver of pressing 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, as reviewed above. Von Helmholtz (1866) made the same assumption, that pressing on the eye moves it passively, and that the resulting 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

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during their eye press. The two observations are consistent with one another, but both are misinterpretations.

The apparent movement is based on the inference of motion of the retina, but the two kinds of motion are not necessarily linked. The real situation is easily demonstrated – simply pick a fixation target, then slowly press on the outer canthus of one eye while closing the other. You will find that you can 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 at all with respect to the visual world.

If the motion is not coming from retinal slip, it must come from another source. That source originates with the successful effort of oculomotor tracking mechanisms, which cannot be turned off, in keeping the eye on the fixation target despite the eye press. The effort requires oculomotor innervation, and with it a change in efference copy. Far from demonstrating the effect of passive eye movement, the eye press demonstrates the effects of active compensation for oculomotor disturbance and shows that efference copy alone can drive the perception of motion.

The second misinterpreted observation is that the eye of another person performing an eye press appears to move. What the observer sees, however, 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 nasal-ward rotational force, and the other is an equal and opposite force generated by the lateral rectus muscle. The oculomotor innervation is driven by a retinal slip initiated from the finger but compensated by an involuntary optokinetic tracking system. Thus the two rotational forces cancel, and the eye does not rotate.

But each of these forces also introduces a translational component in the medial direction, the finger pushing the anterior part of the eye nasal-ward and the lateral rectus pulling the posterior part of the eye nasal-ward. The translational forces sum to move the eye several millimeters in the orbit, as measured experimentally (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 occluded fellow eye, whose rotation is not canceled by the eye press, provides an objective measure of the forces applied.

Now the eye press technique, which causes a deviation in efference copy without a change in retinal image position, can be applied to the problem of measuring the temporal aspects of efference copy. It was possible to use scleral search coils in both eyes simultaneously, and also to press on the eye without popping out the required scleral contact lens (the experiment is not for the fainthearted). Again the nonpressed eye is occluded so that its movements are measured in darkness. In this experiment, extending the static experiments of Stark and Bridgeman (1983), we pressed repeatedly on the viewing eye in a roughly sinusoidal pattern (Ilg et al. 1989). Adding to the complexity of the setup, a force transducer on the fingertip provided an objective record of the frequency and timing of the eye presses.

Replicating Stark and Bridgeman (1983), we found that at low temporal frequencies the viewing eye does not rotate. Only the occluded eye rotates, under its occluder, revealing

the compensatory oculomotor 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 1 Hz the occluded eye still rotated, but in addition the viewing eye rotated passively as it was repeatedly pressed and released. At the surprisingly low rate of 2 Hz, the occluded eye ceased its rotation completely, and only the viewing eye rotated in the passive manner that Purkinje and von Helmholtz would have predicted. Interpolation of our data implied that the oculomotor compensation system ceases to function at about 1–1.5 Hz. The implication is that any efference copy-based system that normally contributes to space constancy must cease to function at these relatively low rates, well within the bandpass of normal perceptual events.

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.

There was also a more qualitative sort of evidence that should have eliminated efference-based theories from consideration, but did not, again because of the lack of an alternative. One bit of evidence came from an experiment on saccadic suppression by Brune and 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, replicating the findings of Bridgeman et al. (1975). But at a slightly higher gain, when the world as a whole continued to appear stable, “prominent objects” would seem to jump or jiggle with each saccade. The efference copy theories, however, do not allow the possibility that parts of the image can move relative to one another – 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 the Brune and Lücking 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 at a faster rate than signals from dimmer parts of the image. In a continuously moving environment, this might result in prominent objects being perceived in different locations than the context. Another possible artifact is that the prominent objects might have been fixated so that signals from them would course through the visual system in slower, high-acuity channels. Again, relative mislocalizations might result.

All of these possibilities were eliminated in a replication and extension of the study that used tessellations of a plane by the Dutch artist Maurits Escher as the stimulus materials (Bridgeman 1981). Escher used two repeated shapes that interlocked to completely cover a surface. For instance, devils and angels might tessellate 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. Because this perception occurred with both figures, without any change in the stimulus, all image

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variables were controlled. Something was wrong with compensation theories – none of them could account for this result.

Another observation, one that had been known since the nineteenth century, is “autokinetic” motion of a small bright dot in darkness. Normally the visual world remains quite stable, but after a few seconds the small dot begins to appear to wander slowly through the dark field. No compensation theory can account for this observation, for these theories require an equal quality of constancy regardless of image properties. Space constancy in the efference copy theory requires an extraretinal signal that matches whatever comes in through the retina, regardless of structure or extent.

Autokinetic motion is now thought to originate from noise in the vestibular system affecting eye movements through a vestibulo-ocular reflex not registered in perception (Leibowitz et al. 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, the optokinetic reflex, which is also not registered in perception, can stabilize the 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 is the use of the extraretinal signals? An answer came from quantitative work on the gains of the efference copy and proprioception signals, building on a half-century of investigations of these signals. The work again exploited the static eye press technique, but with an additional twist. Pressing on the side of the viewing eye changed efference without changing gaze position, but pressing on the occluded eye should change only proprioception. The argument is that the occluded eye when pressed will be forced to rotate under the eyelid because the press does not result in any corrective signal from error feedback. If the proprioceptive signals from the two eyes are summed in the brain (as they must be according to Hering’s law), the resulting binocular gaze signal would equal half the deviation of the occluded eye (Fig. 7.2).

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 eye press deviates the occluded 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, occluded 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 eye press technique it became possible to quantify gains of both outflow and inflow in normal observers in the same experiment. The internal signals could be recovered by algebraic rearrangement of the measured signals (Bridgeman & Stark 1991). Careful measurements of perceptual deviations with various magnitudes of eye press on the viewing or the occluded eye resulted in magnitudes of deviations that could be used

*I Space-time during action*

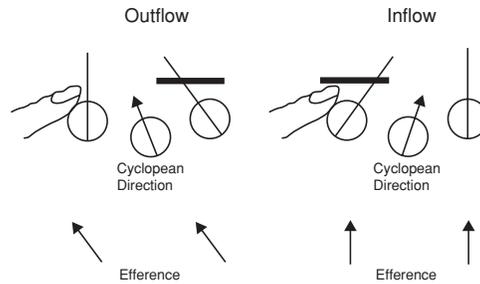


Fig. 7.2 Manipulation of outflow and inflow signals with monocular eye press in monocular viewing. Left: In the outflow condition the viewing eye is pressed, resulting in a compensatory efference (and EC). The cyclopean direction is half of the deviation of the occluded eye because the cyclopean signal is averaged with the undeviated viewing eye. Right: In the inflow condition the occluded eye is pressed, and it deviates mechanically because there is no visual error signal to correct gaze posture. Efference does not change. Again, cyclopean direction, and proprioceptive signal, equals half the eye's deviation.

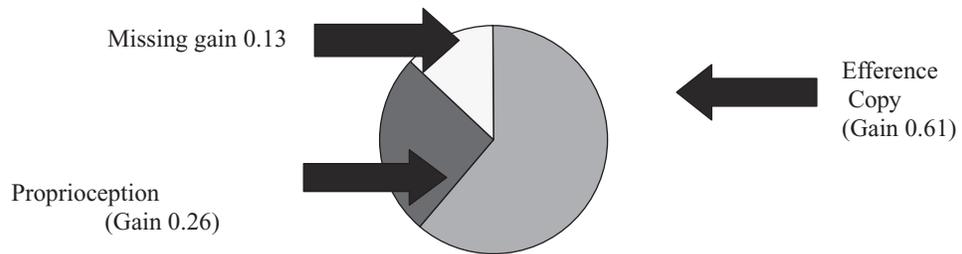


Fig. 7.3 Gains of efference copy and proprioception sum to 0.87, leaving an underregistration of 0.13 that is the origin of an eccentric-gaze illusion.

to recover the internal inflow and outflow signals. The resulting gains were 0.61 for outflow and 0.26 for inflow, a disturbing result because even with perfect summation of the two gains the brain would underestimate how far the eye really moved. There was a “missing” gain of 0.13 (Figure 7.3). Where did it go?

The answer came from an earlier study of the 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 first (Morgan 1978). This implies that eye deviations are registered as being smaller than the actual eccentricity of gaze. Quantifying these observations, Morgan drew a graph of her results but did not go further. 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. Outflow, inflow, and illusion gains sum to 1.00, closing the circle on the signals used in registering eye gaze position and the resulting perceptions.

As a result of this quantitative accounting for the eccentric-gaze illusion, we can draw several previously unrealized conclusions. First, inflow and outflow gains are summed in the brain's calculation of eye eccentricity. Two centuries of work on efference copy and proprioception 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 much higher than the proprioceptive gain, about 2.4 times greater. 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 occluded 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.

#### 7.4 Modern alternatives for space constancy

Despite all of the difficulties with it, efference copy was discarded only recently as a mechanism for space constancy, with a new theory centered on a reanalysis of what information 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 reacquired whenever the observer wants it. What the brain possesses is currently available retinal information and nothing more. This idea, that transsaccadic memory 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 et al. 1994a,b). According to this analysis three information sources are traditionally used to achieve space constancy: proprioceptive inflow from eye muscles, efference copy outflow, 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, by then we did not know all of the details of the dozens of visual areas in the brain, but we did know enough to be certain that no area contained the panoramic, high-acuity representation of our perceptual experience. The experience had to come from something else, something not coded in a topographic visual map in the brain.

Three solutions to the problem of space constancy have been proposed: the elimination, translation, and evaluation solutions. Physiological and psychophysical evidence allows us to reject all three – no subtraction, compensation, or evaluation need take place. Bridgeman et al. (1994a) offered an alternative “calibration” solution: correct spatiotopic positions are calculated anew from inflow, 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 visual system that it isn't still in the same place. The role of extraretinal signals during saccades, if any, is not to compensate the previous retinal

position but to destroy it. Then perception can begin anew with a clean slate during the next fixation interval.

According to a more specific elaboration of this new interpretation, attention shifts to a reference object at the saccade target before a saccade is executed (Deubel et al. 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 currently available information. If no other prominent objects are in the region of the saccade landing point, even an object dissimilar to the original saccadic goal object will be accepted as the target if it is in the right position. The positions of other objects in the visual field are then interpreted 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.

The more radical part of 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 (Irwin, Hollingworth, pers. com.). The stable, rich visual world of our perception is more promise than physiological reality. 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 less, a “flicker” paradigm (Simons 1996; Rensink et al. 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 et al. 1999). Even the abrupt transient has been shown not to be necessary (Turatto et al. 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 masking transients that underlie the effect.

The importance of change blindness for this article, then, is that a willful inattention to previous images prevents their interfering with present perception. This is the final solution to the space constancy problem.

## References

- Bell, C. (1823). Idea of a new anatomy of the brain. In P. Cranefield (ed.), *Francois Magendie, Charles Bell and the Course of the Spinal Nerves*. Mt. Kisco, NY: Futura, 1974.

- Bridgeman, B. (1981). Cognitive factors in subjective stabilization of the visual world. *Acta Psychol* **48**: 111–121.
- Bridgeman, B. (1995). Extraretinal signals in visual orientation. In W. Prinz & B. Bridgeman (eds.), *Handbook of Perception and Action Vol. 1: Perception*. London: Academic Press.
- Bridgeman, B., Hendry, D., & Stark, L. (1975). Failure to detect displacement of the visual world during saccadic eye movements. *Vision Res* **15**: 719–722.
- Bridgeman, B., & Stark, L. (1991). Ocular proprioception and efference copy in registering visual direction. *Vision Res* **31**: 1903–1913.
- Bridgeman, B., van der Heijden, A. H. C., & Velichkovsky, B. (1994a). Visual stability and saccadic eye movements. *Behav Brain Sci* **17**: 247–258.
- Bridgeman, B., van der Heijden, A. H. C., & Velichkovsky, B. (1994b). How our world remains stable despite disturbing influences. *Behav Brain Sci* **17**: 282–292.
- Brune, F., & 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.
- Grüsser, O.-J., Krizic, A. & Weiss, L.-R. (1984). Afterimage movement during saccades in the dark. *Vision Res* **27**: 215–226.
- Helmholtz, H. von (1866). *Handbuch der Physiologischen Optik*. Leipzig: Voss.
- Ilg, U., Bridgeman, B., & Hoffman, K.-P. (1989). Influence of mechanical disturbance on oculomotor behavior. *Vision Res* **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 ed.).
- 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. *Psychol Bull* **81**: 899–917.
- Matin, L. (1972). Eye movements and perceived visual direction. In D. Jameson & L. Hurvich (eds.), *Handbook of Sensory Physiology* (331–380, vol. 7, part 3). New York: Springer.
- Morgan, C. L. (1978). Constancy of egocentric visual direction. *Perception & Psychophysics* **23**: 61–68.
- Nagle, M., Bridgeman, B., & Stark, L. (1980). Voluntary nystagmus, saccadic suppression, and stabilization of the visual world. *Vision Res* **20**: 1195–1198.
- 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. *Psychol Sci* **8**: 368–373.
- Simons, D. J. (1996). In sight, out of mind: When object representation fails. *Psychol Sci* **7**: 301–305.
- Sperry, R. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *J Comp Physiol Psychol* **43**: 482–489.

- Stark, L., & Bridgeman, B. (1983). Role of corollary discharge in space constancy. *Perception & Psychophysics* **34**: 371–380.
- Teuber, H.-L. (1960). Perception. In J. Field & H. Magoun (eds.), *Handbook of Physiology*, sect. 1; *Neurophysiology*, vol. **3** (1595–1668). Washington, DC: American Physiological Society.
- Turatto, M., Betella, S., Umiltà, C., & Bridgeman, B. (2003). Perceptual conditions necessary to induce change blindness. *Visual Cognition* **10**: 233–255.
- von Helmholtz, H. (1866). *Handbuch der physiologischen Optik*. Leipzig: Voss.
- von Holst, E., & Mittelstaedt, H. (1950). Das Reafferenzprinzip. Wechselwirkungen zwischen Zerkelnervensystem und Peripherie. *Naturwissenschaften* **27**: 464–476.
- Wallach, H., & Lewis, C. (1965). The effect of abnormal displacement of the retinal image during eye movements. *Perception & Psychophysics* **81**: 25–29.