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Efference copy and its limitations

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Abstract

Efference copy, an internal brain signal informing the visual system of commands to move the eye, was the dominant explanation for visual space constancy for over a century. The explanation is not viable, however; the signal is to small, to slow, and too unreliable to support the perception of perfect constancy. Newer theories recognize that detailed image information does not survive refixation in any case. Efference copy is a viable explanation of static position perception and sensorimotor interaction, but the rich, stable visual world is an illusion.
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1. Introduction

Perceiving a stable visual world establishes the basis for all other visual function, but the perception seems paradoxical because all of the visual information that we acquire comes through retinal images that jump with each eye movement. There are two components to the space constancy issue. One relates to the non-experience of the actual track of the image across the retina of the moving eye, while the other relates to the perception of target position relative to the body of the observer. Explanatory mechanisms for these components of space constancy may, of course, differ.

A half-century ago the first problem had not yet been recognized, and it seemed that the second problem of space constancy had been solved with 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 space constancy. The idea is now called efference copy, an extraretinal signal [1] affecting vision but not originating at the retina. It is also called 'outflow', because a signal flows out from the oculomotor centers [2].

2. History

The first explicit formulations of the efference copy idea originated with Bell in 1823 [3] and Purkinje in 1825 [4], who apparently described the idea independently. Both descriptions are based in part on perceptions that occur when the side of an eye is pressed with a finger, a technique introduced by Descartes in the 17th century. 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 observations could be explained if an active eye movement elicited an extraretinal signal to compensate for the eye movement, but the eyepress did not. The afterimage fails to move with the eyepress in darkness because the afterimage would remain fixed on the retina while the eyepress 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

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Table 1

	Retinal image motion	No retinal image motion
Efference copy	**A. Normal eye movement**	Afterimage with saccade
No efference copy	Eypress in normal field	**B. Eyepress in darkness**

in a normal environment would not elicit apparent motion because the retinal image motion would be matched by the efference copy, but the eyepress 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, as summarized in Table 1.

The two lettered conditions in bold type result in space constancy. In the other two conditions, space constancy fails because of a mismatch between efference copy and image movement.

Both Bell and Purkinje went further to conclude that gaze movement signals cancelled retinal image displacements to achieve space constancy.

For more than a century after this, efference copy was the major mechanism assumed to mediate space constancy. The dominance of outflow mechanisms in explaining space constancy was assured in 1866 by Helmholtz [5]. He expanded the empirical base for outflow theories with observations of neurological patients who had muscle pareses, so that they could not use part of their oculomotor fields.

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 patient concludes is that there is an image to his right, though due to the failure of the eyes to move, the 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.

For the perception of a jump of the world in the direction of an intended eye movement, the explanation is similar. 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 with the eye, because eye position (as reported by Willensanstrengung) has changed but the retinal image position has not.

Perhaps because Helmholtz saw his eye movement signal as related to the will, he did not analyze it quantitatively, despite his formidable mathematical talents. The first step in that direction was by Mach [6], another physicist–physiologist, who proposed that a neural copy of oculomotor efference sums algebraically with the retinal signal.

3. Quantitative theories

Building on advances in control theory made during World War II, two papers appeared independently in 1950 that defined efference copy theory for the next generation. In fact the phrase 'efference copy' first appeared in a paper in German by von Holst and Mittelstaedt [7] as 'Efferenzkopie'. This was an empirical paper, describing the results of inverting the head of the blowfly *Eristalis* by rotating its neck 180°. 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. The results were explained by assuming that the fly monitored the output of its locomotor system and compared that output with the retinal flow field. 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 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 formalized their idea with an engineering flow diagram and algebraic analysis, the efference copy exactly cancelling the afferent signal. This seminal paper also introduced the terms exafference, a change in retinal motion signals resulting from motion of objects in the world, and reafference, a change in retinal motion signals resulting from movements of the organism.

Sperry [8] 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 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.

Table 2

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

3.1. Limitations of compensation theories

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 developed rapidly during World War II, made these problems clear.

First, the efference copy is a feedforward, a signal the 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 is not corrected when it is in error. Yet in the real world, 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, and that something else might be all that is necessary to do the job.

The normal stability of the world is surprisingly fragile, though. A full-field world is stable, but a small point in a dark room is not, seeming to jump in the direction opposite each eye movement. Even a large saccade made from one point on the edge of the oculomotor range to another (for instance looking from the upper left to the upper right corner of vision) elicits a breakdown of constancy. Even in the normal range, making saccades too frequently results in oscillation of the visual world. Explaining both the stability and the fragility of space constancy has been a challenge for theorists.

Recognizing that efference copy could not be perfect, Matin [9] 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 [10,11]; 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 did not 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 nearly $\frac{1}{3}$ as large as the saccade itself [12]. 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 functional 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.

Other problems with the efference copy theory soon emerged. 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) that must have driven the behavior. Applied to the oculomotor system, reverse modeling clarified the motor signals that drive voluntary nystagmus, a rapid oscillation of the eyes that can be performed by a small proportion of the population. The oscillations are small in amplitude, usually 3° or less, but high in frequency, up to 20 Hz. The resulting rotatory 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; their 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. [13], who compared suppression during 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; space constancy did not necessarily accompany saccadic suppression. Further, an afterimage in darkness remained motionless during voluntary nystagmus (Table 2), showing that the changes of eye position failed to elicit changes in apparent target position. The mechanism of constancy must have some other basis.

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. A better temporal resolution of the constancy/frequency relationship was achieved in studies of the apparent movement of an afterimage with saccades in darkness. Grüsser et al. [14] 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 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/s) the afterimage appeared to

remain fixed in front of the subject. Space constancy had failed completely. The result confirmed that perceptual compensation occurs only over a low frequency range. Even for saccade 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 eyepress has been misunderstood for centuries, since Descartes's assumption that it elicited a passive eye movement, as reviewed above. Helmholtz [5] 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 eyepress; and second, the eye of another person appears to move when it is observed during their eyepress. The two observations are consistent with one another, but both are misinterpretations.

The observation of image 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 with the other closed. You will find that you continue to hold your gaze at 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 the visual world. The motion originates with the successful effort of oculomotor tracking mechanisms, which cannot be turned off, in keeping the eye on the fixation target. Both the optokinetic and the pursuit oculomotor control systems add innervation to the eye to keep it from deviating from the target. The effort requires oculomotor innervation, and with it both an efference copy and a perception of motion. So, far from demonstrating an effect of passive eye movement, the eyepress demonstrates the effects of active compensation.

Now the results of eyepress in Table 1 can be reinterpreted. The 'Eyepress in normal field' condition moves to the upper right, because the eye does not move relative to the retinal image. Motion perception is due to change in efference copy alone. The interpretation of the other conditions remains the same.

The second misinterpreted observation is that the eye of another person performing an eyepress 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 nasalward rotational force, while the other is an equal and opposite force generated by the lateral rectus muscle. The oculomotor innervation is driven by a retinal slip initiated by the finger, but compensated by an involuntary optokinetic tracking system. Thus, the two rotatory forces cancel. But each of these forces also introduces a translation in the medial direction, the finger pushing the anterior lation in the medial direction, the finger pushing the anterior part of the eye nasalward and the lateral rectus pulling the posterior part of the eye nasalward. The translational forces sum to move the eye several mm in its orbit [15]. 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, observers misinterpret the translational motion as rotation. The rotation of the occluded fellow eye, which is not cancelled by the eyepress, provides an objective measure of the forces applied.

Now the eyepress technique, which causes a deviation in the efference copy without a change in the retinal image position, can be applied to the problem of measuring the temporal aspects of efference copy. It was possible to apply scleral search coils to both eyes simultaneously, and also to press on the eye without popping out the required scleral contact lens. Again the non-pressed eye is occluded, so that its movements are measured in darkness. In this experiment, rather than replicating the static experiments of Stark and Bridgeman [15], we pressed repeatedly on the viewing eye in a roughly sinusoidal pattern [16]. A force transducer on the fingertip provided an objective record of eyepress frequency.

We found that at low temporal frequencies the viewing eye does not rotate, replicating Stark and Bridgeman [15]. Rather, the occluded eye rotates under its occluder, revealing the compensatory oculomotor innervation; according to Hering's law, 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 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 was converging on the idea that efference copy could not be responsible for space constancy. It was too slow, and its gain too low to support a perceptual compensation for saccades. There was also evidence of a more qualitative sort that should have eliminated compensation theories, 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 [17], who fed an eye movement signal into a mirror that moved an image with the eyes, but at variable gain. At low gains, when the image was moving one-tenth as far as the eye, the image appeared always to be stable, replicating Bridgeman et al. [12]. 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. Efference copy theories, however, do not allow parts of the image to move relative to one another. The observation would seem to eliminate all efference copy and related theories in a single stroke.

The Brune and Lücking experiment might have resulted in dissociations for uninteresting reasons, however. The prominent objects might have been brighter than the background, for example, so that signals coding them would move through the visual system faster than the 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 background. Another possible artifact is that the prominent objects might have been fixated, so that signals from them would course through slower, high-acuity channels, with the same result.

All of these possibilities were eliminated in a replication and extension of the study that used tesselations of a plane by the Dutch artist Maurits Escheras the stimulus materials [18]. Escher used two repeated shapes that interlocked to completely cover a surface. For instance, images of devils and angels might tesselate 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 for both figures, without any change in the stimulus, all image variables were controlled.

No compensation theory can account for this result. One possible explanation is that figure-ground segregation establishes an apparent depth difference, so that the figure is seen to move when the ground is stable. Figure-ground considerations are a long way from efference copy theories, however, a new approach is needed.

4. The alternative—no compensation

Efference copy was finally discarded as a space constancy mechanism with a new theory, centered on visual search and on a reanalysis of what information is carried over from one fixation to the next. According to the visual search interpretation, attention shifts to the saccade target before the saccade is executed [19]. Due to the attention shift, location and visual attributes of the target and of surrounding objects are stored in transsaccadic memory. After the saccade, the visual system searches for the previous object of attention 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. The system works even for large saccades, where extreme peripheral information must be used, because the correspondence between presaccadic and postsaccadic position need not be exact for the mechanism to operate.

Computationally this theory is even simpler to instantiate than the classic efference copy compensation theory, because under normal conditions no recalibration need be performed at all. Only if the object is not found do outflow and other information sources come to bear.

If the saccade target were to be removed after the saccade was triggered, would non-constancy be the result? The answer to this question is 'yes'; a target extinguished during a saccade, and reestablished in a slightly different position only after the eye comes to rest, can be localized quite precisely relative to its position before the saccade began [19]. This precise information is apparently discarded if the target is present when the saccade ends.

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. The stable, rich visual world of our perception is more promise than physiological reality, because there is no unified visual representation at all. In this reanalysis, then, it does not make sense to ask about the constancy of the visual world because there is no visual world that survives changes in fixation. Change blindness studies, in which large changes in an image can go unnoticed if a saccade-like blanking of about 100 ms separates the changed image from the original, offer further evidence for the absence of a precise transsaccadic image storage. Extraretinal signals are used in static conditions, though, especially for controlling motor behavior [20].

Acknowledgments

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