

Visual stability

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The problem of visual stability is normally posed somewhat as follows: When my eye roves over the visual scene, the image of the world dances about on my retina, yet I perceive that world as stable. How does my visual system succeed in restoring and maintaining stability? Conversely, when I press on the canthus of my open eye so as to rotate the eyeball, the visual world seems to move. What differentiates this case from one in which a similar displacement of the retinal image is brought about by the use of my eye muscles?

A partial answer to the last question is that, whereas normal exploratory eye movements are saccadic, the image movements produced by pressing on the canthus are usually much slower, and may excite "drift-sensitive" elements in the visual system¹ which are not stimulated by normal saccades. But this is not the whole story, for the world is still seen to move even when such artificially produced image displacements are as rapid as saccades. We must therefore conclude that the central nervous system has access to information about a voluntary eye movement which is absent when an image displacement is brought about in some other way.

This conclusion raises two questions which are sometimes confused:

1. What is the source of such information?

2. What use is made of it?

This paper is *not* concerned with Question 1. The two most favored answers to

it have invoked either proprioceptive "inflow" from eye muscle spindles,² or a "corollary discharge"³ or "efferenzkopie"⁴ derived from the oculomotor "outflow" to the eye muscles. Current evidence favors the "outflow" hypothesis⁵; but whatever the source of eye movement information, the question that now concerns us is Question 2: What need is there for such information? What function do we suppose needs to be performed in order to bring about our experience of a stable visual world during voluntary eye movements?

The "suppression" hypothesis

Here again two answers have traditionally been offered. Both are agreed in presupposing that the need is to *eliminate* from the sensory input to the CNS the changes that have been produced by the eye movement. The first we may call the *suppression* hypothesis. This postulates that the information about an eye movement is used to suppress or attenuate the transmission of signals during the rotation of the eye. In support of this hypothesis it has been noted that visual sensitivity is reduced for test flashes presented during or *just prior to* a voluntary saccade. The apparent "anticipation" of the eye movement has been widely interpreted as evidence that an "outflow" signal from the oculomotor system must be responsible.

It is difficult to see how such a suppression mechanism could help much to explain perceptual stability, since it could do nothing about the change in image *position* brought about by the saccade. In any case the inference from "anticipation" turns out to be fallacious, for a series of control experiments^{6, 7} have shown

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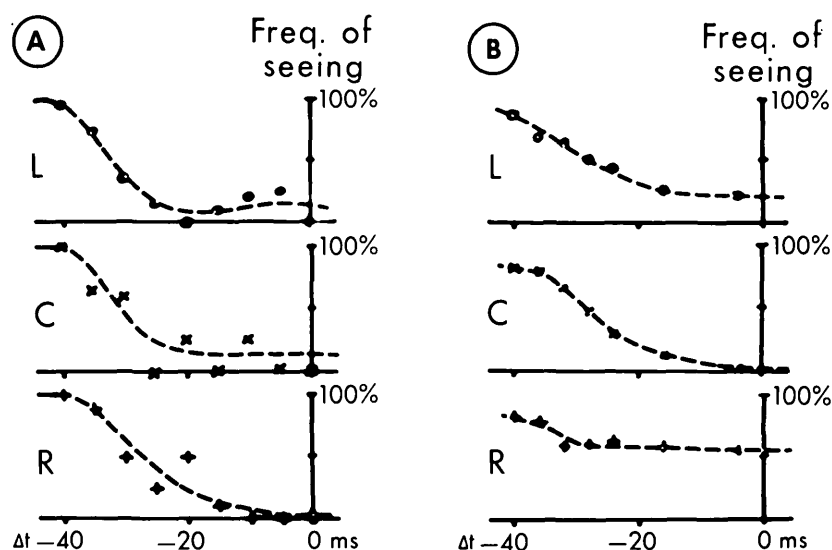


Fig. 1. A, Frequency-of-seeing curves for a test flash presented at varying times (Δt) before a circular background field was suddenly displaced. Fixation approximately two degrees to left (L), center (C), two degrees (R) of test flash. B, Corresponding results where the test flash was presented to one eye and the background field to the other. (See MacKay.⁷)

that with a stationary eye before an artificially displaced visual field there is a similar reduction in sensitivity for test flashes presented even 40 msec. or more before the displacement (Fig. 1, A). The effect is still found, however, and has a similar time course (Fig. 1, B) if the flash is presented to one eye and the jumping field to the other, suggesting that it is due to interference at some higher level between the activity generated by displacement of the peripheral retinal image and the neural processing of the signal generated by the test flash. If the processing of an earlier flash signal is still going on when the displacement occurs, the latter will appear to have a retroactive or "anticipatory" effect.

The "subtraction" hypothesis

The second answer offered to Question 2 may be called the "subtraction" hypothesis. This postulates that eye movement information is used to generate a "copy" of the changes in retinal signals due to voluntary eye movement, which is then *subtracted* from the sensory input before

it passes to higher centers, thus keeping it invariant. Fig. 2 shows von Holst's diagram of this proposal,⁸ in which the oculomotor command signal gives rise to an "efference copy" equal and opposite in sign to the "reafference" (changes) due to eye movement, and the two are combined so as to cancel out the changes before the signal passes onward.

It should be noted that although in this form the hypothesis relies on "outflow" it would be possible to apply the subtractive principle using proprioceptive "inflow." Indeed this is just what is sometimes done to maintain the stability of a radar display on board ship, against the effects of turning the ship's head. "Inflow" from a gyro compass is used to bring about a compensatory rotation of display coordinates, so as to cancel the angular displacement that would otherwise be suffered as the ship turns. In the visual case, however, it is known that when the eye muscles are paralyzed, the subject reports a sensation of "movement of the world" when he tries to move his eyes.⁹ This would be predicted on von Holst's

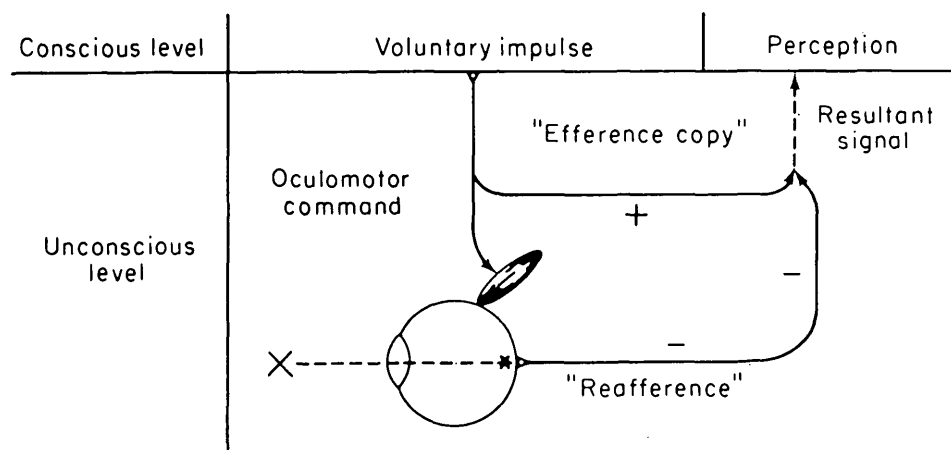


Fig. 2. Von Holst's proposal to account for visual stability by the subtraction of an "efference copy" from incoming visual signals. (From von Holst, E.: *Stud. Gen.* 10: 234, 1957.⁸)

"outflow" theory (Fig. 2), since in the absence of any visual "reafference" from the paralyzed eye the compensatory "efference copy" would be added unopposed to the resultant signal. It would not be predicted if the postulated compensatory signal were derived from proprioceptive "inflow," since the eye muscles are here immobilized.

Further support for von Holst's theory has been claimed from the fact¹⁰ that the position of a target briefly illuminated at the time of a voluntary saccade is misperceived in relation to a fixed scale. Here again "anticipation" is observed, flashes presented even 50 msec. or more before the eye moves being perceptually mislocated. It has seemed natural to take this as evidence of a "compensatory shift of internal coordinates" performed by a corollary discharge from the oculomotor system in advance of the eye movement; but unfortunately for this conclusion, a similar illusory mislocation is observed if the eye is at rest and the visual field (a luminous graticule) displaced saccadically by external means.¹¹ Moreover, the effect is again "anticipatory," in that test flashes presented well before the field jumps are perceptually mislocated (Fig. 3).

The explanation is presumably that the neural response to the test flash is still

reverberating at the time at which the retinal coordinates of the graticule change. Thus whatever the central process involved in judging the position of the flashed target relative to the graticule, it has to cope with two conflicting pieces of evidence and must reach a compromise based on their relative weight. On this theory (neglecting differences in response latency for simplicity) the biggest illusory shift should be seen for targets flashed just before the graticule moves, since the retinal location of the target would then correspond to the *original* location of the graticule image, whereas the bulk of the neural response would overlap in time with signals representing the *new* location of the graticule image. On this basis, moreover, the magnitude of the maximal illusory displacement should depend on the speed with which the graticule moves. As will be seen from Fig. 3, *B*, both of these predictions are confirmed. The illusory displacements observed with voluntary eye movements thus provide no evidence of a subtractive corollary discharge from the oculomotor system.

A further crumb of negative evidence has come from the work of Brindley and Lewin,¹² who used occipital electrodes in a blind woman to generate phosphenes which were apparently perceived as sharp-

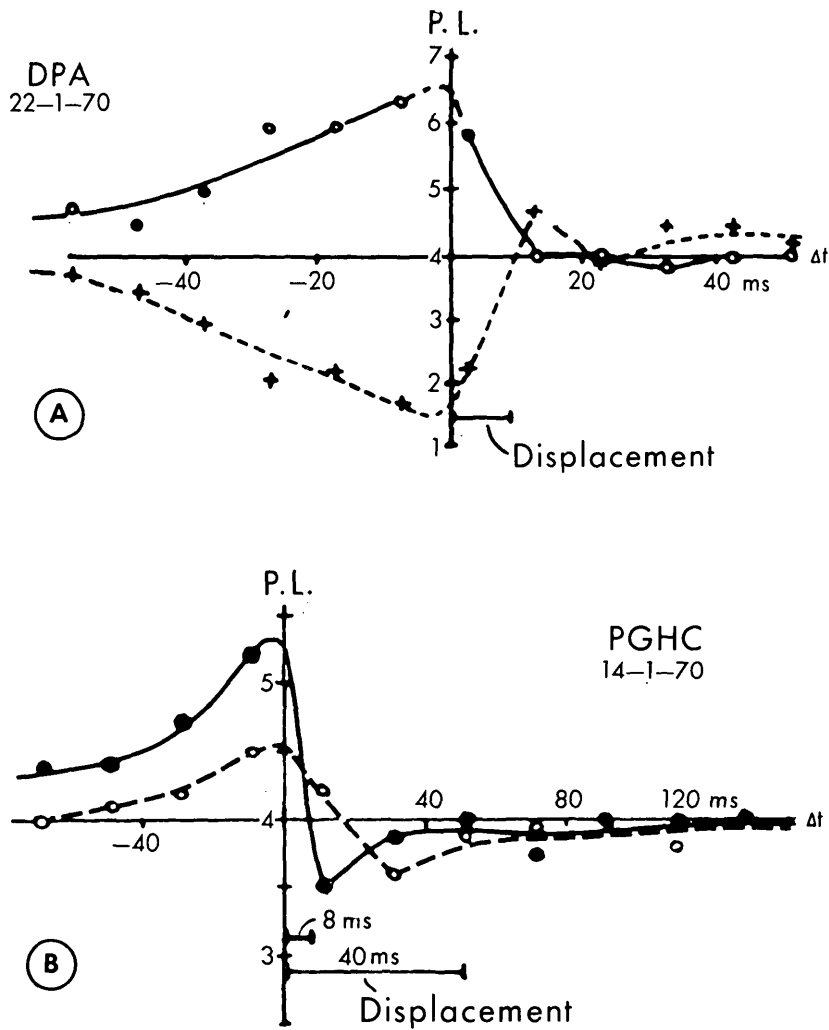


Fig. 3. A, Perceived location (P.L.) of flash on scale as a function of time interval between flash and onset of displacement. Actual location was fixed at 4. Displacement took 8 msec. Measured displacement to left was slightly larger (2.8 divisions) than to right (2.4 divisions). \circ , Left; +, right. B, Effects of duration of image motion on perceived location. \bullet , 8 msec. (500 degrees per second); \circ , 40 msec. (100 degrees per second). (See MacKay.¹¹)

ly defined spots having an external location. When the subject made an eye movement, she reported that the phosphenes seemed to move with her eyes (just as a retinal afterimage would). This shows that it is not sufficient for visual stability that the "neural image" should be stationary on the visual cortex and also throws doubt on the idea that it is necessary. Whatever the stable neural representation of our world may be, it must apparently

be at a still more central level than that stimulated by Brindley and Lewin.

Is "elimination" necessary?

At this point it seems appropriate to question the presupposition upon which both "suppression" and "subtraction" theories are based: namely, that it is necessary for the changes due to eye movements to be *eliminated* from the incoming sensory signals if the perceived visual world

is to remain stable. There is, after all, a strong counterexample in the case of tactile exploration. When the arm muscles are used to move the sensory surface of the palm over the tactile world, we are perfectly well aware of the succession of changing signals sent up from the exploring surface. The "tactile image" moves over our palm, admittedly not saccadically (unless we explore by a series of hopping movements), but still quite perceptibly; yet nobody to my knowledge has ever proposed either a "suppressive" or a "subtractive" process to account for the fact that our tactile world is perceived as *stable* throughout the exploration.

Such a theory would clearly make no sense; for the sensory changes taking place as we move our palm over a stationary surface are not awkward consequences to be eliminated; they are rather the *object* of the exercise. Properly evaluated, they offer *positive evidence* of the stability of the explored surface; for if they were absent, we would be justified in inferring that whatever was under our palm must be moving with it.

Now there are nontrivial differences between visual and tactile exploration which must not be overlooked. In particular, we have joint receptors that give us accurate knowledge of hand position which is lacking in respect of eye position¹³; and our ability to explore by smooth hand movements has no analogue in vision, where smooth drifting of a retinal image (as opposed to saccadic jumps) almost always gives rise to sensations of illusory world movement.¹⁴ Nevertheless the tactile example serves well enough to illustrate the principle that in order to maintain perceptual stability it is unnecessary, and even undesirable, to *eliminate* changes from sensory signals due to exploratory movements. What is needed here is not elimination, but *evaluation*. If this argument is correct, the presupposition behind both the suppressive and the subtractive theories is false.

Eye movements as questions

The logic of the situation is perhaps most easily clarified in terms remote from physiology and general enough to apply to any sensory system.¹⁵ Suppose we ask a series of questions about a stable world. According to the form of our questions, the correct answers will in general vary; but the variations in those answers, so far from suggesting that our world is changing, will merely be part of the evidence that it is not. Any idea of tinkering with the answers so as to make them invariant as we change our questions would be absurd.

On the other hand, it is clear that in order to evaluate or interpret an answer, we must know to what question it is the answer. Thus evaluation entails the bringing together of information in the form of an answer, with information as to the form of the question. The interaction between the two is a logical operation, which can doubtless be mechanized like other computing operations, but will generally involve something much more complex than either "suppression" or "subtraction."

The suggestion emerges, then, that we should think of exploratory eye movements, and indeed of other bodily movements that affect the positions, sizes, or other attributes of retinal images, as changing the form of the questions put to the visual world by the central nervous system. For the resulting changes to be properly evaluated, the CNS must of course supply its evaluative system with information as to the nature of the movements responsible; so there is no disputing the need for "corollary motor discharges," or perhaps better, "corollary motor *information*" to that end. But we must expect the integrative process, whereby the CNS evaluates the operational significance of the resulting changes, to be much more complex in general than a suppression or subtraction of components from the visual input; and we have indeed no reason to expect to find the physiologic

correlates of this process at the level of the afferent visual pathways.

Conclusion

Our suggestion, in effect, is that theories of the physiologic basis of perceptual stability have been bedevilled in the past by a confusion between the *physical attributes* of a sensory signal and its *information content*. One way of putting our present argument is that the sensory changes resulting from exploratory movement in a stable world have *no selective information content* justifying any change in the internal representation of that world: In the jargon of communication engineering, they are "100 per cent redundant." If we suppose that the mechanism for updating the internal representation (whatever that may be) operates on the statistically efficient principle of the "null hypothesis," then it is not the maintenance of stability, but the recognition of change, that will require informational justification. On this basis, "corollary motor information" is needed not to interfere with incoming data, but to *set appropriate criteria of evaluation*—to determine the conditions upon which the null hypothesis can be deemed to be falsified by the sensory evidence. The accuracy required of such information can in general be much lower than if it had to be subtracted from the sensory signal, since it need now be no more precise than the motor performance it represents.

It should be emphasized that this argument in no way disputes the appropriateness of subtractive processes in neural sensorimotor servo loops, such as that which Robinson¹⁶ proposes to account for ocular fixation. It may well be that the corollary oculomotor signals found in the superior colliculus reflect the operation of just such a subtractive mechanism. Our objection is not to the original von Holst–Mittelstaedt conception of the *efferenzkopie* as the basis of sensorimotor coordination, but only to the idea that it either need be or could be invoked as a device also for eliminating

from the sensory input to the perceptual system the changes due to voluntary movement.

Negative though it is, this conclusion may not be unimportant for the visual physiologist if it helps us to keep a more open mind about the possible functions of such "corollary discharges" as we may come across and to develop a clearer idea of the sorts of physiologic process we might try to look for as the basis of visual stability.

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Discussion

HORRIDGE: When I press on one eye with both eyes open I can make the image of your nose move any distance across your face. Now that is a small angle, but it is an angle. I can bring such images together if I voluntarily change my convergence. Now if I look at you with two eyes I can't separate you at all. If my evaluation system knows that you don't have two faces how is it fooled by this small movement?

MACKAY: Your example illustrates the point that evaluation has to take place at different levels. Under a condition of retinal image disparity, however brought about, there are certain low-level readinensses that must be organized to reckon with the double image, for example, oculomotor readinensses to scan the visual field. At this level, the evaluative criteria take no account of your knowledge that people don't have two faces. At the higher level that determines your conscious readinenss to reckon with the objects in your world, factors such as familiarity with normal objects and with the experience of diplopia play their part in determining the criteria of evaluation and prevent you from developing a conscious readinenss to reckon with a two-headed monster. In other

words, evaluation in the sense I was using is a hierarchic process.

WURTZ: One of the hopes of this kind of analysis I think is that it predicts hypotheses which can be tested at the physiologic level which one could differentiate. We didn't see any input from the oculomotor system to cortex in monkey but in colliculus we find cells which are inhibited in total darkness in synchrony with eye movements. From the model proposed here one could say something is being cancelled or perhaps evaluated. Could you comment on this result and suggest specific physiological results your model would predict?

MACKAY: Conceptual analysis of itself does not predict hypotheses; it offers rather an interpretive framework which affects the *kinds* of alternative hypotheses (or further questions) that spring to mind in response to our observations. Thus on the older view of the problem of visual stability that I was rejecting, your findings might suggest the hypothesis that the collicular units suppressed during eye movements are "way stations" for visual signals on their way to some neural "map" forming the basis of our perception of the visual world. This would perhaps lead to a hunt for psychophysiological evidence of such a map where these units terminate. If my analysis is correct, on the other hand, our experience of visual stability offers no logical incentive to make this hypothesis. The suppression you observed raises quite different questions. Are these units part of a fixation servo loop, which must be momentarily suppressed to allow a saccade to occur? Are they part of a comparator-system that normally evaluates the magnitude of the image-jump against a goal-criterion represented by the inhibitory input? And so on.

It might take a long time and a lot of further ancillary data before specific physiologic tests of any of these various hypotheses could be made. The importance of conceptual analysis is to save us as far as possible from wasting time on non-starters.