ADAPTATION TO AN ALTERED RELATION BETWEEN RETINAL IMAGE DISPLACEMENTS AND SACCADIC EYE MOVEMENTS[1]

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Abstract—The normal relation between retinal image displacement and saccadic eye movement was experimentally altered by moving a stimulus vertically up or down contingent upon a subject's horizontal saccades. For half the subjects the stimulus moved up with a rightward and down with a leftward saccade, while for the other subjects the reverse was the case. Prior to and following 45 min of exposure to this novel situation, detection thresholds for vertical up and down motion during rightward saccades were determined. The exposure condition produced a significant mean increase of 7.8% in the threshold for vertical motion in the same direction as the adapting stimulus had displaced with rightward saccades during exposure, and a mean decrease in the threshold for motion in the opposite direction of 6.4%. The exposure condition also produced a significant post-test change in saccadic trajectory. The results are evidence of a significant tendency toward the re-establishment of position constancy when there is an altered relation between image displacements and saccadic eye movements. Based on the change in saccadic trajectory, an argument is made that the adaptation is caused by a recalibration of registered eye movement direction.

INTRODUCTION

Movements of our heads normally produce displacements on the retina of images of the objects in our visual fields. Nevertheless, stationary objects continue to be perceived as stationary and this is an example of a phenomenon referred to as position constancy. A number of investigators have established that the perceptual system can adapt to a consistent change in the normal relationship between head movements and retinal image displacements (Wallach and Kravitz, 1965; Wallach, Frey and Rodney, 1969; Rock, 1966; Hay, 1968). While such a change initially produces an apparent loss of visual stability, or position constancy, this loss of constancy begins to disappear after brief exposures to this novel perceptual situation, and in time stability or constancy is re-established. In an elegant experiment Hay (1968) has shown that this adaptation is produced by a change in the eye movement pattern associated with movements of the head. Despite the fact that position constancy occurs during saccades (Mack, 1970; Matin, 1972; Bridgeman, Hendry and Stark, 1975), albeit with less precision than during head movements, there has been no analogous investigation of the modifiability of the relationship between saccadic eye movements and image displacements which produces position constancy. Evidence of such modifiability would not only provide additional evidence of visual plasiticity but would also yield support for the hypothesis that position constancy results from the action of a compensatory mechanism which evaluates retinal image motions in terms of eye and head motions (von Holst, 1954; Teuber, 1960). According to this hypothesis image motions which "match" eye movements provide the occasion for perceived object stability, whereas all other image displacements result in the perception of object movement.

As with head movements, when the eye saccades images of stationary objects in the visual field normally displace rapidly across the retina by the same amount and along the same dimension that the eye has moved; within certain limits, these objects appear stable. If position constancy during saccades is modifiable, then, following a period of exposure to a situation in which the images of all visible objects are caused to displace in a novel manner during saccades, only objects whose images displace in this novel way (during a saccade) should appear stationary while objects whose images behave normally should appear to move. The reserach described here is an attempt to determine whether the visual system is modifiable in this way. It is modelled on the work concerning the modifiability of position constancy during head movements. Like all visual adaptation studies, these experiments involved three phases: An initial pre-test phase in which a baseline measure is established against which an adaptive change can be evaluated; an exposure phase in which the observer experiences the distortion; and finally a post-test phase in which the pre-measures are repeated and the changes assessed. In these studies the pre- and post-measures consisted in determining the detection thresholds for the perception of vertical up and down motion of a single stimulus during a horizontal saccade. In the exposure period a visual stimulus was caused to move vertically contingent upon a subject's horizontal saccades.

METHOD

The visual display was presented on a fast phosophor (p. 15) CRT. A similar CRT (p. 7) was used by the experimenters to monitor the display. The stimulus elements consisted of a small uniformly lit square which subtended a visual angle of 0.5° and two briefly flashed horizontally

aligned light points, separated by 6'. Eye movements were monitored by a double Purkinje image eyetracker (Cornsweet and Crane. 1973) which has a resolution of better than 6' and outputs the horizontal and vertical positions of the eye on two orthogonal channels while remaining highly insensitive to small movements of the head. This eyetracker has an estimated bandwidth of approximately 200 Hz and typically does not lag behind the eye by an interval of more than 4 msec. An analogue record of the subject's eye movements was obtained with a two channel chart recorder. A Waveteck function generator and TTL logic were used to time the audible clicks and brief flashes used to cue the saccades in the several experimental conditions. The stimulus elements were multiplexed onto the CRT. Subject. eyetracker optical assembly. and display oscilloscope were housed in a light-tight cubicle.

A rigid bite-plate with dental impression wax was used to secure the subject's head position. The subject was seated 61 cm in front of the CRT and viewed the display binocularly. Calibration procedures were then begun. Calibration was complete when the following conditions were obtained. The eyetracker was locked onto the subject's right eye and the subjective straight-ahead position was determined. The luminous display square was positioned so that its center coincided with the subjective straight ahead. (The luminance of the square. determined by a photographic light meter, was set at a constant value for all subjects. It was dim but clearly visible.) The output of the eyetracker was adjusted so that a 3° horizontal excursion of the subject's eye to the left and right of straight ahead produced a 1.5° upward and downward displacement of the square. This was accomplished by feeding the horizontal output of the tracker into the vertical (Y) channel of the multiplexer used to display the square on the CRT. Since the eye travelled approximately a distance of 6° as it moved from left to right of the square, the square displaced through a total distance of 3°. Whether the square displaced up when the subjects' eyes moved right and down when they moved left or vice versa depended on the position of a polarity reversal switch. A 24-position step-attenuator placed in the signal path between the horizontal output channel of the eyetracker and multiplexer allowed the experimenter to reduce the vertical displacement of the square produced by a horizontal eye movement from its maximum calibrated value of 50% down to 0% in 23 uniform steps of 2.17%. With the attenuator set for 0 displacement, the square was fixed in the center position regardless of the subject's horizontal eye position. One step up from 0 the square displaced vertically by 2.17% of the horizontal distance traversed by the eye, and so on. Any vertical component in the subject's eye motion did not influence the position of the square. Finally, two additional points were positioned on the CRT, one 3° to the left (the left point) and one 3° to the right (the right point) of the center position and level with that position. These points were normally not visible but each could be flashed in the appropriate position for 10 msec.

After calibration was complete, a series of training trials were run to determine whether the subject was able to perform the required experimental tasks. These involved saccading left and right between the two briefly flashed points which were flashed at 2 sec intervals, while the display square was present and stationary in the field. In addition. the subject was required to saccade to the left and right of the stationary square in time with a 0.5 Hz sequence of audible clicks in the absence of the flashed points. Subjects who could not. with reasonable practice, learn to saccade approximately the correct (6°) distance between the flashes. which, of course were no longer visible when the eyes began to move. could not hold their eyes steady between flashes, or control the impulse to saccade to the square, were eliminated. This constituted a considerable number of subjects. All subjects who were able to

saccade adequately between the flashes also succeeded in performing the task to the audible clicks.

Pre-test threshold determination

Prior to the initial threshold determination subjects were dark-adapted for 0.5 hr. Following threshold determination subjects were given a rest period in a normally lit room. However. from the onset of the exposure phase to the completion of the final post-test measurements. subjects were kept in complete darkness except for the stimulus display.

Thresholds for the detection of vertical up and down motion during a rightward saccade were determined in the following manner. The left point was flashed several times allowing the subject to fixate its position and the eyetracker to capture the eye, the display square appeared. the right point flashed (no more than 1 sec after the square appeared), and the subject saccaded to it. If a saccade did not occur. the right point was flashed again 1 sec later. Immediately following the saccade the display was blanked and the subject reported whether the square had moved up. down. left. right or remained stationary (Oblique movements were reported as up-left or down-right. etc.).

Thresholds trials were begun with four trials in which the square was stationary. Then the square was moved up or down in successive increments of 2.17% of the horizontal saccadic distance. When the subject reported vertical motion in the correct direction on three successive trials the threshold was recorded as the first of these trials. and a descend series was begun. Up and down motion trials were intermixed according to a predetermined randomized schedule and "no" motion trials were intermixed with these with an average frequency of one for every ten trials. This procedure may be thought of as a modification of the random double staircase technique (Cornsweet. 1962). since the subject could not predict the probable behavior of the square on any trial from its behavior on the previous trial. It should be noted. however. that there was a possible cue to the direction of square displacement that the subject might have used. On each trial the initial position of the square was displaced up or down from the level of the flashed points by an amount equal to the feedback percentage setting of the step attenuator multiplied by 3° (assuming the subject was fixating accurately). Since this displacement was always in the direction opposite to that in which the square would move. the level of the square could have been used to predict the direction of motion. despite emphatic instructions to the subject only to report motion if it was actually perceived. Some subjects. with very low detection thresholds. may have used this information. However. should this have occurred. it ought not to have affected the final outcomes. since this information was equally available in post-threshold trials.

A total of two ascend and two descend series of trials were run. although if the thresholds obtained in the first series were highly deviant from those subsequently obtained. a fifth series was added and the data from the first discarded. Trials in which saccades were very short (under 4°) were discarded and these trials rerun. A mean of these four threshold measurements was used as the pre-baseline threshold estimate.

Adaptation trials

Adaptation trials were begun following threshold determinations. In this phase of the experiment subjects saccaded to the right and left of the stimulus square in time with the audible clicks. The square was displaced vertically by 26.04% of the horizontal distance of the saccade and its displacement was completely contingent on the saccade. For half of the subjects the stimulus displaced up when they looked right and down when they looked left. while for the remaining subjects the reverse was true.

Subjects saccaded in this manner for 90 sec, rested for 60 sec and saccaded back and forth again for another

90 sec. This sequence was continued until the subject had completed 30 such adaptation episodes. Since there was a 5-min rest period after the 15th episode. the subjects experienced a total of 45 min of adaptation training in 1 hr 20 min. During adapting trials, an eye blink or a saccade which caused the eyetracker to lose the eye would act to blank the CRT until the eyetracker recaptured the eye. Except for a few flashes of the left point at the start of each series of trials which were necessary to bring the subject's eye into capture position for the eyetracker. the square was the only visible object during this entire period.

Post-threshold determination

Final threshold determination began immediately following the adaptation trials and was carried out in the same manner as the initial threshold determination with the exception of the following changes. Determination of up and down detection thresholds were based on only one ascend and one descend series. Two rather than three veridical reports of square motion were used to obtain the ascend and descend thresholds. The start point for the initial ascending series was the step-attenuator setting one step below the threshold setting established in the pre-test ascend series for up and down motion. (If the subject reported motion at this setting, the series became, of course, a descending one.) These changes were instituted to minimize the number of trials necessary to obtain a threshold estimate. since it was likely that the very procedure for obtaining thresholds would tend to disrupt the adaptation effect we were attempting to measure.

Following both pre- and post-threshold measurements an attempt was made to determine how the subject moved his/her eyes in response to the instruction to move them horizontally, since pilot studies suggested that there might be some change in saccadic direction during and following exposure. This was accomplished by asking subjects to fixate the flashed left point and then to saccade on verbal command horizontally to the right the distance he/she remembered from previous trials had separated the points. The right point. of course. was not flashed. and the square was not present in the field. This was repeated 4 times.

Subjects

Eight subjects with normal uncorrected vision were tested, four in each of the two exposure conditions. Subjects were paid for participation.

RESULTS

If the visual system is able to adapt to a situation in which, during a saccade, a stimulus (the only visible object) is consistently caused to move vertically by some fraction of the horizontal saccadic distance (e.g. up when the eye saccades right and down when it saccades left). then, following exposure to this situation, a stimulus which moves up when the eye saccades right should appear stationary. An upward stimulus displacement has become the normal consequence of a rightward saccade. If now, following adaptation, the visual stimulus remains physically stationary when the eye saccades right, it should be perceived as moving down since only if it moved up would it appear stationary. Finally, if the stimulus actually moves down when the eye saccades to the right, it should always be perceived as moving down. Thus the threshold for vertical down motion should decrease and the threshold for vertical up motion

should increase. The converse should be true if during exposure the stimulus had always moved down when the eyes moved to the right and up when they moved to the left. Therefore. given the fact that all pre- to post-motion threshold determinations involve only rightward saccades. adaptation is indicated by a pre- to post-increase in the threshold for vertical motion detection in the same direction as the stimulus was moved during rightward saccades in the exposure period, hereafter to be referred to as "same" motion (S). and a corrrelative decrease in vertical motion detection in the opposite direction. hereafter to be referred to as "opposite" motion (O).

The mean pre- and post-thresholds obtained for motion matching (S) and motion opposing (O) the direction of stimulus motion during rightward saccades in the adaptation period are presented in Table 1. Adaptation is indicated by an increase in the S and a decrease in the O thresholds. This occurred for all eight subjects. There was an overall mean increase in the S threshold of 7.79% ($t = 6.63$, d.f. = 7, $P < 0.001$) and a mean decrease in the O threshold of 6.44% ($t = 10$, d.f. = 7, $P < 0.001$).[2] These changes are highly significant.

Presenting the data in this way requires that the thresholds for up and down motion be collapsed together. The threshold changes for up and down motion may also be considered independently for the two groups of subjects, one of whom experienced an upward and the other a downward stimulus displacement during a rightward saccade in the exposure field. This will indicate the effect on the initial up and down thresholds produced by the two kinds of adaptation experiences. These data are shown in Table 2. For the group of subjects that experienced upward motion of the adapting stimulus during rightward saccades, there is a mean increase in the up threshold of 8.31% ($t = 4.51$, d.f. = 3, $P < 0.05$), and a mean decrease in the down threshold of 6.17% ($t = 5.30$, d.f. = 3, $P < 0.05$). For subjects in the other group who experienced a downward displacement of the adapting stimulus when they saccaded to the right in the adaptation period, the threshold changes were, as expected, in the opposite direction. There was a mean decrease in the up threshold of 6.15% ($t = 11.75$, d.f. = 3, $P < 0.01$). and a mean increase in the down threshold of 7.27% ($t = 4.29$, d.f. = 3, $P < 0.05$).

From these figures it should be clear that substantial threshold shifts were produced by the adaptation procedure, such that thresholds for the detection of motion in the direction matching that which was seen during adaptation were elevated and thresholds for motion in the opposite direction were decreased. Thus

Table 1. Mean pre-adaptation and post-adaptation motion detection thresholds stated as percentages of the horizontal saccadic distance transversed

	S motion	O motion
Pre	6.32	7.34
Post	14.11	0.90

Vertical motion in the same direction as that seen with rightward saccades during adaptation is labelled S motion: vertical motion in the opposite direction is labelled O motion.

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[2] All threshold values are stated as the percentage of the horizontal saccadic distance traversed by the square as it moved vertically.

Table 2. Mean pre-adaptation and post-adaptation upward and downward motion detection thresholds stated as percentages of the horizontal saccadic distances transversed

	Group 1		Group 2	
	Pre	Post	Pre	Post
Motion thresholds up	3.90	12.21	7.24	1.09
Motion thresholds down	7.43	0.72	8.73	16.00

Group 1 are subjects who experienced upward motion with rightward saccades during adaptation and Group 2 are subjects who experienced downward motion with rightward saccades.

the differences between eye-movement–stimulus displacement contingencies in the adaptation period for the two groups produced clear and opposite effects of the kind that would be predicted had adaptation to position constancy occurred.

The fact that the initial pre-test thresholds are somewhat lower than those previously reported for the detection of vertical motion during horizontal saccades (Mack, 1970; Stark, Kong, Schwartz, Hendry and Bridgeman, 1976) and for a few subjects were extremely low (e.g. 0.54% for up and 2.6% for down motion), merits a comment. As previously noted, it was possible for a subject to use the initial level of the square relative to the flashed points to predict the direction of target movement. Use of this information by some of the subjects might account for these low detection thresholds. However, since this information was equally available during the post-threshold trials, its effect, if any, should have been to reduce the magnitude of the experimental effect. In view of the strength of the effects obtained despite this, this factor could not have played a determining role in the results.

It will be noted that the mean threshold for up motion detection in the pre-test is 2.15% lower than the mean threshold for down motion. However, this difference is not significant ($t = 1.92$, d.f. $= 7$). Similarly, the tendency for the O values to be slightly smaller than the S changes is not statistically significant ($t = 1.5$, d.f. $= 7$).

There is an aspect of the data yet to be considered which, however, may be important in understanding the adaptation-like shifts. The eye movement records reveal that, as the exposure period went on, subjects' saccades became more oblique and the direction of this added vertical component in the eye movements always matched the direction of the adapting stimulus motion. (This occurred in pilot studies in which, dur-

ing the adaptation period, subjects saccaded left and right to the sequentially flashed and horizontally aligned right and left points, as well as in the experiment reported here in which the saccades were directed only by the audible sequence of clicks.) Furthermore, and perhaps more important for an understanding of the results, there was a small increase and a consistent change in direction in the vertical component of the saccadic eye movements in the post-test threshold trials where the eye movements were always cued by the horizontally aligned flashed points. In these post-test trials the vertical component of the saccade relative to pre-test trials was always in the direction of the vertical stimulus motion which had been associated with rightward saccades in the exposure period. Thus, for those subjects who had experienced the square moving up when they saccaded to the right in the adaptation period, there was a pre- to post-test upward shift in the vertical component of their eye movements. (These subjects tended to saccade obliquely upward after adaptation, regardless of whether the square displaced up or down.) The converse was true for subjects who experienced the square moving down when they saccaded to the right in the adaptation period. They tended to saccade obliquely downward in the post-test trials. The extent of these eye movement shifts are reported in Table 3. For the first group there was a mean increase in the vertical upward component of their eye movements of $0.41°$ while for the latter group there was mean increase in the vertical downward component of the eye movements of $0.51°$.[3] These shifts in eye movement patterns could, at least logically, produce the obtained threshold shifts. If motion detection during saccades is solely a function of the absolute magnitude of retinal displacement, then these eye movement shifts, which have the effect of decreasing vertical retinal slip in the S direction and increasing it in the O direction, could account for the increase in the threshold for S and the decrease in the threshold for O motion detection following adaptation exposure.

An additional change in eye movement pattern also appeared in the results. It may be recalled that, following both the pre-test and post-test threshold trials, we asked subjects to execute rightward horizontal saccades without cueing these saccades by flashing the right point. This was an attempt to determine whether subjects responded differently to these instructions following adaptation. The mean change in the vertical component of these eye movements was $0.4°$ up for subjects who experienced the square moving up during rightward saccades and $0.55°$ down for subjects in the other group who experienced the square moving down during rightward saccades. Again, these changes are in the expected direction.[4]

Available data concerning motion detection during saccades (Mack, 1970; Bridgeman et al., 1975) provides grounds for doubting this explanation of the results since those data indicate that it is not the absolute value of retinal image displacements during saccades which determines whether or not object motion is perceived. Failure to perceive stimulus motion during a saccade seems to be independent of the direction of the eye movement relative to the target motion, and if this is in fact the case, then

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[3] Combining this eye movement change data for both groups of subjects by scoring changes which decrease retinal slip in the S direction as positive and changes which increase retinal slip in the S direction as negative, we find that the changes are highly significant ($t = 5.28$, d.f. $= 7$, $P < 0.01$).

[4] Combining this eye movement change data for both groups of subjects by scoring the changes as either in the correct or incorrect direction, we find they are significant ($t = 2.86$, d.f. $= 7$, $P < 0.05$).

Table 3. Mean vertical eye motions associated with rightward saccades during pre- and post-adaptation threshold detection trials for subjects who experienced upward motion with rightward saccades during adaptation (Group 1) and for subjects who experienced downward motion with rightward saccades during adaptation (Group 2)

	Group 1	Group 2
Pre	−0.07	−0.30
	(−1 99°₀)	(−4 18%)
Post	+0.37	−0.82
	(+5.90%)	(−12.17%)
Change	+0.43	−0 52
	(+7.89%)	(−7.99%)

All eye motions are expressed both in degrees and as a percentage of the mean horizontal saccadic distances transversed (in parentheses). A positive sign (+) indicates an upward direction and a negative sign (−) indicates a downward direction.

the absolute magnitude of image displacement is not the critical factor in motion detection during saccades. Both the Bridgeman *et al.* and Mack data indicate that it is the absolute size of the error between the saccade and retinal displacement that is the critical factor in motion detection during saccades. Since the oblique direction of the eye movements in the test situation does not affect the size of this error—that is, does not affect the magnitude of the mismatch betwen image displacement and eye movement—it does not seem likely that the pre- to post-shift in eye movement direction is responsible for the threshold shifts.

Despite the weight of this evidence, we chose to examine directly the question of whether a shift in eye movement direction comparable to the shift we observed in our eye movement records from pre- to post-test trials would, in fact, produce predictable and comparable changes in motion detection thresholds. If the pre- to post-threshold shifts can actually be accounted for by the changes in vertical retinal slip produced by the change in the vertical component of the eye movements, then this should be demonstrable in a threshold determination situation in which oblique eye movements—comparable to those found in the post-threshold testing trials—are generated. In other words, it should be possible to generate the kinds of threshold shifts obtained following adaptation under conditions in which there is no adaptation but the eye movements during threshold determination mirror those during post-threshold trials in the main experiment. To this end we performed a control experiment in which we determined detection thresholds for vertical up and down motion for six subjects—two of whom had been subjects in the main experiment and four of whom were new—under the

following three conditions: (1) the flashed points were horizontally aligned and separated by 6° as they had been in the main experiment; (2) the right flashed point was located 6° to the right and 0.5° above the level of the left point; and (3) the right point was located 0.5° below the level of the left point. We chose a vertical offset of 0.5° because the mean change in the vertical component of the eye movement from pre- to post-test trials was approximately 0.5°. Thresholds with horizontally aligned points were always determined first and served as the baselines against which possible shifts could be evaluated. The order of the two remaining conditions was counterbalanced across subjects and the procedures were otherwise identical to those used for pre-threshold determinations in the main experiment.

The results are presented in Table 4. There was essentially no mean change in the threshold for the detection of upward motion (0.17%) when the right point was above the level of the left, although there was some decrease in the down threshold (4.78%) in this condition. With the right point below the level of the left one, there was essentially no change in the threshold for down motion (0.84%) and some decrease in the threshold for up motion (4.71%). The threshold shifts that did occur are smaller than those obtained in the adaptation experiment and are not statistically significant. An analysis of the eye movement records reveals that locating the right point above the left did produce a mean upward shift in the vertical component of the eye movement of 0.62° relative to the eye movement when the points were horizontally aligned, which is comparable to the shift in eye movement direction obtained in the adaptation experiment. Locating the right point below the level of the left, however, produced only a 0.3° mean downward shift in the vertical component of the eye movement. The reason for this may be that all six subjects tended to saccade obliquely down when the points were horizontally aligned (this was also true for six of the eight subjects in the pre-test trials of the main experiment) and the mean downward vertical component was 0.59°, which was 0.09° greater than the subsequent downward vertical offset of the right point. Thus, to saccade accurately in the down condition, no change in eye movement direction was called for. Whatever the reason for this, the result is that only the upward oblique condition of the control experiment is fully comparable to the experimental post-threshold condition in which there was an upward shift for all subjects in the vertical component of their eye movements.[5] Nevertheless, the small threshold shifts that occurred were not exclusive to this comparable condition, and none of the changes were significant. The results of our control experiment would therefore seem to be in line with available data concerning motion detection during saccades and lead us to reject the view that the post-adaptation shifts in threshold obtained in the main experiment are accounted for by a decrease in retinal displacement in the S and an increase in retinal displacement in the O directiion caused by the shift in the vertical component of the eye movements.

Ruling out this explanation of our results, it becomes clearer that the results are in fact evidence of position constancy adaptation during saccadic eye

[5] It is relevant to note that three of the four subjects who observed the square move down when they saccaded rightward on the adaptation trials of the main experiment also had a small initial downward vertical component in their pre-test saccades. Nevertheless, these subjects had a greater downward vertical component in the post-test saccades which of course made their eye movements less accurate.

Table 4. Mean vertical motion detection thresholds for six control subjects who saccaded rightward between flashed points when the right flash was (1) horizontal, (2) 0.5 up and (3) 0.5 down with respect to the left flash

	Horizontal	Right flash up	Right flash down
Up threshold	5.79	5.95	1.08
Down threshold	10.55	6.77	11.39

Thresholds are expressed as percentages of the horizontal saccadic distance transversed.

movements. The question then arises as to its source. There seem to be at least two possibilities. The adaptation might be based on a recalibration of the direction of eye movements such that a horizontal saccade is no longer registered as horizontal or. alternatively, the direction of retinal image displacement signifying position constancy associated with horizontal saccades might have been altered. (Conceivably some combination of these factors might also account for the adaptation.) Both these explanations involve the assumption that a comparator mechanism which evaluates image displacement in terms of eye movement information is responsible for position constancy and motion detection during saccades. (Evidence that position constancy adaptation occurs during saccades would seem to be the strongest evidence currently available to support that assumption.) Both explanations also provide a basis for the perceptual system to account for the novel but consistently contingent oblique image displacements during the adapting period. Since the adapting square always displaced vertically contingent on the subject's horizontal saccades and consequently displaced obliquely on the retina, recalibration of intended horizontal saccades so that they are objectively oblique would allow the system to account for the contingent oblique image displacements in terms of the eye movements, and thus re-establish position constancy. With this maneuver an oblique image displacement would come to "match" a registered horizontal eye movement.

For example, assume the adapting stimulus displaced upward as the subject made rightward saccades during the adaptation trials, and this resulted in the recalibration of eye motions so that a registered horizontal saccade was obliquely upward. The upward displacement of the eye during the intended horizontal saccades would act to null the upward displacement of the stimulus, re-establishing retinal and perceptual stability. It follows that in this situation an objectively horizontal saccade would be registered as obliquely downward. The upward motion of the adapting stimulus during this objectively horizontal saccade would provide the upward retinal displacement needed to "match" the registered downward displacement of the eye and again perceived stability would result. Since most of the available evidence suggests that the information about eye movements used by the perceptual system in evaluating image behavior is derived from outflow and not inflow signals (Brindley and Merton. 1960; Skavenski, Haddad

and Steinman. 1972), an explanation of position constancy adaptation in terms of a recalibration of eye movement direction could properly be labelled efferent.

Assuming that it is the discrepancy between registered eye movement information and retinal image displacement which determines the perception of object motion and stability. the above model will account for an increase in the detection threshold for objectively upward and a decrease in the threshold for objectively downward movements during saccadic eye motions, following exposure to a situation in which the adapting stimulus moves upward contingent upon a subject's horizontal eye motions.

Alternatively, if no recalibration of eye movement direction occurs, the re-establishment of position constancy could result from the perceptual system learning to accept oblique image displacements as the normal consequence of horizontal saccades. Thus. if the adapting square had moved up contingent on rightward horizontal saccades during the adaptation trials. and the perceptual system learned to accept oblique downward image displacements as the normal consequences of these eye movements, this too would lead to the obtained increase in the threshold for up motion and the decrease in threshold for down motion and to the re-establishment of position constancy. However, unlike the former explanation of adaptation, this would constitute an afferent change.

While these are theoretically distinguishable events, they are not easy to isolate experimentally and nothing in our procedures allows us to assert with certainty that one or the other of these events underlies the adaptive change. The eye movement changes that we observed both during the adapting trials and during post-threshold testing are, however, consistent with an efferent explanation of the adaptation. If the adaptation is based on a recalibration of eye movement direction. we should expect that an oblique eye movement would flow from the intent to move the eyes horizontally. Thus. the fact that the eye movements became more oblique in the expected direction both during the adaptation trials where subjects were expected to make horizontal saccades, and in the post-threshold determination trials where saccades were cued by horizontally aligned flashes. is suggestive.

To be more specific, we would expect that, for subjects who experienced the adapting stimulus displacing upward during a rightward saccade, a horizontal saccade would be recalibrated as an oblique downward saccade, so that the eye movement response to the intention to move the eyes horizontally would be an upward oblique eye movement. All of the four subjects in this group did evidence an upward shift in the vertical component of their eye movements in the post-test trials in which saccades were cued by horizontally aligned points. Exactly the reverse of this pattern would be expected for the four subjects in the other adaptation group and all four of these subjects showed a post-test downward shift in the vertical component of their eye movements. The fact that following adaptation subjects saccaded obliquely in response to instructions to move their eyes horizontally when the eye movements were not cued by flashing the right point also supports this

explanation. It would seem to be rather good evidence that a recalibration of eye movement direction had occurred, for in response to instructions to move their eyes horizontally subjects, after adapting, respond with oblique eye movements which are oblique in the expected direction. This eye movement change, along with the change that occurred in post-test trials (where eye movements were cued by the horizontally aligned flashed points and their executed eye movements were, nevertheless, oblique in the expected direction). lead us to tentatively conclude that adaptation to position constancy during saccades is based on a recalibration of eye movement direction.

There is still another aspect of the data which supports this explanation. If we compare the change in the vertical component of the eye movements from pre- to post-threshold trials with the obtained threshold changes, we find that they are comparable. (Since thresholds are stated in terms of the percentage of the horizontal saccadic distance traversed by the vertically moving square, it was necessary to translate vertical eye movement data presented in degrees of visual angle into a percentage of the subject's mean horizontal saccadic distance in order to compare the changes.) We find that for the four subjects who experienced an upward movement of the square during rightward saccades in the adapting period, there is a 7.89% upward shift in the vertical component of their eye movements, while for the other four subjects there is a 7.99% downward shift. Reinspection of Table 2 will reveal that these figures are similar to threshold change figures for both groups of subjects. If we assume that the saccades during both pre- and post-threshold trials were intended to be horizontal—an assumption that is made tenable by the data from those trials in which the subjects were instructed to simply make horizontal saccades in the absence of the right point, and following adaptation make oblique eye movements comparable to those in the post-threshold trials—then the threshold shifts follow directly. For example, if, for the four subjects who experienced an upward movement of the square during rightward saccades in the adapting trials. an oblique upward eye movement, whose vertical component is greater by 7.89% of the horizontal saccadic distance following adaptation than before. is registered as horizontal, then the target square should have to move up approximately 7–8% farther in the post-threshold trials in order to be perceived as moving up, and move down about 7–8% less in order to be perceived as moving down. This is so because coding this oblique eye movement as horizontal means that an upward stimulus motion of the same magnitude could not be detected if motion detection during saccades is based, as it seems to be, on a mismatch between eye movement and image displacement information. The potential downward image displacement of an upwardly moving stimulus would be nulled by the actually upward oblique eye movement (the vertical stimulus displacement was contingent only on the horizontal component of the eye movement), and if that eye movement were registered as horizontal, the absence of any vertical image dis-

placement would constitute a match between eye and image displacement input and movement would not be seen. Assuming that the pre-threshold values reflect the magnitude of the mismatch between eye movement and image movement information necessary to detect vertical motion, then the stimulus would have to move up by the amount the eye moved up plus that value in order to be perceived as moving up. This is what occurred. The converse of this argument holds for downward motion detection. Thus, the fact that the change in the vertical component of the eye movements is comparable to the obtained changes in thresholds following adaptation seems to support the view that the threshold changes are based on a recalibration of eye movement direction.

Whether or not this conclusion is justified, the data reported seem to be clear evidence of a recalibration of the relationship between image displacements and saccadic eye movements signifying position constancy and, as such, demonstrate a new kind of perceptual modifiability.

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