

Spatial discordance is a sufficient condition for oculomotor adaptation to prisms: Eye muscle potentiation need not be a factor

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In three experiments, each of the stationary standing subjects inspected his right foot via 20-diopter base-right prisms. Each subject was arranged so that the eyes in his head, the head on his body, the trunk, and the legs were at all times symmetrical about the vertical through the body midline. Subsequent judgments of the visual straight-ahead and pointing to a visual target revealed a significant adaptive shift of 2°, whereas there was an insignificant shift of 2.5 mm in pointing to the nose. These results show that substantial recalibration of visual direction takes place when discordance of sensory spatial information is the only relevant stimulus. It follows that eye muscle potentiation (Ebenholtz, 1976) is not a necessary condition for adaptation of visual direction.

When humans wear prisms and are exposed to sight of their own body parts (Craske, 1967; Craske & Crawshaw, 1974) or the less well-defined stimuli associated with chronic exposure (Held & Bossom, 1961), it is now clear that one adaptive response is a change in registered eye-in-head position. The resultant errors of visual direction lead to the misreaching, which is characteristic of the prism aftereffect.

The mechanism of adaptation has been argued to be one of recalibration of the ocular positioning system due to cross-modal (eye-in-head position/kinesthetic) spatial discordance (Craske & Crawshaw, 1974, 1975).

Analysis of the idea of recalibration suggests that it can operate in a very straightforward fashion. First let us assume that, in order to maintain the functional integrity of the organism, each of the sensory systems responsible for spatial localization has modifiable parameters. Overall, the set of systems will operate to optimize performance of spatially organized behavior. Thus, it is expected that the brain will seek to minimize any between-system spatial discrepancy.

Now, when the operation of the spatial senses is veridical, then from each sense the spatial information about any set of points near the observer is essentially identical; spatial maps constructed from this information would be homeomorphic. The im-

position of a prism in front of the eyes destroys this homeomorphism, visual direction is biased, and there is consequent between-sense spatial discordance.

To use the example of looking at the feet through displacing prisms: the feet will be seen to be in one position in space, yet, via the position sense inherent to the limbs, they will feel to be in a different, veridical, location. A self-optimizing system will seek to eliminate this discordance. The term recalibration refers to the consequent internal changes of the set of spatial coordinates for a given stimulus in one sensory system with respect to some other spatial sense.

The present authors have claimed that the procedure of viewing the feet will produce adaptation that is restricted to a change in perceived eye-in-head position, and this is due primarily to recalibration as a result of spatial discordance (Craske, 1967). They have also shown that a 3-min inspection of the feet through base-out prisms significantly changed the observer's judgments of both distance and direction, whereas a control condition in which a virtual image of a disk replaced the feet showed no significant change in either judgment (Craske & Crawshaw, 1974). However, post hoc analyses of these data have led Ebenholtz and Wolfson (1975) to dismiss the recalibration notion in favor of an alternative mechanism. The basis for this mechanism follows from a number of observations. Thus, skeletal muscle exhibits spontaneous contractile activity as a result of previously maintained contraction

(Kohnstamm, 1915). It is also known that, subsequent to the eyes' being held in a position of strained asymmetrical convergence, there is a change in the judgment of visual direction (Craske, Crawshaw & Heron, 1975; Park, 1969) and that after suitable exposure conditions similar oculomotor aftereffects can be in opposite directions in the two eyes (Ebenholtz, 1974; Ellerbrock & Fry, 1941). Recently, it has been argued that these spatial aftereffects in muscle may belong to a common class (Ebenholtz, 1976; Ebenholtz & Wolfson, 1975). Further, it has been pointed out that the exposure condition in prism adaptation experiments may involve asymmetrical posture of the eyes, and hence entail a directional bias in muscular contraction. From this it has been argued that the particular kind of prism aftereffect that is misjudgment of the direction of gaze could be due to eye muscle potentiation (EMP) that results from previous ocular posture.

The general argument is that perceptual aftereffects of EMP underlie both the spatial aftereffects resulting from asymmetrical convergence and prism aftereffects resulting from wearing prisms. The mechanism of EMP has been envisaged to be a continued involuntary innervation of the previously contracted muscle. Thus, to fixate any visual target would require an extraordinary innervation of the contralateral muscle. If eye-in-head position is known by monitoring the voluntary efference to the eye musculature, as is commonly accepted (Merton, 1964), then this will lead to errors of judgment of eye-in-head position. The errors of localization would be in the direction in which the contralateral muscle pulls the eye. Ebenholtz (1976) and Paap and Ebenholtz (1976) argue that, in the context of prism adaptation, the operation of the above mechanism provides an alternative explanation to that of recalibration of the ocular positioning system (Craske & Crawshaw, 1974, 1975).

Consistent with the recalibration hypothesis, Craske and Crawshaw (1975) have shown that prism adaptation to the right occurs despite the eyes being turned to the left during base-left prism exposure. Ebenholtz (1976), however, has argued that Craske and Crawshaw's results may be due to the combined spatial aftereffect resulting from EMP to the left and a much larger postural (head-on-shoulders) aftereffect to the right. This latter is the result of the twist to the neck that the exposure condition required. His data support this notion, but are not altogether convincing. It is certainly not necessary to adopt the view he espouses, namely, that "The results of Craske and Crawshaw can be fully accounted for and are therefore best interpreted in terms of additivity of the aftereffects of head and eye rotation" (Ebenholtz, 1976).

In order to draw this conclusion, Ebenholtz has assumed that it is reasonable to compare a 6-min

prism exposure condition (with head turned) with a 10-min period of lateral duction of eyes (with head turned). Further, he has assumed that it is reasonable to compare data on the aftereffects of these two conditions when the first set was collected over a period of a minute or so while the latter set was collected within seconds of the completion of the exposure. These assumptions are not justified, for there is evidence to support the idea that the time-course for the decay of ocular postural aftereffects and that for the prism aftereffect are quite different, the former decaying far more rapidly than the latter (Craske, Crawshaw, & Heron, 1975). Indeed, the rapid decay of ocular postural aftereffects is borne out by the observations of Paap and Ebenholtz (1976).¹

The time-constant for spatial aftereffects due to previous rotation of the head is not known; data from one of our laboratories (BC) suggest that it is relatively short, something less than 1 min. If this is of the right magnitude, then Ebenholtz (1976) has collected data in which head-on-shoulders spatial aftereffects are strongly present, while Craske and Crawshaw (1975) collected about half their data when these aftereffects were largely absent.

The above argument suggests that the comparison made by Ebenholtz (1976) was not strictly correct. Furthermore, the conclusion that prism adaptation could be due to EMP ignores the fact that exposure to prisms produces an effect that is absent after lateral duction. Prism exposure causes a disturbance of the oculomotor system that takes the form of low-frequency, large-amplitude pendular oscillation of the resting position of the eyes (Craske & Templeton, 1968). Lateral duction, however, has not been shown to give such an effect (Craske, Crawshaw, & Heron, 1975).²

The fact that previous eye posture can affect subsequent judgments of visual direction is not in question, for there is a lot of evidence to support this view (Carr, 1910; Craske, Crawshaw, & Heron, 1975; MacDougall, 1903). It is also known that there are spatial aftereffects following previously held bodily postures (Hoff & Schilder, 1925). It is also quite clear that both could be factors in the explanation of prism aftereffects. However, the issue to be resolved is not whether oculomotor prism aftereffects can involve these components, as is certainly the case, *but whether these aftereffects can result solely from cross-modal spatial discordance.*

The experiment that must be carried out is quite clear. It is to seek evidence of prism adaptation in the presence of cross-modal discordance, but in the absence of all postural asymmetry, whether of the eyes in the head, the head on the shoulders, or of any other component that might yield contaminating postural aftereffects. The EMP hypothesis predicts that there should be no aftereffects, but the hypoth-

esis that recalibration can occur as a result of discordant spatial information predicts that normal prism aftereffects be exhibited.

EXPERIMENT 1

Method

Apparatus. A horizontal wooden platform was arranged to allow unobstructed pointing beneath its surface. A rigid dental impression could be attached at head height, and the height of the subject could be adjusted until his shoulder was just beneath the under-surface of the platform. Projecting from the top surface was a vertical luminous target, 1 mm wide and 10 mm high. This was mounted 1 m away from the subject in his median sagittal plane.

Subjects. Twenty-two volunteer right-handed subjects with measured phoria in the range of 0 ± 2 prism diopters were tested on a pointing task before and after a 6-min exposure to base-right 20-diopter prisms.

Procedure. In the testing situation, the laboratory was darkened, and with undeviated vision the standing subject was required to make 10 judgments of the direction of the target. From a randomized set of starting positions clustered about his right hip, he was asked to raise his right arm, point to the target, and in so doing make a mark with a fibre-tip pen on a scale beneath the platform.

The subject then underwent an exposure condition in which he was required to wear base-right 20-diopter prisms for 6 min. He was asked to stand upright, incline his head forwards, and inspect his right foot. It was essential that the subject's eyes remain in symmetrical convergence throughout the treatment. The right foot was thus positioned so that it was offset from the vertical through the body midline by an amount equal to the displacement of the prism. The left foot was moved by an equal amount in the opposite direction to preserve symmetry of stance. The positions of the head and trunk were also arranged to be symmetrical about a vertical through the body midline. The position of the head was controlled with a bite bar. The treatment took place under conditions of normal laboratory lighting. The subject's field of view was restricted to a patch around his feet, 1 m in diameter. At the end of the treatment, the lights were extinguished and the prisms removed. The subject then stood normally, moved forwards to the testing apparatus and fitted his teeth to the bite bar. He was then asked to make a further 10 judgments of the direction of the target.

Results

There was a significant mean shift of pointing of 2.0° to the right, $t(21) = 3.44$, $p < .005$.

EXPERIMENT 2

It has already been claimed that the experimental procedure used here is a sufficient condition for the production of uncontaminated adaptation of visual direction. However, it would seem prudent to repeat the experiment and use judgments of visual direction as a measure.

Method

Apparatus. In the testing condition, a modified Aimark projection perimeter was used. The subject's head was held by a dental bite, and was maintained in a position such that the point midway between his eyes was coincident with the axis of the arms of the perimeter. The subject could see only a 4-mm spot of white

light 327.5 mm distant, which, by means of a reversing servomotor, the subject could smoothly drive around the perimeter.

Subjects. There were 20 volunteer subjects, with a measured phoria of 0 ± 2 prism diopters.

Procedure. During the pretest, each subject sat with his head secured by the dental bite in front of the perimeter. The arms of the perimeter were set to horizontal, and the room made completely dark. The observer's task was to set the spot of light to his subjective straight-ahead. The subject drove the spot smoothly around the perimeter until he was satisfied that it was central. He then closed his eyes for 10 sec, the experimenter took the reading and drove the spot to a randomly selected starting position, which could be to the left or right of the objective straight-ahead. Data on 10 judgments were collected. This was followed by a treatment that was identical to that of Experiment 1, which in turn was followed by a posttest identical to the pretest above.

Results

There was a significant shift of 2.3° to the left of the judged straight-ahead, $t(19) = 3.82$, $p < .002$.

EXPERIMENT 3

The previous experiments seem to indicate that spatial discordance plays a prominent role in the genesis of adaptation. However, it may be argued that while the subject is inspecting his right foot in the experimental condition, even though there is no postural asymmetry, the subject may feel that his head is rotated with respect to his shoulders. Such "cognitive" asymmetry may subsequently yield a postural aftereffect whereby the head appears to be rotated to one side, and this could yield results similar to those so far reported. Therefore, it was decided to carry out an experiment in order to look for such changes in head-trunk proprioception.

Method

Apparatus. The subject was instructed to stand so that his head was close to a $\frac{1}{4}$ -in.-thick Plexiglas sheet mounted vertically in his coronal plane. On the index finger of his preferred hand he wore a rubber thimble with a single raised dot on the tip. After this had been stamped on an ink pad, the subject was told to touch the tip of his nose. This made a mark of area approximately 3 mm^2 on millimeter graph paper attached to the further side of the Plexiglas sheet.

Subjects. Nineteen subjects with measured phoria of 0 ± 2 prism diopters were tested under both control and experimental conditions.

Procedure. The pretest for both control and experimental conditions was carried out under normal laboratory lighting. The subject freely positioned his head, approximately "straight ahead," and then pointed to his nose 10 times while keeping his eyes closed. In the control condition, the subject stood symmetrically as described in the procedure of Experiment 1. He then inclined his head forward in order to inspect a black spot located on the floor midway between his feet. The position of the head was controlled by a foreheadrest.

The experimental condition was identical to that of the first two experiments, and required exposure to base-right 20-diopter prisms for 6 min, during which the subject was asked to inspect his right foot. During the treatment, with all room lights extinguished, the only illuminated area was around the object of inspection. The posttest followed each of these conditions.

The lights were turned on and the subject pointed to his nose 10 times with his eyes closed, as before. In both pre- and posttests, the true positions of the nose were recorded by the experimenter. The errors of judgment were obtained by measuring the distance between the true position of the nose and each of the 10 localization points made by the subject.

Results

There were no significant differences between the pre- and posttests of each of the control and experimental conditions or between the posttests of the control and the experimental conditions.

The mean shift in judgment of the position of the nose was 2.51 mm in the experimental condition and 4.41 mm in the control. For pre- to postexperimental condition, $t(18) = 1.23$, $p > .20$; for pre to post-control condition, $t(18) = 1.44$, $p > .10$. Comparison of posttests in experimental and control conditions resulted in $t(18) = 1.10$, $p > .20$.

DISCUSSION

These three experiments show that prism adaptation of registered eye position can take place under circumstances in which discordant cross-modal spatial information is present and postural after-effects involving eye muscle potentiation (EMP) are precluded. The possibility of spatial aftereffects due to previous head or body positions are also eliminated in the experiments. These data therefore lead to the unambiguous conclusion that *a sufficient condition for adaptive adjustment of registered visual direction exists when vision and kinesthesia give the brain different information about position.*

It should be pointed out that those experimenters who favor naturalistic exposure conditions, such as walking about a campus or along hallways when wearing prisms, should not expect necessarily to observe clear-cut consequences as a result of their manipulations. Such uncontrolled conditions leave it open to the subject to adopt strategies, such as turning the head on the shoulders, which give rise to subsequent postural aftereffects. It also allows subjects to sample a variable amount of cross-modal (visual/kinesthetic) information. A subject may choose to see very little of his body and hence collide with various obstacles, or may move with great caution and watch hands and feet continually. Thus, a subject may show a significant EMP effect (if he kept his head straight on his shoulders) or a head-on-shoulder aftereffect (if eyes were kept straight and head turned in the direction of displacement), or if eyes and head were moved from side to side little or no EMP effect at all. The extent of the adaptation is unpredictable and will depend upon the extent to which the subject can receive and process information relating to cross-modal discordance. These uncontrolled situations could also involve adaptation of

felt limb position to a variable degree in either or both of the upper limbs. Hence, if the localizing systems do self-optimize, any adaptation in the limb component can only reduce the likely extent of adaptation in the eye positioning system. Limb adaptation is an unwanted contaminant when the eye-position system is being investigated; it may be avoided by using as an exposure condition inspection of the feet via prisms, which is a sufficient condition for producing change in registered eye position.

In conclusion, the evidence shows that recalibration of eye-in-head position does take place as a result of cross-modal discordance. It is thus possible to reject the idea of Paap and Ebenholtz (1976) that displacement adaptation is due *solely* to potentiation in the extraocular muscles. We do know, however, that EMP and postural effects can add or subtract from adaptation effects resulting from discordance.

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NOTES

1. Paap and Ebenholtz (1976) show that decay functions for 2- and 4-min ductions of the eyes are at baseline value by about 70 to 80 sec. Further, these data result from 22°-42° ductions; presumably, 11.3° ductions (which are typical of prism experiments) would be expected to give an initial aftereffect of mean

value of 1.5° (from their Figure 1) with a drop to 0.75° within 40 sec.

The above data should be compared with a mean aftereffect of 1.1° when data is collected over a period of a minute after a 3-min exposure to 20-diopter prisms (Craske & Crawshaw, 1974).

2. Pilot experiments carried out by the senior author have failed to support the notion that lateral duction can generate subsequent oscillation of the eyes, even when the duration of prior exposure is 10 min.

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