Dissociation of corollary discharge from gaze direction does not induce a straight-ahead shift

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Pressure on the outer canthus of the eye can change the oculomotor innervation, and thus the corollary discharge, while a subject maintains monocular fixation on a visual target. We tested the possibility that sensory and motor effects of pressing an eye were due to a shift in the subjective straight-ahead direction. Subjects set an auditory source to straight ahead with and without a structured visual field and with and without eyepress. We also measured matching of auditory and visual targets under the same four conditions. Eyepress biased audio-visual matching with and without a structured field, but did not induce a straight-ahead shift. The deviation of the occluded eye was correlated with the amount of perceptual shift in audio-visual matching ($r = .83$). We conclude that perceptual offsets during eyepress are caused by a bias in extraretinal signals, and not by a cognitive straight-ahead shift.

Many factors contribute to the perception of visual direction. This paper will address two of them: (1) corollary discharge (CD) (Sperry, 1950), also referred to as "effort of will" (Helmholtz, 1867) and "Efferenzkopie" (Von Holst & Mittelstaedt, 1950) and (2) visual capture (as defined by Matin, Picoult, Stevens, Edwards, & MacArthur, 1982).

Corollary discharge is an extraretinal signal which informs the visual system of the intended position of the eye. Normally, the CD signal matches the eye position, but in subjects with oculomotor paralysis the two signals are readily mismatched, providing an opportunity to study CD independently of true eye position. Helmholtz (1867) reported that patients with oculomotor paralysis noticed displacement of visual images when they tried to gaze into the paretic field. He proposed that this displacement could be attributed to the efferent "effort of will" controlling eye position, since the paralysis prevented any change in position of retinal images. Matin et al. (1982) administered systemic d-tubocurarine to subjects and instructed them to fixate a display of illuminated points located at a constant offset from primary position. Constant oculomotor effort was required to maintain fixation, and the reduced gain of the oculomotor system meant that CD was offset more than the resulting eye position. Under these conditions, perception of straight ahead was perfectly normal as long as a structured visual field (a laboratory environment) was present. When the lights were extinguished,

the illuminated points seemed to drift in the direction of the deviated CD and then to remain in their eccentric locations. These results led Matin et al. to suggest that the extraretinal signal was superseded by contextual cues in the presence of a structured visual field. In the absence of a structured visual field, however, CD is the predominant factor governing perception of location. Matin et al. also reported that when subjects were asked to match the position of a visual stimulus with an auditory stimulus, their judgments were biased by extraretinal signals in both the presence and absence of a structured visual field.

Eyepress

A series of experiments has replicated and expanded upon the findings of Matin et al. (1982) using the eyepress paradigm to mimic the effects of oculomotor pareses (Bridgeman & Stark, 1981; Stark & Bridgeman, 1983). A subject can fixate a target monocularly, then press on the outer canthus or the lower lid of the eye. The extra innervation required to maintain fixation in the original position is reflected in a biased CD. Like paresis or paralysis of the extraocular muscles, then, the eyepress paradigm induces a mismatch between CD and eye position, with the CD changing while retinal image position remains constant. A press on the monocularly fixating eye will cause (1) the illusion of object displacement in the world (a press on the right side of the right eye leads to perceived displacement to the right), presumably due to the discrepancy between the CD and retinal signals; and (2) the secondary deviation of the unencumbered occluded eye as the oculomotor system counters the effect of the press with a binocular change in innervation. The second-

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dary deviation of the occluded eye can provide an objective, quantitative measure of the CD.

Among other findings, Stark & Bridgeman (1983) found that judgments of a target set to appear straight ahead were unaffected by eyepress under normally illuminated lab conditions, an example of visual capture. But in darkness, judgments were consistently offset, presumably due to the influence of CD on perception. CD was also found to be the predominant source of information for intersensory coordination, as suggested by data from visual-motor coordination and visual-auditory matching experiments.

Recently, another theory has provided an alternative interpretation for many of these results (Post, Shupert, & Leibowitz, 1984). This oculomotor-oriented theory postulates two influences on the processing of visual direction: the first is a phylogenetically old visual stabilization system that drives optokinetic nystagmus (OKN) and optokinetic afternystagmus. It functions to stabilize the image on the retina, integrating information from throughout the visual field. Its gain is relatively low, but spatial summation assures that the eye will follow the visual world with a gain approaching one if there is texture throughout the field. Because of its small subtended visual angle, the fovea contributes relatively little to this system. Vection illusions demonstrate that activation of the OKN system is not registered in perception. The second mechanism is a phylogenetically newer pursuit system which tracks an image on the fovea, working against the OKN system if a foveally fixated object is moving relative to the optic array. Activation of this system is perceived as visual motion. An advantage of the theory is that it uses only systems and mechanisms already known to be present in the nervous system, and requires no additional "black boxes." The OKN system should stabilize the eye against the static perceptual effects of eyepress or paresis in a structured visual field.

Straight-Ahead Shift

Harris (1974) has raised the possibility that the results of experiments involving judgments of the straight ahead were often erroneously interpreted as indicative of a perceptual change, when in fact they were a function of a cognitive bias, the "straight-ahead shift." A straight-ahead shift may be defined as a change in the egocentric spatial direction that is treated as "straight ahead" by the subject; the straight-ahead shift affects all tasks that involve judgments of the straight ahead, including nonvisual tasks, but does not affect other spatial estimates. The definition of egocentric includes three types of directional axes (Howard, 1982): (1) oculocentric direction, specific to the center of the eye and the visual axes; (2) headcentric direction, specific to the center of the head and the median or midtransverse section of the head; and (3) bodycentric direction, specific to some point in the spinal axis and orthogonal to the spinal axis. Harris's change in egocentric spatial direction presumably refers to the bodycentric direction, since straight-ahead shifts can induce corresponding shifts in static eye-in-head or head-on-body orientations.

Harris and Gilchrist (1976) reported a series of experiments that demonstrated a straight-ahead shift without prisms and without adaptation. The main apparatus was a large cardboard box, with the subject's head inside it. Inside the box was a vertical metal rod that the subjects could set to appear straight ahead. Rotating the box 10° about a vertical axis resulted in a 4° shift in the settings of the rod, and a similar shift in pointing to straight ahead with a hand outside the box, but no significant change in pointing to the rod without being able to see the hand. The interpretation was that a straight-ahead shift had biased both visual and nonvisual estimates of straight ahead, but had left visual-manual matching unaffected because the matching task did not require a calibration with the straight-ahead direction.

An eyepress in the light has several perceptual characteristics in common with the straight-ahead shift. The most striking is "immediate correction," a phenomenon named by Rock, Goldberg, and Mack (1966) and later reinterpreted as a result of a straight-ahead shift (Harris, 1974). In immediate correction, a subject looking at a structured visual field through a displacing prism immediately finds that "objects in the scene do not appear as displaced as they ought to, given the magnitude of the displacing power of the prism" (Rock et al., 1966). Similarly, pressing on the eye results in no change in the exocentric position perceived to be straight ahead, especially if vision is occluded at the beginning of the press when the world appears to move. The oculomotor system is deviated as though the eyes were rotated toward the press (and indeed the occluded eye is rotated medially), implying that the opinion about what is straight ahead may have changed. Like the subjects in prism studies, our subjects must deviate the innervation of the eyes to look straight ahead, and, like the immediate correction subjects, our subjects view a static scene without opportunity for adaptation. Thus, a straight-ahead shift might explain the differences we obtained in straight-ahead judgments in the light and in the dark (no shift would be expected in darkness).

The present study is an attempt (1) to determine whether the effects of the eyepress may be attributed to either a cognitive bias (straight-ahead shift) or a perceptual change, and (2) to further delineate the roles of CD and visual capture in space perception. We present two experiments which measured subjects' abilities to judge the auditory straight ahead and to match visual and acoustic stimulus positions while pressing on the monocularly fixating eye.

The first experiment was intended to determine whether or not a shift in the CD mediated by an eyepress would influence a subject's judgment of the auditory straight ahead. That is, would a shift in the visual straight ahead be accompanied by an analogous shift in other sensory modalities, in this case audition? If this were found to be true, it could be concluded that judgments recorded during an eyepress were reflective of a cognitive straight-ahead shift rather than a perceptual change. If it were not true, the lack of shifts might be an artifact of insensitivity of

the dependent measures under our conditions. The purpose of the second experiment was to control for this possibility by showing a clear effect of the eyepress on intersensory coordination, using the same subjects and apparatus as the first experiment.

EXPERIMENT 1: AUDITORY STRAIGHT AHEAD

Method

Apparatus. The study was conducted in a laboratory setting providing extensive visual environmental information. The subject sat at a table (150×91 cm) facing a black opaque screen (106×51 cm). Above the horizontal edge of the screen, near eye height, the subject could see a structured laboratory environment. Corners of the room and wall-ceiling intersections were visible. Head position was fixed by using a bite bar which was adjustable for height and angle of regard. The distance from eye to screen was 90 cm. Paper was fastened behind the screen in order to record the subject's judgments: headcentric straight ahead was marked on the paper as a reference point.

The auditory stimulus consisted of a speaker attached to the base of a metal tube, 22 cm long and with a diameter of 38 mm. A sharp pointer was fastened to the aperture of the sound source in order to mark the subject's judgments on the paper. Stimuli were broadband clicks presented at a rate of 3 clicks/sec.

Procedure. Ten subjects (two naive, eight nonnaive) participated in the study. There were four trial types: (1) press, in the light; (2) no press, in the light; (3) press, in the dark; and (4) no press, in the dark. In the light conditions, the subject maintained a stable gaze position, so that the effect of eyepress was actively countered. In the dark conditions, one would not expect a straight-ahead shift unless proprioception of extraocular muscles could somehow affect the judgments, since there was no visual stimulus to stabilize gaze position. These conditions served as controls to determine the distracting effects of eyepress on straight-ahead judgments. Sixteen trials of each type were presented in a randomly determined order. The subject pressed on the outer canthus of the right eye with the right index finger. Gaze was slightly elevated from primary position, so that apparent motion was horizontal and out of phase with finger motion. For 5 of the 10 subjects, both eyes were occluded during the dynamic phase of the press. When the subject felt that his or her press was steady, the pressed right eye was unoccluded and the trial was initiated. The left eye was always occluded.

For each trial, the experimenter positioned the sound source directly behind the screen. The sound source was then moved laterally at 2°/sec. Half of the trials were begun from the left side of the screen and the other half from the right. The subject was instructed to direct the movement of the sound by using the commands "left, right, stop" until he or she was satisfied that the auditory stimulus was directly straight ahead (headcentrically). The experimenter worked without visual feedback in order to prevent bias in controlling the sound source. Use of verbal commands prevented the subject from attempting to use proprioceptive cues from the apparatus in adjusting the position of the sound source.

Results

For each subject, the distance between the objective reference point and each judgment mark was measured, and mean pointing directions were calculated for each of the four trial types. The data were then entered into a two-way ANOVA (repeated measures). No significant effects of press [$F(1,9) = .9638$, $p = .352$], light [$F(1,9) = .013$, $p = .911$], or interaction [$F(1,9) = .189$, $p = .674$] were found (Table 1, Figure 1). The subjects set the target

Table 1
Auditory Straight Ahead

Variable	F	df	p
Subject	1.79	1,9	.214
Press	0.96	1,9	.352
Light	0.0131	1,9	.911
Press/light interaction	0.189	1,9	.674

Figure 1. Judgments of auditory straight ahead. Each arrow represents 16 trials from each of 10 subjects, and the error arcs represent $\frac{1}{2}$ SD in each direction. All angles in this and the following figure are exaggerated 10-fold for purposes of illustration. The data given here are analyzed statistically in Table 1. Direction is given as deviation from the subjective straight ahead, determined by the average position of the auditory source set to straight ahead with full ambient illumination and no eyepress (light arrow, solid line).

almost exactly straight ahead whether they were in a structured laboratory setting or in darkness, and whether the eye was pressed or not.

EXPERIMENT 2: AUDITORY-VISUAL MATCHING

Method

The stimulus conditions in Experiment 2 were similar to those of Experiment 1, except that a luminous point was positioned directly in front of the subject (distance from eye to point was 71 cm). The subject was instructed to make a judgment when he or she was satisfied that the auditory and visual stimuli were superimposed. Thus, the task was unrelated to subjective straight ahead, although the luminous point was located on the subject's median plane.

For each subject, the average magnitude of the deviation in CD was objectively measured by assessing the deviation of the occluded eye with an infrared system that offered high spatial resolution without contacting the eye. The eye was illuminated with infrared light from a small LED, and infrared-sensitive photocells were aimed at the iris-sclera border. The difference between the signals from the two photocells provided a measure of horizontal eye position (Stark, Vossius, & Young, 1962). Steady-state eye position during eyepress on the fellow eye was compared with eye position without eyepress for each subject.

Table 2
Auditory-Visual Matching

Variable	F	df	p
Subject	26.29	1,9	.001
Press	8.83	1,9	.016
Light	6.47	1,9	.031
Press/light	12.18	1,9	.007

Figure 2. Matching of localized visual and auditory sources. Display conventions as in Figure 1. Each arrow is based on 16 trials from each of 10 subjects. Statistical analysis of the data is given in Table 2.

Results

In this experiment, all subjects showed deviation of auditory-visual matching when the eye was pressed. A two-way ANOVA showed a significant main effect for press [$F(1,9) = 8.83$, $p = .016$], a smaller effect for light [$F(1,9) = 6.47$, $p = .031$], and an interaction effect [$F(1,9) = 12.18$, $p = .007$] (Table 2, Figure 2). One-way ANOVAs were performed between groups to determine the source of the interaction. Press was significantly different from no press in the dark [$F(1,9) = 10.32$, $p = .010$] and in the light [$F(1,9) = 6.99$, $p = .026$], and press in the dark was significantly different from press in the light [$F(1,9) = 15.76$, $p = .004$]. For all subjects, the magnitude of the shift due to eyepress was greater in the dark than in the light (binomial sign test, $p = .0020$). This difference was smaller among subjects who were highly practiced and/or were readily able to master the eyepress.

Bias in the CD, as measured by deviation of the occluded eye, accounted for most of the perceptual offset (Figure 3). The correlation between mean perceptual effect and mean eye deviation accounted for 70% of the between-subjects variance in eye deviation.

GENERAL DISCUSSION

These experiments have shown that eyepress and the resulting offset of CD do not change the subjective straight-ahead direction, as determined with an auditory measure (Experiment 1), whereas the same subjects in the

same apparatus show a strong effect of CD bias on matching of visual and auditory position (Experiment 2). Furthermore, most of the individual differences in the auditory-visual matching effect are accounted for by the magnitude of CD, as determined by the secondary deviation of the occluded fellow eye.

It remains to be explained why no straight-ahead shift was found here when many prism experiments do find a straight-ahead shift (reviewed by Harris, 1974), and the possible roles of straight-ahead shift, oculomotor influences, and CD in perception and visually guided behavior are yet to be analyzed.

Harris (1974) defined the straight-ahead shift as a non-perceptual change in the egocentric direction treated as straight ahead. We made an effort to create conditions in which no straight-ahead shift would occur. Our structured visual field consisted of a rectangular laboratory room, with the subject's axis parallel to two of the walls. The table, screen, and experimental apparatus were oriented in the same rectangular coordinates. The subject's head was restrained with its medial plane parallel to a wall, so that only the eyes were free to move.

Evaluation of eye movement during the eyepress requires measurement of both eye rotation and translation during eyepress. Stark & Bridgeman (1983) determined psychophysically that fixation could be maintained on a small target before and during eyepress, suggesting that the motion of the eye when pressed is a translation in the orbit rather than a rotation. The amount of translation was measured by asking subjects to fixate a reference point mounted halfway between the subject and a tangent screen

Figure 3. Relation of deviation of the occluded eye to deviation of an auditory target set to match the position of an objectively straight-ahead visual target during eyepress. Subjective offset data are based on auditory-visual matching in the light condition with a structured visual field.

Figure 4. Top view of the method for estimating the translation of the eye in the orbit during eyepress. The dashed contour represents eye position in the control condition; the solid contour represents position during eyepress. The angle of eye deviation and the distance D have been exaggerated for purposes of illustration. In Stark and Bridgeman (1983), the maximum deviation was about 0.12% of the distance from eye to screen; in the present experiments, the estimated deviation D is 0.067%. With the tangent screen in our psychophysical experiments moved back to 90 cm from the eye, deviations from straight ahead during eyepress are negligible.

(Figure 4), with the head immobilized. The difference between the projections of the point on the screen before and during an eyepress corresponds to the translation of the eye in the orbit. This difference is small compared with the auditory-visual matching effects obtained in Experiment 2. We conclude that body, head, and eye orientation were stabilized, and that only CD changed during the experiment; Experiment 1 shows that these precautions were adequate to prevent a straight-ahead shift. Thus, the CD does not contribute to a straight-ahead shift by itself.

The remaining results can be interpreted by the oculomotor theory of Post et al. (1984). We can apply the theory to our experiments by extending it to static situations. The OKN and pursuit systems always have some state of activation, even when it is static. A press on the eye in a structured visual field should induce an unregistered OKN effort to maintain eye position, with no perceptual change in apparent position of the visual world. In the absence of a structured visual field, stabilization can be achieved only by activating the pursuit system, so that an offset of the visual target is perceived.

This theory explains why Stark & Bridgeman (1983) found an effect of eyepress on the perceived straight-ahead position of a point in darkness but not in a structured visual field. The effects on pointing and auditory-visual matching were similar with and without a structured field, however, implying that the mechanism that drives these effects is different from the mechanism that drives the perception of apparent straight-ahead position. Matin,

Stevens, and Picoult (1983) noted a similar paradox in their paralysis results. Because the motor theory can explain all of the effects on the perceived straight ahead, we conclude that, in the context of this theory, the CD never influences perceived visual direction. Rather, CD influences only the interaction of vision with nonvisual measures (pointing and auditory matching).

The oculomotor theory can also explain the dynamic effects of eyepress. If one pushes relatively quickly on the eye, but still allows fixation to remain on a single point, one experiences motion of the visual world. In this case, the relatively slow OKN system is not adequate to stabilize the eye, and some registered pursuit innervation is added to the final oculomotor signal. This added pursuit innervation is perceived as motion. If one pushes very slowly on the eye, however, using several seconds to reach a complete press, there is no apparent motion of the visual world. In this case, the OKN system is adequate to stabilize the eye, and therefore no motion is perceived.

The contrast between oculomotor control and CD can be summarized by proposing that a copy of the pursuit innervation branches off to a perceptual level before the OKN and pursuit systems converge on the oculomotor controller. At a stage after the convergence of these two systems on oculomotor control, the CD branches off to influence the interaction of visual and nonvisual sources of spatial information.

In Experiment 2, auditory and visual stimuli were superimposed at a greater offset from the center without a structured visual field than with one. The same trend is evident in Stark and Bridgeman (1983, Figure 5), which reported that both pointing and auditory matching showed greater offsets without a structured visual field. The effect was not significant in that paper. Matin et al. (1982) also found auditory matching to be "indistinguishable" in light and dark. Both the Matin et al. and the Stark and Bridgeman studies used a small number of subjects and observations, though; with a larger number of subjects and trials, the present effect is statistically significant. The interpretation of this difference is still a question; it may mean that there is some influence of visual capture or of the OKN system on the visual signal that is used for the matching process, but not enough influence to abolish the bias effect. The result is in agreement with the results of Shebilske (1984). In a structured visual field, he found smaller, but still significant, effects of gaze bias on ballistic motor activities. Thus, the results obtained with eyepress are consistent with those obtained from the minor motor anomaly method.

Matin et al. (1982) used drug-induced paresis to reduce the gain of the oculomotor system. With this method, the largest differences between eye position and oculomotor output, and the largest expected experimental effects, are obtained at the largest deviations from primary position. Our method, in contrast, introduces a constant offset between eye position and CD rather than a reduced gain, so that we can obtain equally large effects at the primary position and at eccentric positions. Thus, we have pre-

ferred to work near primary position where human subjects ordinarily perform spatial tasks. At this position, the present data show no straight-ahead shift. It is still an open question whether a straight-ahead shift will occur at the eccentric gaze positions used in paralysis and paresis experiments.

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