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# PHYSIOLOGICAL CORRELATES OF ADAPTATION TO A ROTATED VISUAL FIELD

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## SUMMARY

1. Perceptual adaptation to a 30 or 45° visual tilt was induced in human subjects by means of prismatic spectacles worn for 5–7 days. Relative contrast thresholds and the amplitudes of the occipital potentials to vertical and oblique gratings were studied.

2. During continuous exposure to the tilted visual environment the normal differences between contrast thresholds for vertical and oblique targets decreased or were no longer significant. In all subjects the change from control threshold differences was significant at the 0·005 level.

3. During the course of adaptation the difference in amplitude of the potentials evoked by vertical and oblique oscillating gratings also decreased. The changes with respect to control differences were significant at the 0·005 level in each subject.

4. Intermittent exposure to tilt in one subject resulted only in minor adaptation of the apparent vertical, and the evoked potential differences did not change from control levels.

5. The changes are interpreted as suggesting that plastic changes in the extraretinal mechanism responsive to target orientation occur during adaptation to prismatic tilt.


## INTRODUCTION

When the visual field is systematically inverted, tilted or displaced by prismatic spectacles, human subjects eventually adapt and perceive the surrounding world in its proper orientation. Following removal of such prisms a so-called 'after-effect' occurs during which the visual world temporarily appears distorted in the opposite direction to which the subject had become adapted (Taylor, 1962; Harris, 1965). Although several factors have been shown to influence the rate and extent of this

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complex adaptive process (Held & Freedman, 1963; Michaelian & Held, 1964; Morant & Beller, 1965; Ebenholtz, 1966), the site and nature of the underlying neural mechanisms remain obscure.

The present study represents an attempt to gain some insight into these mechanisms based on the observations that the vertical and horizontal visual axis enjoy particular psychophysical and electrophysiological properties. Visual acuity and contrast sensitivity are known to depend upon the orientation of the target (Taylor, 1963): gratings are better resolved when they are vertical or horizontal than when oblique with respect to the subject. Neither optical factors (Campbell, Kulikowski & Levinson, 1966) nor ocular movements (Higgins & Stultz, 1950) can account for these psychophysical features which reflect characteristics of central neural mechanisms sensitive to orientation. Moreover, the amplitude of the occipital potential evoked by an oscillating grating has also been shown to be a function of its orientation (Maffei & Campbell, 1970). Vertical and horizontal gratings give rise to larger evoked potentials than oblique ones. For any spatial frequency of the grating, the extrapolated contrast threshold for the evoked potential approximates the psychophysical threshold (Campbell & Maffei, 1970; Campbell & Kulikowski, 1972).

In this study we undertook to determine if perceptual adaptation to prism-induced visual tilt is associated with changes in the orientation giving optimal contrast resolution and maximal evoked potentials.

## METHODS

Four non-astigmatic adult subjects were selected for the experiments. In two subjects both contrast thresholds and evoked potentials were studied (L.M. and A.F.) and in two subjects (M.B. and S.B. respectively) either contrast thresholds or evoked potentials alone were evaluated. Selection of subjects was found to be necessary since in some the evoked potentials were irregular (using only 500 averages) and of variable amplitude from determination to determination. In others, the differences between potentials evoked by vertical and oblique gratings was small or inconsistent (evoked potentials of subject M.B. could not be studied for this reason).

It is of interest that astigmatic subjects in particular did not show consistent differences in evoked potentials despite optical correction. The relationship between the angle of the astigmatism and the evoked potential differences were not however investigated.

Unfortunately the difficulty in finding appropriate subjects was compounded by the fact that among those with reproducible evoked potentials some were either unreliable or unwilling to wear prism for the long period required. In no case could a lack of demonstrable difference in evoked potential amplitude for vertical and oblique targets be ascribed to the spatial frequency or to the contrast level of the grating, nor was placement of the recording electrodes critical.

Visual tilt was obtained with two pairs of dove prisms mounted in tandem in front of a helmet allowing binocular vision without right–left reversal. The field viewed by the subjects was approximately 15° in all directions. Peripheral vision was occluded. The subjects wore the prisms continuously during waking hours for 5–7 days. At night when the prisms had to be removed for sleeping, the subjects covered their eyes with a black bandage. While wearing the prisms the subjects were encouraged to walk about and keep as active as possible.

The prisms were set to produce a counter-clockwise rotation of 30 or 45°. In one subject (A.F.) the tilt was changed from 30 to 45° during the course of the experiment. Also in this subject an additional trial of adaptation was attempted using the method advocated by Taylor (1962). She was then exposed, for only 4 hr each day for 6 days, to a tilt of 45°. The data for this subject will be considered separately.

Subjective perceptual compensation was periodically assessed by having the subjects adjust to the vertical a bright bar which was viewed through the prisms against a dark background. The angle between this apparent vertical and the real vertical orientation was measured. Intermittently, determinations of the tilt after-effects were made in a similar manner, though with the prisms removed and, in total darkness, such that only the bright bar was visible to the subject.

Contrast thresholds were measured for gratings set at two orientations, (1) vertical and (2) either 30 or 45° clockwise from the vertical according to the prism setting used for the subject. As viewed through the prisms the vertical grating gave an oblique and the oblique a vertical retinal image. The grating was generated on an oscilloscope screen and the oscilloscope tube could be rotated to any desired angle. The target was viewed from a distance of 2 m and subtended an angle of about 3·5°. The spatial frequency of the grating was 5·5 c/deg. The contrast between light and dark bands could be varied by the subject and adjusted to threshold by means of a potentiometer. The average luminance was maintained constant despite the variations in contrast. Within each session the thresholds for the oblique grating as well as S.D. and S.E. were expressed as a percentage of the mean threshold for the vertical grating. Daily measurements and the differences were then generally grouped together.

Visual evoked potentials were elicited by alternating the phase of a 1·5 c/deg grating 8 times/sec. In this way the light flux entering the eye remained constant. A lower spatial frequency of the grating was chosen for the evoked potentials in order to reduce the time necessary to average the responses. The contrast was set approximately 1 log unit above the psychophysical threshold to keep the potential amplitude below its saturation level. The potentials were recorded from the occipital area of the scalp, filtered and averaged (generally 500 times) with a computer of average transients (see Campbell & Maffei, 1970, for details of the technique). A roughly sinusoidal wave form is thus obtained (Fig. 2). Potentials evoked by vertical and oblique gratings were always done in immediate succession and the percent difference in amplitude of the potential evoked by the oblique as compared to the vertical grating was taken for each pair. Generally groups of 4–6 pairs of evoked potentials were done in one session.

It has to be noted that this technique does not enable us to specify absolute changes in the amplitude of the evoked potentials during the course of the experiment.

## RESULTS

All subjects reported progressive diminution of apparent tilt. The difference between their apparent vertical and the real vertical decreased most rapidly in the first several hours, in accord with the findings of

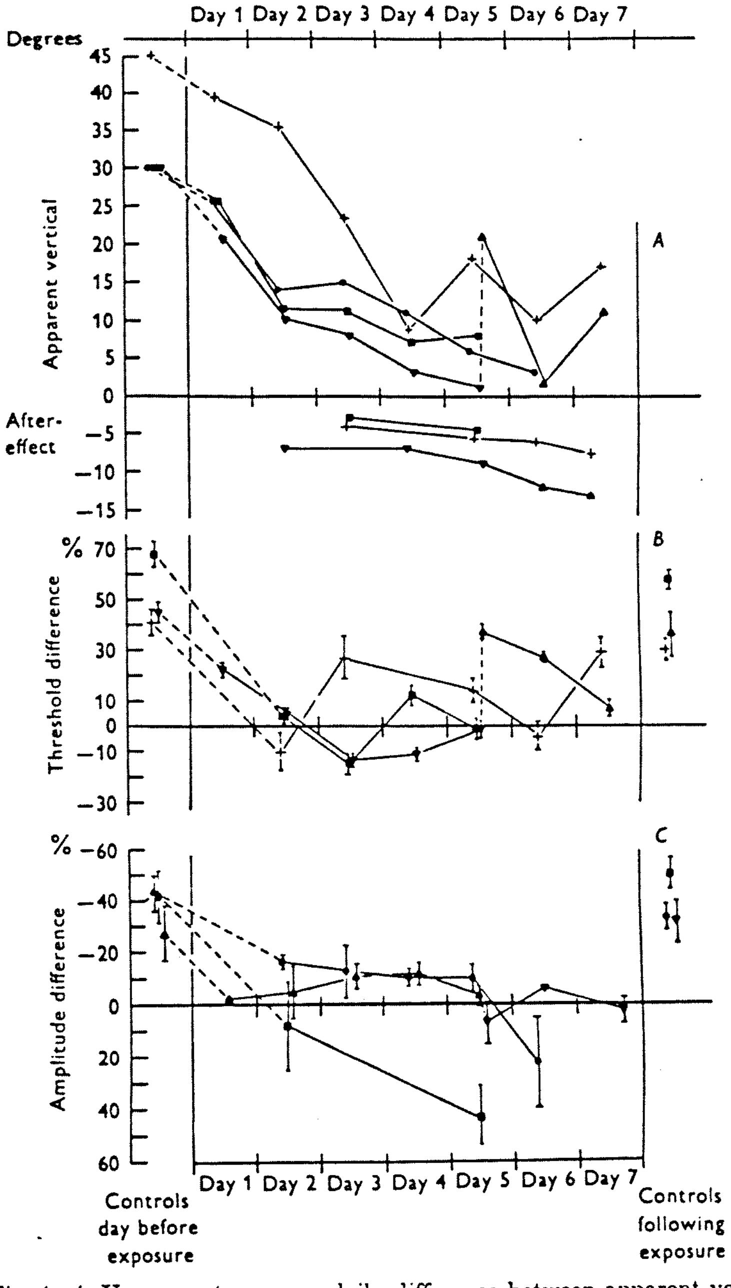


Fig. 1. *A*, Upper part; average daily difference between apparent vertical and real vertical; lower part; tilt after-effect. *B*, daily threshold differences for all subjects. *C*, daily evoked potential differences for all subjects; in subject S.B. (circles) the control determinations following exposure are those obtained 2 hr after the prisms were reset to eliminate the visual tilt. Vertical bars in *B* and *C* are S.E. ●, S.B.; +, M.B.; ■, L.M.; ▼, A.F., 30°; ▲, A.F., 45°.

previous authors (Ebenholtz, 1966). Adaptation continued albeit at a lesser pace during ensuing days (Fig. 1*A*). By the fourth day the subjects commonly felt that some familiar objects occasionally no longer appeared tilted while in general the visual world seemed almost normal.

Perceptual after-effects increased at a considerably slower rate (bottom part of Fig. 1*A*) and continued to increase even after the subjects experienced nearly complete subjective compensation. By the end of the period of adaptation the tilt after-effect never exceeded 14° in any subject.

*Changes in contrast thresholds*

Control threshold determinations were done on 5 or 6 separate days in each subject. Averaging the mean daily threshold difference for each subject, control thresholds for oblique targets (30 or 45°) were from 35 to 54 % greater than for vertical targets. Means varied from day to day with a S.D. between 12 and 18 % according to the subject. Threshold differences were always highly significant in each subject and each day (when comparing 10–20 single values the standard errors were generally of the order of 5–7 %). Furthermore, the difference in threshold for gratings with vertical or oblique retinal images was similar whether the target was viewed directly or through the prisms irrespective of the angle setting of the latter.

Following exposure to the prismatic tilt, the normal differences in contrast threshold decreased or disappeared. Indeed, the pattern was similar in each subject: during the period of exposure, thresholds for vertical gratings were commonly not significantly different from those for oblique gratings. On some days there were differences in thresholds in the normal direction, on other days there was relative inversion. Thus on occasion the target with an oblique retinal image was seen at a significantly lower contrast level (see Fig. 1*B*, subject A.F. on days 3 and 4). In each case, comparison (*t* test) of the grouped data for control threshold differences with those obtained during exposure to tilt showed changes which were significant at the 0·005 level (see Table 1).

In one of the subjects (A. F.) the threshold changes occurred over a 2-day period when exposed to a 30° tilt. When the prisms were reset at 45° there was progressive decrease in threshold difference over an additional 2½-day interval (Fig. 2*B*). During the intervening period and during the entire period of adaptation in the other subjects no trend was observed for the threshold changes. Specifically, the changes in threshold did not parallel the gains in subjective adaptation to the visual tilt and correlation coefficients between the changes in apparent vertical and threshold were not significant when control values were excluded.

A control experiment was performed on one subject (L.M.) to ensure

TABLE 1. In each subject control determinations and determinations made during exposure to tilt are grouped together. Means and S.E. of threshold differences are expressed as percentages of the mean threshold for vertical targets. Means and S.E. of the evoked potential differences are expressed as percentages of the potential amplitude evoked by the vertical grating. *P* values were computed by means of the *t* test

| Subject and angle tilt | Controls *n* | Controls Mean | Controls S.E. | Exposure to tilt *n* | Exposure to tilt Mean | Exposure to tilt S.E. | *P* |
|---|---|---|---|---|---|---|---|
| S.B. 30° | | | | | | | |
| Apparent vertical (last day of expt.) | | | | | 3° | | |
| Evoked potential difference | 53 | −33·95 | 2·17 | 48 | −2·49 | 5·0 | <0·005 |
| M.B. 45° | | | | | | | |
| Apparent vertical (last day) | | | | | 17° | | |
| Threshold difference | 55 | 38·14 | 3·29 | 61 | 14·57 | 2·93 | <0·005 |
| L.M. 30° | | | | | | | |
| Apparent vertical (last day) | | | | | 7·9° | | |
| Threshold difference | 66 | 50·06 | 4·04 | 85 | 1·36 | 1·89 (n.s.) | <0·005 |
| Evoked potential difference | 15 | −31·06 | 7·4 | 11 | 29·91 | 8·59 | |
| A.F. (1) 30° | | | | | | | |
| Apparent vertical (last day) | | | | | 1·0° | | |
| Threshold difference | 53 | 36·32 | 3·7 | 117 | 2·09 | 1·16 (n.s.) | <0·005 |
| Evoked potential difference | 6 | −21·83 | 5·29 | 22 | −7·91 | 2·59 | <0·005 |
| A.F. (1) 45° | | | | | | | |
| Apparent vertical (last day) | | | | | 11·2° | | |
| Threshold difference | 45 | 39·73 | 3·52 | 50 | 21·15 | 1·38 | <0·005 |
| Evoked potential difference | 6 | −35·0 | 5·96 | 10 | 3·1 | 3·95 (n.s.) | <0·005 |
| A.F. (2) 45° | | | | Intermittent exposure | | | |
| Apparent vertical (last day) | | | | | 33·6° | | |
| Evoked potential difference | 14 | −30·785 | 3·80 | 32 | −28·94 | 2·78 | n.s. |

that the changes observed were not consequent upon the severe restriction of the visual field. In a second trial run, the subject wore the prisms oriented to produce a tilt of 30° for 1½ days. Before exposure, the threshold difference between vertical and oblique targets was 38·3 % (S.E. 6·2), after 1½ days there was no longer any significant difference (mean −1·7 %, S.E. 3·6). At that point the prisms were reset to the vertical eliminating all tilt and the subject continued wearing the prisms. Two hours later the threshold difference had reappeared (mean 74·0 %, S.E. 10·4) despite the continued restriction of visual fields.

*Changes in evoked potentials*

Average control differences in occipital potentials evoked by vertical and oblique oscillating gratings varied between subjects from 22 to 34 %. These differences were always significant and reproducible from day to day: S.D. of daily control determinations varied from 7 to 12 %. As observed for the contrast thresholds, the same differences occurred when the grating was viewed with or without the prisms.

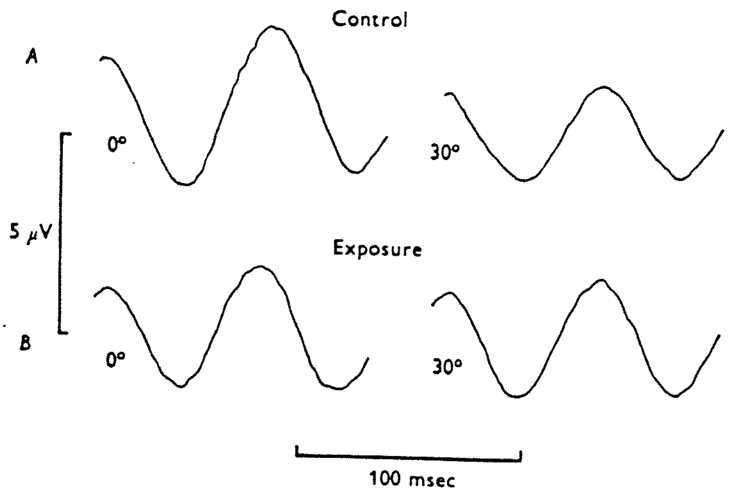


Fig. 2. Sample evoked potential records from subject S. B. *A*, control tracings. *B*, records obtained during exposure to tilt. 0 and 30° indicate the orientation of the retinal image of the grating.

During the period of adaptation the differences in potentials evoked by the two orientations of target stimuli decreased and often the evoked potentials were of similar amplitude (Figs. 2 *B*, 1 *C*). In only one subject on one day was significant inversion observed. In every case the change in amplitude difference from control levels was highly significant: *t* tests on the grouped data comparing control differences with differences during the period of exposure yielded $P$ values better than the 0·005 level (see Table 1).

As we observed for the contrast thresholds, no trend was apparent and it was not possible to correlate the variations in apparent vertical with the changes in evoked potentials.

Whereas a good correlation exists between evoked potential amplitude and psychophysical thresholds in normal unadapted subjects (Campbell & Maffei, 1970) no such correlation was seen during prism adaptation. Nevertheless the major changes in both psychophysical thresholds and in evoked potentials took place within a 2-day period following application of the prisms. Some isolated evoked potentials done within 2 hr of exposure did not reveal any substantial differences from control determinations.

In one subject (S.B.), at the end of the period of adaptation when there was no significant difference in potentials evoked by vertical and oblique gratings, the prisms were reset to eliminate the tilt. After 2 hr a difference of 37·0 % (S.E. 7·9) was again present (Fig. 1 *C*) and did not change on the subsequent day during which the now straightened prisms continued to be worn.

Several months after the first run, one subject (A.F.) was exposed to a visual tilt of 45° for 4 hr each morning for 6 days. Whereas during the first exposure subjective compensation was progressive and virtually complete by the fourth or fifth day, only partial adaptation was achieved now (Table 1), and did not increase after a final 2½ days of continuous exposure. During this trial run, evoked potentials did not depart from control values (see Table 1).

## DISCUSSION

Our findings indicate that the greater contrast resolution and the larger visual evoked potentials associated with vertical targets represent a labile property of the visual system of man.

It has been argued that the orientation sensitive potentials in human subjects are determined by the activation of extraretinal neurones with orientation specific properties (Maffei & Campbell 1970). The changes in the relative amplitudes of the visual evoked potential might derive from the presence even in the adult human of a group of central visual neurones with labile orientation-sensitive properties. The preferred orientation of such units might then be determined by particular characteristics of the environment to which they are exposed. Such a characteristic could be the greater preponderance of contours in the vertical and horizontal directions. In kittens selectively exposed to lines of a single orientation, Hirsh & Spinelli (1971) and Blakemore & Cooper (1971) observed that the directional specificity of cortical neurones largely conformed to the orientations to which they had been exposed. Although it does not seem likely that such properties might persist in primary visual areas in the adult (Wiesel & Hubel, 1970) a similar phenomenon might occur in visual association areas. Alternatively, the preferred orientation of some units responding to visual stimuli could depend upon concomitant converging influences from other sensory modalities or from association areas concerned with the elaboration of peripheral information. Vestibular influences in particular could be important and are known to affect unitary responses in both cortex (Horn & Hill, 1969; Hornl Stechler & Hill), and superior colliculus (Bisti, Maffei & Piccolino, 1972) to specific orientational stimuli. It has also been claimed (John, Shimokochi & Bartlett, 1969) that within visual and other evoked potentials is embedded an 'endogenous' component reflecting in some fashion the significance of the stimulus for the subject. The latency of this component is extremely brief (35 msec) and might be included in the wave form which we studied.

Summing up, our data do suggest that from the first days of prism adaptation there occurs a process of dedifferentiation in the orientation specificity of some visually responsive units. Whether stable inversion in relative size of evoked potentials and contrast sensitivity would occur cannot be stated. This matter and the related question of the relationship of these changes to the nature of adaptation to a tilted environment would probably require much more prolonged periods of exposure, perhaps more readily accomplished in the experimental animal. Although there was not a clear-cut relationship between the changes in contrast thresholds or evoked potentials and the degree of subjective adaptation, the results obtained with the subject exposed intermittently to the prismatic distortion may constitute indirect evidence. Indeed, in this subject exposed to a tilted visual field the absence of adaption was not associated with changes in evoked potentials such as those observed in the same and other subjects when subjective adaptation occurred.

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