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Orthogonal adaptation and orientation discrimination

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Abstract

The change in apparent orientation of lines and gratings induced by surrounding or preceding patterns of a different orientation (the tilt illusion and tilt after-effect) has been abundantly documented, but there is no unanimity about the effect of such inducing patterns on orientation discrimination thresholds. In particular, because inducing contours that are almost orthogonal cause the direction of the tilt illusion to reverse, evidence for an improvement of orientation discrimination with orthogonal adaptation has been welcomed on theoretical ground as supporting concepts of inversion of polarity of neural connection between cortical cells with oriented receptive fields for large orientation differences. In careful psychophysical experiments on human observers with several kinds of test and orthogonal adaptation patterns the average ratio of adapted/unadapted discrimination thresholds in paired sets of data was 1.027 ± 0.13 , which does not differ significantly from unity and hence constitutes evidence that orthogonal adaptation does not improve orientation discrimination.

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1. Introduction

Adaptation to oriented contours has a profound influence on the perceived orientation of visual pattern. Most widely known is the so-called tilt illusion in which lines or gratings surrounded or preceded by oriented patterns experience a shift in their apparent tilt. When the inducing lines differ in orientation by up to about 60° , the induced shift is repulsive, making the difference in the orientation of the inducing and test patterns appear to increase. For differences that approach 90° , the effect is reversed, producing an apparent attraction between inducing and test patterns (Wenderoth & Johnstone, 1988).

The standard interpretation of the tilt illusion involves interaction between neurons with orientated receptive fields in the primary visual cortex. Both excitatory and inhibitory signals are thought to be involved. When the direction of the tilt illusion is reversed for large values of the induced/test orientation differences, this can be interpreted as an inversion of the sign of the interacting signals.

The bulk of the literature on the tilt illusion deals with induced changes in the apparent direction of contours. Only a few studies concerned themselves with the orientation discrimination sensitivity in the presence of such induced changes in mean orientation (Barlow, Macleod, & van Meeteren, 1976; Clifford, Wyatt, Arnold, Smith, & Wenderoth, 2001; Regan & Beverley, 1985). Discrimination thresholds are widely used as indicators of neural sensitivity; it is, therefore, of interest to know whether the reversal of sign of the tilt illusion as the inducing angle approaches orthogonality is also associated with a change in orientation sensitivity.

There is, unfortunately, no unanimity about the influence of orientation adaptation on discrimination thresholds. Barlow et al. (1976) found no effects. Regan and Beverley (1985) reported a reduction in performance for small inclinations of the inducing patterns and an actual improvement when inducing and test patterns were parallel. The most recent research duplicated these effects (Clifford et al., 2001), but also included a startling claim: an actual improvement of up to 50% in thresholds over the plain, unadapted situation for adapting angles of 90° and thereabouts. That an artificially induced state of the visual system, in this case extended previous exposure to an orthogonal grating, should permit performance to be twice as good

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as normal is indeed surprising and unprecedented; hence this specific issue of improved thresholds for orthogonal adaptation was here revisited.

2. Method

One may distinguish between the tilt illusion or simultaneous orientation contrast and the tilt after-effect, i.e., when the visual system has been adapted by inspection for some time to an influencing oriented pattern. The two phenomena are closely related and show similarity in many respects. Because there are difficulties in measuring the orientation of a line or grating in the presence of a superimposed pattern of a different orientation, the experiments referred to above and the ones to be reported here utilized the tilt after-effect. The visual system was exposed for long periods to the inducing pattern which was interrupted for brief periods (<1 s) by stimuli designed to probe the sensitivity for orientation differences.

We used three different approaches to test the effect of orthogonal adaptation on spatial orientation discrimination. For all experiments, the observers' task was to discriminate the direction in which a test stimulus was tilted relative to an immediately preceding standard. In each trial, a stimulus was shown first in the comparison orientation, usually vertical and, following a short pause, a test stimulus appeared which was randomly positioned in one of seven orientations at equally spaced intervals centered on the comparison. The observers' task was to judge the direction of the deviation of the test from the comparison. The two-interval forced-choice judgment was registered by pressing a button on the computer mouse. Two to five runs of 150 trials for each comparison situations were obtained on different days and the orientation discrimination threshold was calculated from the summed results by the method of probits, yielding a threshold (half the difference between the 25% and 75% responses on the psychometric curve) and its standard error.

The display was generated on a 15 in. Sony monitor by a Pentium-based PC with a refresh rate of 60 Hz. All programs were written in the C language, using an anti-aliasing algorithm for smooth oblique lines, and were run under DOS control with interrupts disabled. Observation was binocular at a distance of either 5 m or 114 cm, depending on the experiment, and no error feedback was provided. The authors and three undergraduate biology students in their early 20s and naïve as to the purposes of the experiments, served as observers. Their refractive and visual status was normal. Except where indicated otherwise, they had sufficient training in the task for perceptual learning not to have been a factor.

Test patterns consisted either of a single line, 20 arcmin in length, or of circular patches of sinusoidal gratings of defined contrast, spatial frequency, orientation and phase. Their parameters are given in each instance in Section 3. As will be described, the testing sequence was shown either by itself at regular intervals of 2.5 s, or during temporal gaps in a continuous display of adapting gratings consisting of either lines or circular patches of sinusoidal gratings. In two of the experiments the observation was foveal. In another it was peripheral with a central fixation square exposed continuously.

The experimental procedure and protocol were approved by the institutional Review Board for the Protection of Human Subjects.

3. Results

The specific aim of this research was to investigate the influence of orthogonal adaptation on orientation discrimination thresholds. This objective was accomplished by conducting experiments in a strictly controlled fashion: in every situation on every day there were paired runs of 150 trials with and without adaptation, one or the other alternating as the first run on sequential days.

In the first experiment, orientation discrimination of a 20 arcmin vertical foveal line, 300 ms in duration and separated from the comparison by a 600 ms pause, was measured with and without adaptation to a set of eight 100 arcmin long horizontal lines, 4 arcmin apart, displayed for 1500 ms. The sequence of events in a single trial is laid out in Fig. 1. Including the initial observation before data-taking commenced, the observer was subjected to the adapting lines for about 8 min, interrupted at regular intervals by the testing sequence.

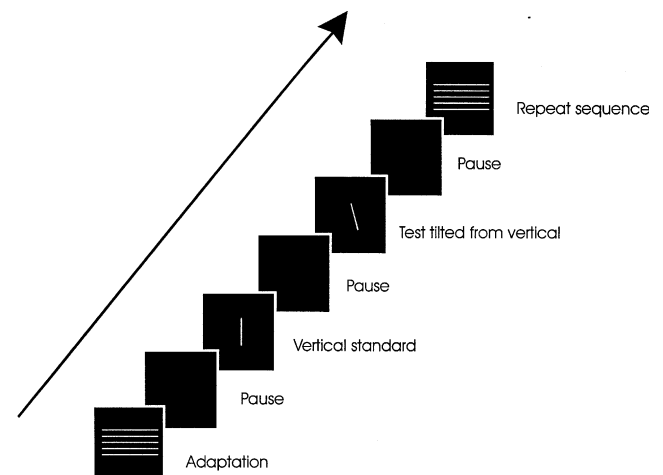


Fig. 1. Sequence of events in a single trial with adaptation. The length of the pauses and the exposure duration of comparison and test line differed among experiments. Similar sequences were used in all experiments.

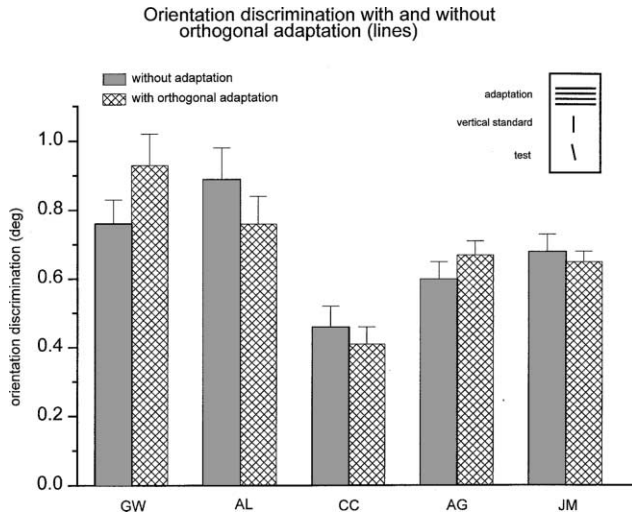


Fig. 2. Orientation discrimination thresholds for a 20 arcmin foveal line displayed for 300 ms in five observers with and without adaptation to a set of eight orthogonal lines, 4 arcmin apart and 100 arcmin long. Inset shows, schematically, the vertical standard and test stimuli, the adapting pattern and which were separated by a 600 ms pause, during the trial. Thresholds with and without adaptation are not distinguishable.

Succeeding runs were separated by at least 10 min to allow full decay of any adapting effects. The results for five observers are plotted in Fig. 2. In strictly paired experiments with and without orthogonal adaptation, thresholds were not distinguishable.

In the second experiment, the stimuli whose orientations were judged consisted of foveal 20 arcmin diameter sinusoidal grating patches, 0.8 contrast and 10 cycles/deg spatial frequency. Orientation thresholds were obtained with and without adaptation to an orthogonal 1.66° diameter circular patch of sinusoidal gratings, 0.8 contrast and 12 cycles/deg spatial frequency. Timing of the sequence was identical to that of experiment 1. Again thresholds with adaptation were indistinguishable from those without adaptation (Fig. 3). Fragmentary data with grating patches of a range of spatial frequencies did not reveal any influence of spatial frequency on this finding.

In view of these results, it was decided to duplicate in all details the stimulus conditions used by Clifford et al. (2001). With central fixation, the observers were shown two circular patches of sinusoidal gratings, 186 arcmin in diameter, 6 cycles/deg spatial frequency, contrast 0.8, whose centers were 154 arcmin to either side of the central fixation point. In the comparison configuration the patches were vertical whereas in their perturbed state they had oppositely directed orientations centered on the vertical. Orientation discrimination was measured in paired separate runs with and without horizontal adapting gratings whose parameters were identical to those of the test gratings. The duration of the comparison and test stimuli was 100 ms and there was a 50 ms

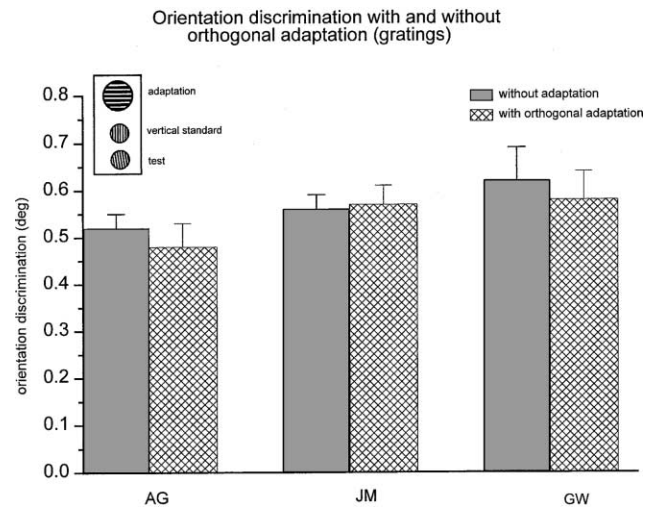


Fig. 3. Orientation discrimination thresholds for three observers for foveal 20 arcmin diameter grating patches, 0.8 contrast and 10 cycles/deg spatial frequency. Data collected with and without adaptation to an orthogonal 1.66° diameter circular patch of sinusoidal gratings, 0.8 contrast and 12 cycles/deg spatial frequency. Inset shows, schematically, the adapting, comparison and test stimuli. Timing of sequence was identical to that of Fig. 2. Again, thresholds with and without adaptation do not differ significantly.

blank screen between them and between the immediately preceding and succeeding adaptation stimulus shown for a 5-s interval between trials. The adapting grating was given a phase jitter at a rate of 0.8 Hz. Viewing distance here was 114 cm. The observers' task was to decide whether the orientation of the two test patches appeared to incline towards or away from each other. The results (Fig. 4) again show no distinguishable effect of adaptation.

To ascertain that the vertical did not constitute a special case, experiment 2 was duplicated in one observer with the whole configuration tilted by 22°, 45° and 78° out of the vertical. Orthogonality between test and adaptation patterns was maintained. Here, Fig. 5, if anything adaptation has a slightly deleterious effect.

Finally, the time parameters of experiment 1 were varied to assure that adequate adaptation to the orthogonal was sustained throughout all trials. Both the duration of the test and comparison presentations was shortened from 300 to 100 ms and the pause intervening between them was cut from 600 to 100 ms. Thus, the interruption of the otherwise continuous adaptation state, which was needed to test its effect on orientation discrimination, was reduced. Using these time parameters, observer AG showed a discrimination threshold of 0.71 ± 0.06 without adaptation and 0.67 ± 0.05 with adaptation ($p > 50\%$). Because these results are comparable to our other experimental data, we do not implicate a decay of adaptation in our findings.

Overall, averaging the ratio of adapted/unadapted thresholds in the 16 paired sets of data in 3 experimental

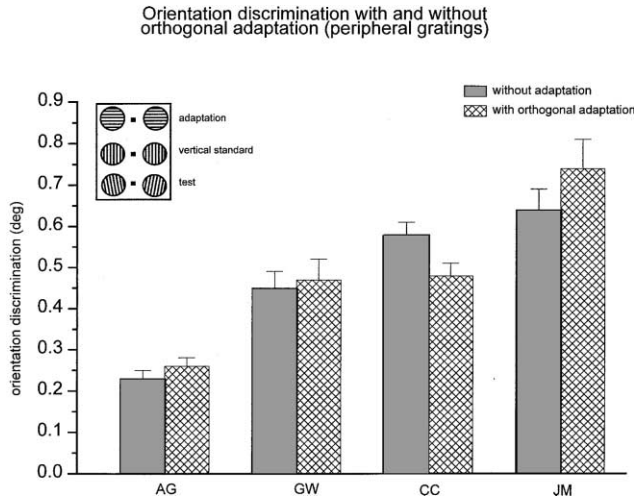


Fig. 4. Orientation discrimination thresholds for circular patches of sinusoidal gratings displayed for 100 ms, 6 cycles/deg spatial frequency, 186 arcmin diameter, 0.8 contrast, centered 154 arcmin from a central fixation spot. Adaptation patches, 5s in duration and with the same dimension and spatial parameters, were orthogonal in orientation and had their phase jittered at 0.8 Hz. Orientation discrimination with and without orthogonal adaptation showed no significant differences in four observers. Adapting, comparison and test configurations, which were separated by a 50 ms blank screen during the trial, are displayed schematically in the inset.

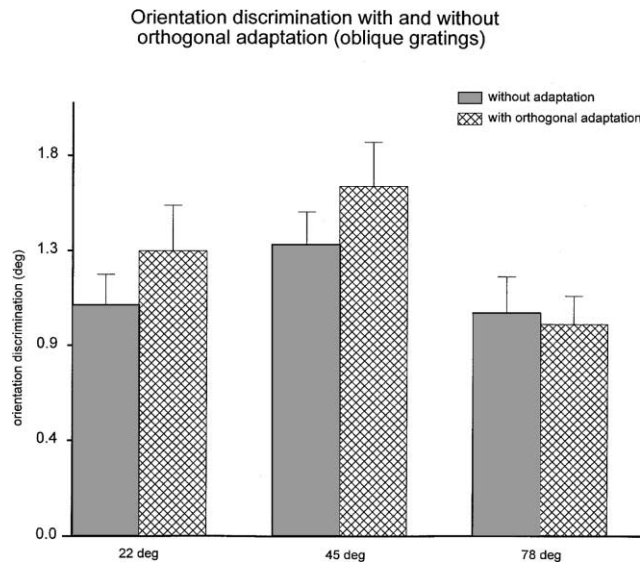


Fig. 5. Same conditions as Fig. 3 except that the basic orientations were rotated into the 22°, 45° and 78° oblique meridians, in each case with and without an orthogonal adaptation patch. Adapted and unadapted conditions show no significant difference. Observer AG.

procedures and 5 subjects, a value of 1.03 ± 0.13 is obtained which does not differ significantly from unity.

4. Discussion

Ever since Hubel and Wiesel's (1962) identification of orientation and direction selectivity of neurons in the

primary visual cortex, the nature of the synaptic circuitry through which this selectivity emerges has commanded interest. This question becomes even more relevant in the present context because human orientation sensitivity for pattern elements like lines, whose neural substrate might very well be located in the primary visual cortex, is at least one order of magnitude better than the width of even the narrowest orientation tuning curves of cortical neurons. There is as yet no complete understanding of the circuitry through which the orientation attribute of a contour is generated, but there is consensus for a vector summation model (Gilbert & Wiesel, 1990; Vogels, 1990) as proposed for motor control by Georgopoulos, Schwartz, and Kettner (1986). Any oriented contour would stimulate orientation-selective cortical cells of a range of preferred orientations, each signaling with a strength depending on its tuning width and the orientation difference between the stimulus and its preferred orientation. These signals, with fixed orientation labels but of varying strengths, could, via an operation akin to vector summation, yield a pointer to a mean orientation with arbitrary precision depending on the number of involved cells and their tuning widths. Both excitatory and inhibitory components have been identified in the confluence of synaptic changes in cortical neurons (see Ferster & Miller, 2000 for a review; Ringach, Bredfeldt, Shapley, & Hawken, 2002).

One model for the tilt illusion involves inhibitory interaction between adjacent neurons of like orientation (Kapadia, Westheimer, & Gilbert, 2000). The reversal of the tilt illusion for inducing angles approaching 90° could then be thought of as a manifestation of change-over of polarity of synaptic connection when there is a large angular separation of neurons' preferred orientation. For example, if orientation repulsion for small inducing angles has its origin in suppressive interactions then the reverse tilt illusion for an almost orthogonal inducing pattern might very well involve activating ones.

It is this kind of reasoning that made Clifford and co-workers welcome the apparent improvement in orientation discrimination with orthogonal adaptation. By comparison, they, as well as Regan and Beverley, saw a worsening performance with near-parallel adaptation, which induced a prominent tilt illusion. In this connection, it is of interest to note that masking of Vernier acuity is also strongest for near-parallel masks (Waugh, Levi, & Carney, 1993) though these authors showed some elevation of thresholds for orthogonal masks, as indeed did Li, Wehrhahn, and Westheimer (1996) when they measured the influence of mask orientation on line-orientation discrimination.

On the other hand, it has been suggested that the direct and indirect tilt illusions are not simply expressions of an interaction opponency at a single neural level, but that they are manifestations of processing at

different levels. Specifically, the experiments of Wenderoth and van der Zwan (1989) led the authors to conclude that the direct tilt illusion is due to interaction at the level of V1 and the indirect at V2 and Poom's (2000) experiments further extended the disparity of stimulus attributes between the direct and indirect tilt illusions.

It remains to conjecture about the reason for the difference between Clifford et al.'s results on orthogonal adaptation and those presented here. Because it could be argued that the reverse tilt illusion is the key, and a stimulus configuration needs to manifest it in order to fit in with their conceptual structure, we ascertained that our patterns do indeed show the classical tilt illusion in both its normal and reverse phases. In any case, because experiment 3 is in all respect a duplication of Clifford et al.'s it is not subject to such a stricture.

We have, however, performed an experiment which in some respect replicates a finding of Clifford et al. Because there is a prominent component of perceptual learning in some spatial visual tasks, especially in the periphery (e.g. Beard, Levi, & Reich, 1995; Ito, Westheimer, & Gilbert, 1988) we have measured the unadapted threshold in two observers and one condition first. This was followed on the next experimental day, after much of the perceptual learning had already taken its course, by a measurement of orientation threshold with orthogonal adaptation and indeed the latter is 35% better (Fig. 6). But an immediately following measurement without adaptation was also much better and a

paired comparison of the latter two showed no adaptation effect.

Acknowledgements

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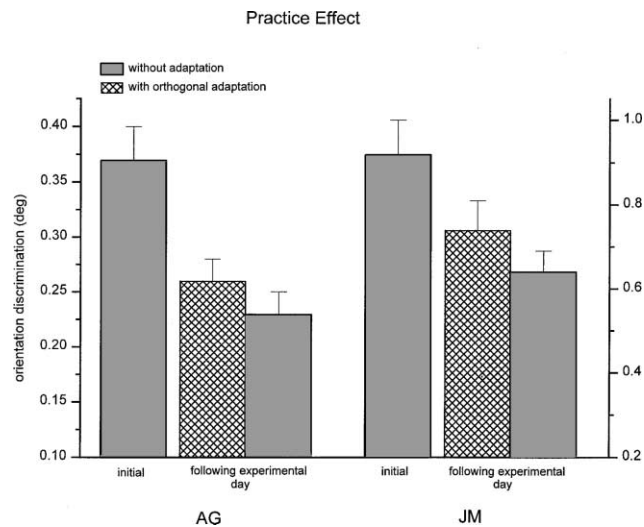


Fig. 6. Learning sequence in experiment 3 for two observers. An initial unadapted run was followed on the next experimental day by paired adapted and unadapted runs. The unadapted threshold on the second day fell to an average of 72% ($p < 0.01$) of its initial value, while on the second day the ratio between the adapted and the unadapted thresholds was not significantly different from unity ($p > 0.5$).