Orientation and spatial frequency effects on linear afterimages: The retinal reference for selectivity—A supplementary report*

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Afterimages of gratings oriented vertically or at 45 deg relative to gravity were generated with the head upright or tilted so that the retinal meridian was inclined 45 deg. The duration of visibility of the whole afterimage was longer for the vertical grating when the head was upright and for the 45-deg grating when the head was tilted. It was concluded that this orientation selectivity of afterimages is dependent upon the orientation of the grating with respect to the retinal meridian rather than to the direction of gravity.

Afterimages of gratings oriented vertically are visible in unitary form for longer than those at 45 deg (Wade, 1973). The evidence for this orientation selectivity was obtained from Ss maintaining a normal upright head posture so that the retinal meridian was aligned with the direction of gravity. Accordingly, the reference axis for the selectivity could be either the retinal vertical meridian or the gravitational vertical.

An experiment which examined the visibility of grating afterimages with the head both upright and tilted is reported.

METHOD

Afterimages were generated by the discharge of a Multiblitz Report flash gun (with an output of 120 J in 2 msec) passing through the apertures of a grating. The spatial frequency of the grating was 2 cycles/deg, and it subtended 4 deg at the eye. The S's head position was controlled by means of an individual dental-composition biteboard, which could be rotated to achieve lateral tilt. The degree of head tilt could be read from a protractor scale. Two switches were positioned in front of S, and these were connected to timers and separate channels of a Rustak event recorder.

Three Ss, well practiced in observing afterimages, were tested. Each used the left eye only, and the right eye was occluded. One S (S 1) had slight (20/30) uncorrected myopia, S 2 was emmetropic, and S 3 had corrected myopia.

Each S was tested in eight sessions. A session was initiated with a procedure, detailed below, to determine the degree of head tilt to employ within that session. There followed 10 min of dark adaptation, after which four afterimage trials were given, two with the head upright and two with the head tilted. In each head position, afterimages of 0- (vertical) and 45-deg gratings (measured with respect to gravity) were generated in the left eye. The afterimages were observed with the eyes closed for 2 min, during which one switch was depressed when the grating was visible in its entirety and the other when only part of it was visible. The intertrial interval was 5 min, during which S was dark adapted. The orders of presentation of the grating orientations and the head positions were counterbalanced, with the restriction that the trials for a given head posture be successive.

The initial procedure was designed to minimize any effects of ocular countertorsion. When the head is tilted laterally, the eyes rotate slightly in the direction opposite to tilt. Thus, in order to ensure that the retinal meridian was tilted by 45 deg, the head

would need to be tilted somewhat in excess of this. At the beginning of each session, an afterimage of a vertical grating was generated with the head upright. The grating was then rotated to 45 deg clockwise and dimly illuminated while S rotated his head to the right until the afterimage was aligned with the grating. The average of two such head adjustments was taken as the degree of head tilt to be employed in that session.¹

The experiment was designed to distinguish between the possible retinal or gravitational reference for afterimage selectivity. According to the retinal hypothesis, the selectivity of 0- over 45-deg gratings should be reversed upon head tilt. That is, a grating aligned with the retinal meridian should be visible in whole form for longer than one inclined to it irrespective of the position of the retinal meridian relative to gravity. The gravitational hypothesis, on the other hand, predicts that a gravitationally vertical grating will be visible for longer than one at 45 deg for both head positions.

RESULTS AND DISCUSSION

The mean durations and frequencies of unitary and partial afterimage visibility for each S are given in Table 1, together with the means. The orientation selective effect was evident for each S with the head upright, i.e., the vertical grating was visible in its entirety for longer than that at 45 deg. This effect was reversed upon head tilt. The grating that was vertical with respect to gravity but inclined to the retinal meridian was visible in whole form for a shorter period than the grating aligned with the retinal meridian. Both of these effects were statistically significant, using the method of planned comparisons [$F(1,6) = 8.88$ and 13.80 , $p < .05$ and $.01$, respectively]. The duration of visibility of the vertical grating with the head upright did not differ significantly from that for the 45-deg grating with the head tilted.

The reverse pattern of results was evident for the partial duration measures. The 45-deg grating was visible in partial form for longer than the vertical grating when the head was upright, but the difference was in the opposite direction during head tilt. Both of these differences were statistically significant [$F(1,6) = 8.69$ and 14.72 , $p < .05$ and $.01$, respectively]. The duration of partial visibility of the vertical grating with the head upright did not differ significantly from that of the 45-deg grating with the head tilted.

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Table 1
Mean Durations (Seconds) and Frequencies of Whole and Partial
Visibility of 0- and 45-Deg Grating Afterimages With the Head
Either Upright or Tilted So That the Retinal
Meridian Was Inclined 45 Deg

		Eye Orientation			
		0 Deg		45 Deg	
		Grating Orientation (Deg)			
S		0	45	0	45
Whole Visibility					
Duration	1	88.9	82.3	84.5	90.0
	2	89.7	79.0	79.9	90.4
	3	42.7	38.3	29.0	40.2
	Mean	73.8	66.5	64.5	73.5
Frequency	1	7.1	4.8	5.9	5.2
	2	7.5	10.0	10.4	7.5
	3	6.9	6.2	4.9	6.9
	Mean	7.2	7.0	7.1	6.5
Partial Visibility					
Duration	1	20.9	28.9	26.6	22.9
	2	26.2	35.0	35.1	25.8
	3	68.9	70.9	79.6	69.2
	Mean	38.7	44.9	47.1	39.3
Frequency	1	6.8	5.4	5.8	4.2
	2	7.4	10.6	10.4	7.6
	3	7.4	6.4	5.6	7.4
	Mean	7.2	7.5	7.3	6.4

The frequencies of whole and partial visibility did not differentiate between any of the conditions.

Under all conditions, the afterimages were visible in either whole or partial form for almost the total 2-min inspection period. That is, whole fades were infrequent. The longer overall visibility was due, most probably, to the larger angular subtense of the gratings (4 deg) relative to the previous study (Wade, 1973). Otherwise, the results are in good general agreement. The whole durations of visibility of S 1 and S 2 were in very close correspondence and were longer than those for S 3. Nonetheless, the same pattern was clearly evident for each S with respect to the different conditions.

The results indicate that the orientation selectivity in afterimage visibility is dependent upon the retinal rather than the gravitational reference axis. This conclusion has certain implications for the possible basis of the effect within the visual system. It was previously suggested (Wade, 1973) that the orientation selectivity could be considered to reflect the operation of functional units responsive to orientation and spatial frequency at the cortical level. Of late, it has been demonstrated physiologically in the cat that a small proportion of cortical cells sensitive to orientation can be influenced by head tilt (Denney & Adorjani, 1971; Horn & Hill, 1969; Horn, Strechler, & Hill, 1972; Spinelli, 1970). That is, their orientation specificity is modified both during and after tilt. The dependence of such analyzers upon head inclination may provide a basis for the various gravitationally dependent visual orientation effects (see Day & Wade, 1969). They do not appear to

be implicated in the effects at present under investigation.

The orientation selectivity demonstrated for grating afterimages corresponds to a wide range of similar effects in human spatial vision (see Appelle, 1972; Howard & Templeton, 1966). It is tempting to relate these as a class to the orientation selectivity that has been evidenced in human cortical potentials: averaged potentials evoked by oscillating vertical gratings are larger in amplitude than those generated by 45-deg gratings (Campbell & Maffei, 1970; Maffei & Campbell, 1970). However, it seems unlikely that the former represent a single class of effects, as the reference axes to which the selectivities are dependent are not the same. That is, some of the effects are dependent upon orientation of the stimuli to the retinal meridian and others to the direction of gravity. For example, orientational variation in acuity is maintained relative to the retinal reference during tilt (Luria, 1963). Discrimination reaction times to single lines, on the other hand, are dependent upon their orientation relative to gravity (Attneave & Olson, 1967). It is improbable that the same cortical processes would mediate both of these effects. Unfortunately, the reference axes for many of the orientation-selective effects remain to be determined by experiments involving head inclination. This would enable grouping the effects with respect to their reference. Those that were dependent upon the gravitational vertical would require the convergence of inputs from both the postural and visual systems—in the manner of those cortical cells sensitive to head posture that were mentioned above. The retinally dependent effects would be mediated by processes within the visual system alone. It should then be possible to determine which class of visual effects is mediated by the orientation selectivity of the evoked potential, when similar head inclination experiments have been conducted to determine its reference. It was previously suggested (Wade, 1973) that the orientation selectivity with grating afterimages is related to that for visual evoked potentials. If this suggestion is correct, it could be predicted that selectivity of the evoked potential is dependent upon the orientation of the grating relative to the retinal meridian.

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NOTE

1. This task proved to be very easy as misalignment of the gratings resulted in the appearance of moiré bands. The extent to which the head was tilted in excess of 45 deg was the measure of countertorsion. The mean degrees of countertorsion for each S were 5.7, 6.1, and 5.3, with corresponding standard deviations of 2.0, 1.7, and 1.5 deg.

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