Interocular Transfer of Orientational Effects

Abstract. *Prolonged exposure of one eye to a diagonal line grating produces masking or decreased sensitivity for similar test gratings presented to the contralateral eye. These aftereffects are orientationally selective and suggest that narrow orientationally tuned channels found by electrophysiological methods in the visual cortex of the cat and the monkey may have neural correlates in the human brain.*

Recent studies (*1*) have established that some channels in the visual system of man are selectively sensitive to the angle of orientation of contours. These orientationally selective channels in human vision may be compared with Hubel and Wiesel's (*2*) discoveries that single cells in the visual cortex of the cat and the monkey respond only to lines with a certain orientation and show selective adaptation within a narrow range of orientations. In order to demonstrate similar higher-level neural adaptation in human vision, we designed an experiment to show that the masking effects of stimulation by a given orientation are not confined to the retina of one eye, but will show interocular transfer.

Dunlap (*3*) found interocular transfer of the masking effect of a dim spot of light presented to the periphery of one eye following its presentation to the corresponding region of the other eye. By forcing convergence of the two eyes upon a dark bar or a light bar, Krauskopf and Riggs (*4*) demonstrated interocular transfer from the fovea of one eye to the other in the disappearance of stabilized images. These studies suggest that some degree of neural adaptation has to occur at or beyond the level at which the impulses from the two eyes interact.

Attempts to determine whether the selective adaptation effects that result from stimulating some orientationally sensitive mechanisms are central in origin or purely retinal have involved presenting a pattern of lines to one eye for a period of adaptation and then the test pattern to the other eye, and comparing the effects with those obtained when both adaptation and test patterns were presented to the same eye. Here the evidence (*5*) is negative, or at best uncertain. The reason why previous investigators have commonly failed to obtain interocular transfer of orientation aftereffects may be that disparate information presented to the two eyes has not been made to converge on the same cortical cells in a given area of the brain.

Our method attempted to force binocular fusion by the stereoscopic presentation, to corresponding areas of the two eyes, of lighted fields of equal luminance, shape, size, and duration before and after each test trial. A six-channel binocular tachistoscope (Scientific Prototype model GB) was used to provide three different conditions of observation: (i) *dichopic*—masking grating presented to the left eye and test grating to the right eye; (ii) *monopic*—both masking and test gratings presented to the right eye; and (iii) *binocular control*—identical nonstriate adaptation fields haploscopically presented to both eyes, and test grating to the right eye.

Both the masking grating and the test grating consisted of 35-mm transparencies containing alternate parallel dark and light stripes each 1 mm wide and subtending 8′ of visual angle. Although the striate masking grating was never presented to more than one eye preceding a given test trial, the channel in which it was located was not known by the subject, who was unable to discriminate which eye was receiving the experimental stimulus. Under all conditions the eye which was not exposed to the masking grating was never closed or kept in the dark; instead, it was shown a disk of blank light adjusted in position to appear superimposed on the disk containing the masking grating presented to the other eye.

When the subject pressed both eyes up against the twin viewing heads of the dual lenses adjusted for optimal convergence he saw a single 4.5° disk of light transilluminated by 5 ft lam (5.4 mlam). Following a ready signal this disk was replaced for a 5-second period by a similar disk containing the diagonal masking grating which had been inserted in the channel of either the left eye or right eye, depending on the condition, dichopic or monopic. Then after a 50-msec interval during which the preexposure field returned, the test grating was presented at threshold luminance and duration to the right eye. The test grating covered a 3° circular area centered within the preceding field and its orientation was varied in random order on successive trials.

The subject's task was to report the orientation of the test grating or, if no lines were visible, to report "blank." To insure a high certainty criterion, subjects were first trained not to make false positive identifications of blanks inserted as control tests in 5 percent of the trials.

Two trained observers served as subjects. The results for each were analyzed separately and found to agree closely. Their percentage of "blank" responses for each of the three conditions of observation were plotted (see Fig. 1) against the orientation of the test grating. The curves for the monopic and the dichopic conditions both show a strong masking effect that peaks at 45°,

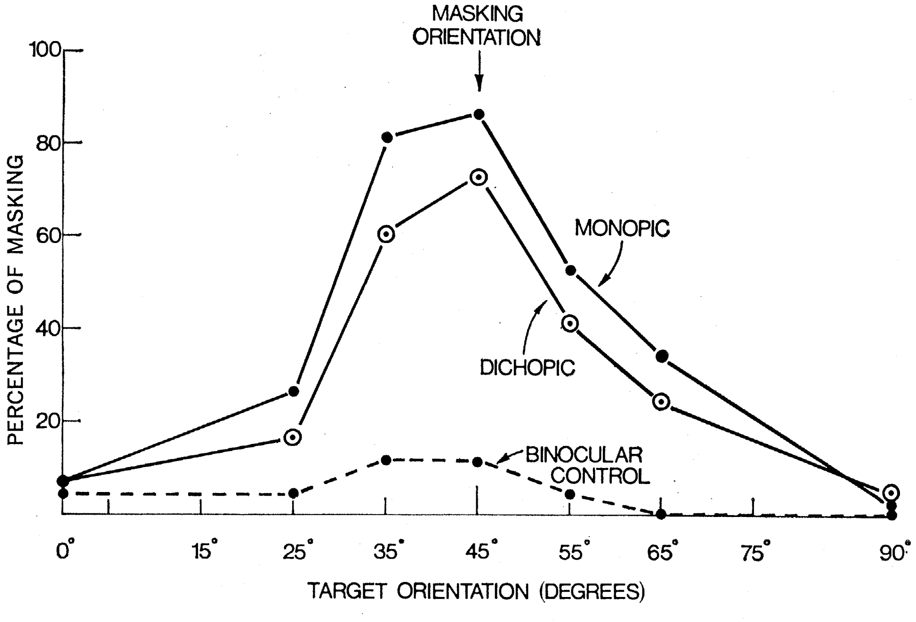

Fig. 1. Percentage of masking or relative frequency of "blank" responses as a function of test target orientation for the three conditions of viewing. Curves for monopic and dichopic viewing peak at 45°, the orientation of the masking grating.

the orientation of the masking grating throughout the experiment. The percentage of masking decreases as the angle of orientation of the target grating deviates on either side from the orientation of the masking grating. Figure 1 shows that dichopic masking clearly parallels monopic masking; both functions are systematically related to the angular separation between the gratings used for adaptation and for testing. The binocular control condition shows a slight hump in the region of the masking orientation, but this possible anchoring effect was not statistically significant.

The effect of the experimental conditions upon the extent of masking was measured by comparing the percentage of "blank" responses under condition (i) and under condition (ii) with the paired trials of the control condition (iii). The paired comparisons for each subject were found by Wilcoxon's test for paired replicates to be significant beyond the .01 level for both the dichopic and the monopic observations.

The significant masking found with dichopic viewing is evidence that interocular transfer of orientational effects does occur. This finding indicates that some higher-level neural adaptation of orientationally selective analyzers takes place in the human visual system and may be the result of contour-detecting mechanisms observed in lower animals that demand cortical integration in primate vision.

The relatively greater monopic than dichopic masking raises a question. But the finding that the masking effect in both conditions is a function of the angular separation between the test and the masking lines is of primary importance. At 10° to 20° away from the masking grating, the masking effect disappears or does not differ significantly from the control. This finding is consistent with a variety of studies (*6*) using different methods that show narrow orientationally tuned channels in the visual system of different species. The angular selectivity characteristic is much narrower than would be expected on a simple Cartesian coordinate system. This characteristic is in remarkable agreement with Hubel and Wiesel's description of the orientation sensitivity of cortical cells found by electrophysiological techniques.

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References and Notes

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Homology and Analogy

The terms homology and analogy (*1, 2*) and their derivatives have had more than a century and a half of intensive, and often confusing, usage in biology (*3*). The term homology has become associated with two of the most important concepts in biology: first, structural correspondence (*1*) and second, common ancestry (*2*). On the other hand, the term analogy has been used to refer to the most diverse kinds of concepts from functional correspondences, especially the use of organs and parts, to structural noncorrespondences, which are the opposite of homology.

Owen's (*4*) definitions of the derivative terms may be considered classical:

> Homologue: The same organ in different animals under every variety of form and function.
>
> Analogue: A part or organ in one animal which has the same function as another part or organ in a different animal.

Now these definitions were in need of further elaboration and extended discussions are to be found in Owen's later works. He gave a report to the British Association for the Advancement of Science in 1846, which was published the following year in the *Report of the Meeting*. The title was "Report on the archetype and homologies of the vertebrate skeleton." This extensive address was reprinted in 1848 with some additional facts and illustrations (*5*). I do not wish to refer to all the types of homology that Owen discusses, namely, general, special, and serial, but only to the "special homology"; that is, the essential structural similarity of the corresponding parts of organisms, and the criteria that were useful in the recognition of these correspondences.

In Owen's words, "These relationships are mainly, if not wholly, determined by the relative position and connection of the parts, and may exist independently of form, proportion, substance, function, and similarity of development." In regard to the latter criterion he stated, "There exists doubtless a close general resemblance in the mode of development of homologous parts: but this is subject to modification."

These quotations indicate that, for Owen, homology meant structural correspondence; and this meaning has been attached to this term longer than any other. On the other hand the term analogy always meant to Owen a similarity in "function" or use to the organism and *never* implied the opposite of homology. This is made absolutely clear in the following words: "but homologous parts may be, and often are, also analogous parts in a fuller sense, viz., as performing the same functions: thus the fin or pectoral limb of a Porpoise is homologous with that of a Fish, inasmuch as it is composed of the same or answerable parts: and they are the analogues of each other, inasmuch as they have the same relation of subserviency to swimming."

So much for the classical usages that were pre-Darwinian. But even after Darwin's *Origin of Species* was published, Owen continued with the same definition of homology. In the first volume of his *Comparative Anatomy and Physiology of Vertebrates* (*6*), he accepts "an ascent from the general or lower to the particular or higher condition of organism."

"The most intelligible idea of homologous parts in such series is that they are due to inheritance." But the occurrence of evolution did not, for Owen, warrant a redefinition of homology so as to include the requirement that homologous parts must be "due to common ancestry." Owen's caution was, to me, quite admirable, for, then as now, inferences in regard to the common ancestry of parts are based chiefly on the kinds and amounts of structural correspondence among them. In discussing homology, Woodger (*7*) commends such caution. "Nothing is more striking in this science [biology] than the contrast between the brilliant skill, ingenuity, and care bestowed upon observation and experiment, and the