

world through the same receptors. From this it follows that in the retina any cell that responds selectively to a particular configuration of the afferent influences must do so independently of specific pathways. By specific pathway we mean a pathway that would be used only for the detection of a particular pattern, to the exclusion of other patterns. We do not refer to the specific excitatory or inhibitory properties of the cells.

These arguments also apply to other retinal and cortical cells that perform specific functions, regardless of whether one can or cannot at present explain analytically their mode of operation. Excitatory and inhibitory processes certainly play a role as components of the input to the cells, but it is to the spatio-temporal configuration of these processes in the input that the cells appear to be specifically sensitive, and thus it is this configuration of the input which we have to consider as the actual stimulus to the cell. Some cells like those which we have discussed may require a very complex configuration, while others may respond to a more simple one, as do ganglion cells in the cat retina (3).

In general we think that the cells of a particular kind will respond to all events that occur in the outside world, in the organism, or in the nervous system capable of producing such a configuration in the input, treating them as equivalent. In other words, we think that a cell will treat these events as members of the same class, the class being defined by the specific configuration to which the cell is sensitive, and hence by some element common to the organization of all the events that produce it. The meaning of the class will arise from the context (functional, behavioral, and so forth) in which the cell activity occurs and the activity developed by a cell when responding will thus represent this class. We believe that neurons behave in this way regardless of their position in the central nervous system. For cells anatomically located further in the central nervous system, the configuration of afferent influences which stimulates them will of necessity depend on the activity of cells in other centers and they are thus able to detect classes made up of other classes. We believe that this mode of operation, in which nerve cells (or part of them) behave as unitary elements capable of class (pattern) recognition independently of spe-

cific pathways, is a fundamental feature of the functional organization of nerve cells in the central nervous system. It seems to us that an adequate understanding of this point leads to a new approach to the problem of the functional organization of the nervous system and the questions of pattern recognition and learning (7).

HUMBERTO R. MATURANA
S. FRENK

Cátedra de Biología and Instituto de Fisiología, Escuela de Medicina, Universidad de Chile, Santiago

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Contour Interaction and Visual Resolution: Contralateral Effects

Abstract. Detection of the gap in a four-position Landolt C presented to one eye is impaired by critically spaced surrounding bars seen only by the other eye. The intensity and spatial extent of this contralateral contour interaction match those obtained ipsilaterally. These results indicate that the neural site for this loss of visual information is suprarretinal.

Human visual resolution is known to depend upon the physical characteristics of the test object, the optical properties of the eye, and the physiological state of the system. Thus, with a given eye and a known or at least constant state of the system, the resolution of a certain kind of target is determined by its size, contrast, brightness, and duration of presentation. Less well known, but none the less important, is the influence of nearby borders or surrounding contours on the visual resolution of a target of interest (1). Such *contour interaction* can be sufficiently powerful to obliterate resolution of an above-threshold test letter (2). This effect has recently been quantified by using a

four-position Landolt C and introducing to the same eye four surrounding bars symmetrically placed at various eccentricities from the test C (3) (Fig. 1).

Visual detection of the gap in the C was maximally impaired when the bars were located about two gap widths from the C. Resolution impairment was generally less for separations smaller than this and was essentially absent when the bars were more than five gap widths away from the C. This was true even though the eyes studied covered a wide range of resolving capacities; the spatial extent of interaction was proportional to the resolving capacity of the eye. Thus, resolution impairment occurred with contours separated by only 2 minutes of arc from the C for eyes having high acuity, but as far out as 24 minutes of arc for low-acuity (amblyopic) eyes. Optical spread in an in-focus image is too small to account for the extensive range of this effect; it has therefore been argued (3) that this contour interaction has a neural basis. The question is whether such neural interaction occurs at a retinal level or somewhere higher in the visual system. The previous monocular studies fail to answer this question; our study was designed to do so by looking for possible impairment of resolution of a target seen by one eye when peripheral contours are presented to the *opposite* eye.

Contralateral presentation of a Landolt C to one eye and peripheral bars to the other was accomplished in the present experiment by means of suitably arranged polarizing filters. For comparison, ipsilateral presentation of the C and bars to one eye, with a matching (56 ft-lam) blank white field for the other eye, was made possible by rotating the filters at the target. Contralateral and ipsilateral presentations of the bars were randomly intermixed; the subjects were unaware of the arrangement. Prior to exposure of the C and bars, the subject binocularly fixated a small spot on a matching white field seen in a mirror. Elevation of the mirror exposed the C and bars for 0.5 second; no eye movements were required for foveal imagery during this interval. Each subject's ametropia was corrected with spectacle lenses. The Landolt C was placed at a viewing distance which permitted about 80 percent correct identifications of gap orientation. At this viewing distance, the frequency of seeing was also determined for each of a series of targets differing only in the

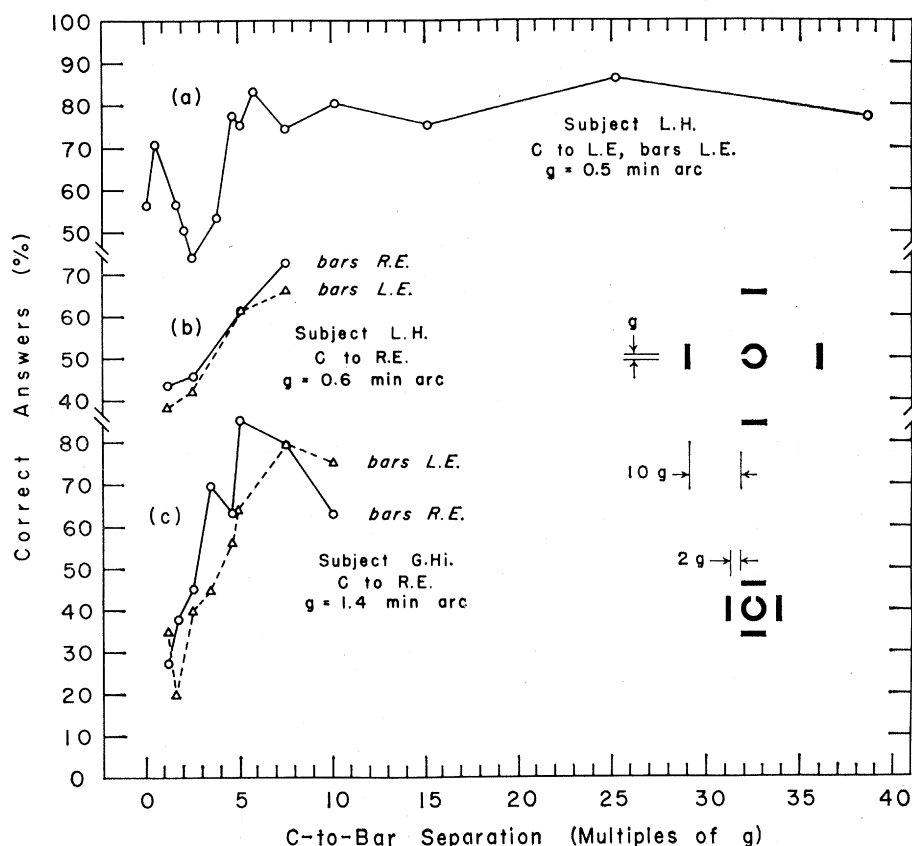


Fig. 1. For targets like those shown at the right, the percentage of correct identifications of gap orientation is plotted as a function of C-bar separation expressed as multiples of gap width, g . The prominent dip in the top curve (a) indicates the critical range of bar separations producing ipsilateral contour interaction; (b) and (c) show the similarity between ipsilateral and contralateral effects within this range. Each plotted point represents about 80 presentations for subject L.H. and about 40 for G.Hi. If the reader increases the distance of this page from his eye until the gap in the lower C just disappears, the gap in the upper C should still be detectable.

separation between C and surrounding bars.

Curve (a) in Fig. 1 is typical of the variation in frequency of seeing obtained ipsilaterally in a previous experiment (3) for a wide range of bar separations. Since contour interaction was evidenced mainly for bar-to-C separations of less than about six multiples of the gap width, the separations in the present study were therefore confined to this range. Curves (b) and (c) of Fig. 1 illustrate the key results of this experiment: presentation of peripheral bars either ipsilaterally or contralaterally gave virtually identical impairment of resolution.

The contralateral interaction for the two subjects in question, as well as for the two others tested, was distinctly more pronounced when the resolution target was presented to the poorer seeing eye, even though the difference in acuity was so slight as to be nearly immeasurable in three of the four subjects (male college students). This greater

effect from bars presented to the better seeing eye suggests a "dominant" or stronger signal reaching the site of interaction from one eye. This led us to attempt to do two things: to weaken the dominant signal and to strengthen the weaker one. First, a 0.4 neutral density filter was placed before the better, left eye of subject L.H.; results showed strong contralateral influence of right-eye bars on resolution of the left eye's C where little interaction had been shown before. Consistent with this "weakening" effect produced by the filter before the left eye, there was now essentially no contralateral effect of left-eye bars on resolution of the C by the right eye. Second, enlarging the overall size of bars to the poorer right eye of subject G.Hi. (by 1.4 times, proportional to the reduced acuity of that eye) increased the previously modest contralateral interaction to equal that exhibited by the other eye. When these larger bars were ipsilaterally presented to the better left eye, resolution impair-

ment was the same as that obtained with bars of regular size. Thus, the intensity and even the direction, but not the spatial extent, of contralateral interaction has been shown to be alterable by changing the relative "strength" of the separate signals for the two eyes.

The contour interaction of the present study is manifested as a loss of information within the visual system. That this loss occurs in the retina is disproved by the contralateral experiments here reported. Even ipsilateral contour interaction is difficult to attribute to the retina—the striking similarity between ipsilateral and contralateral effects makes it highly improbable that separate retinal and suparetinal interaction sites exist. The most probable explanation is that *both* the ipsilateral and contralateral contour interactions take place at a level in the visual system at which sensory information from the two eyes has already come together.

The loss of visual information which results from contour interaction is virtually an inescapable feature of human monocular and binocular vision. Nearly every ordinary visual scene contains numerous near-threshold targets whose resolution is made more difficult or impossible by the presence of nearby contours. In those situations where there is opportunity to control the visual situation (for example, road signs, visual displays, maps, and typography), consideration should be given to the influence of contour interaction along with the more well-known stimulus variables of size, contrast, brightness, and duration of viewing. Unfortunately, only relatively little qualification of this effect is available, and although the present study has established that it takes place suparetinally, neither its exact site nor its underlying physiology is as yet known (4).

MERTON C. FLOM
GORDON G. HEATH*
ELLEN TAKAHASHI

University of California School of
Optometry, Berkeley 4

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