Enhanced Perception of Illusory Contours in the Lower Versus Upper Visual Hemifields

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The visual world consciously perceived is very different from the spatial array of photo-receptor activation present on our retinae; it is composed of segregated surfaces, organized into distinct objects. An important component of this organizational process, the segmentation of an image into figures and background, is shown to be performed much better in the lower visual field. This finding is demonstrated by the performance in two tasks that involve the perception of illusory contours. This asymmetry indicates a neural specialization that may be related to the anatomical discontinuity along the representation of the horizontal meridian in extrastriate visual cortex.

One of the basic problems faced by the visual system is that of segmenting the visual scene into figure and background. Scene segmentation involves difficult computations that go beyond edge detection. This is strikingly illustrated by the phenomenon of illusory contours (ICs) (Fig. 1), in which surface borders are perceived where no luminance boundaries exist. It is widely held that the emergence of ICs reveals the workings of segmentation processes that operate constantly on the incoming visual image (1).

Recent neural models of scene segmentation and IC formation (2) hypothesize that they are carried out in visual cortical areas that are retinotopically organized. This assumption is supported by electro-physiological evidence that cells in such cortical areas respond to the presentation of ICs within their receptive fields (3). A prominent anatomical property of retinotopic visual areas is that the representation of the visual field is split into disjoint portions of the cortical sheet. In addition to the well-known anatomical break between left and right hemispheres, there is a wide separation between the upper and lower hemifield representations in extrastriate visual cortex (4), which has received little attention so far. Introspectively, we are not aware of these splits in the retinotopic representation; surfaces that cross the horizontal or vertical meridians appear unitary and whole. Nevertheless, under careful experimental conditions it is possible to uncover behavioral effects that may be the result of the anatomical discontinuities. Here we report that, in two different experiments, observers exhibit a greater tendency to perceive ICs when the inducing stimuli fall on their lower visual field.

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The stimulus used in our first experiment was a stereogram similar to that depicted in Fig. 2. We let observers view the stimulus freely (that is, no specified fixation point) until they reported that the images were well fused and that they had a vivid impression of depth (5). Then, we instructed them to fixate the upper and lower crosses for 30 s each (order of the fixation points was counterbalanced between observers) and asked whether they perceived a difference in the organization of the scene in the two cases (if they hesitated, they were allowed to move back and forth between the two fixation points). Twenty-two out of 26 observers [P < 0.0003; (6)] reported a noticeable difference in their percepts between the two fixation conditions. When they fixated the upper cross, there was a bright illusory horizontal stripe linking the two filled rectangles (Fig. 2B). In contrast, when they fixated the lower cross, the illusory stripe "faded away" and the two filled rectangles were perceived to be disjoint (Fig. 2C). The stimulus is symmetric with respect to reflection about its horizontal midline, and therefore the only difference is that the (identical) stimulation falls on the upper versus lower visual hemifields. Thus, using a stereoscopic stimulus where occlusion is not strongly suggested in the monocular images, but is still a possible scene interpretation, reveals a difference in the tendency of ICs to emerge in the upper versus lower hemifields (7).

Next, we asked whether such hemifield differences can also be reflected in differential performance in a psychophysical task, and in particular in cases where the stimulus contains only pictorial occlusion cues (that is, no stereopsis). For that purpose, we used a task wherein subjects had to discriminate the shape of a slightly distorted square bounded by ICs, presented briefly, as described in Fig. 3A (8). The left panels in Fig. 4 show the results of an individual observer (9). The upper and lower graphs show the subject's performance when the stimulus fell on the upper and lower hemi-

fields, respectively (10). The lower hemifield shows a marked advantage for the performance of this task. Defining threshold performance as the amount of rotation of the inducing elements needed for the subject to reach 82% correct discrimination (11), the thresholds were 2° and 7.8° for the lower and upper hemifields, respectively. The table in Fig. 3A shows the thresholds of four observers. All performed the task much better in the lower hemifield, with thresholds approximately three times lower than in the upper hemifield (12).

To establish that this differential performance was indeed a result of the perception of an illusory surface, we ran two control tasks. First, we asked whether the lower field has an advantage in shape discrimination in general, and not particularly for illusory shapes. To test this notion, we doubled the diameter of the inducing elements while maintaining the distance between their centers fixed, so that the shapes were bounded by a luminance-defined edge all around (that is, no illusory contours). The "pacmen" figures were again rotated in the same manner (Fig. 3B), and the subject had to discriminate between the two possible classes of shapes. The results are shown in the right panels of Fig. 4. Performance in the shape-discrimination task was very similar in the upper and lower hemifields when the shape was defined by a luminance edge all around (thresholds 1.1° and 0.9°, respectively).

Finally, to control for possible differences in the visibility (or reliability of representation) of the local inducing elements in the upper and lower hemifields, we tested the subject's performance in an orientation discrimination task (Fig. 3C) when all four inducing (pacmen) elements were facing the same direction and rotated above or below the horizon (13). The psychometric functions obtained for the upper and lower fields (not shown) were very similar; subject CT required a rotation of the local elements by 2.6° and 2.5°, respectively, to reach threshold performance. Thus, the superior performance exhibited in the IC-related task in the lower field cannot be accounted for by an advantage in the visibility of the local inducing elements.

The tables in Fig. 3, B and C, summarize the results of all four observers in the upper and lower hemifields for the two control conditions and show that in these cases per-

Fig. 1. Illusory contours (ICs). A white "bloblike" shape is seen in front of a set of partially occluded circles (the inducers). The white-on-white parts of its bounding contour are not supported by luminance-defined edges in the image and are therefore illusory.
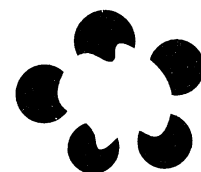
formance in the upper and lower hemifields was similar (12). We tested all four observers and did not find any consistent left/right hemifield asymmetry [(14); see also (15)].

We suggest that the marked up/down asymmetry found in our two tasks is based on an asymmetry in cortical organization. An important physical constraint in brain processing is the extent to which neurons can be richly interconnected. Within a giv-en portion of cortex, information is mediated by a dense host of local connections between neurons within and across cortical layers (16). In contrast, more separated regions of cortex are connected only by nerve fibers from the white matter (16); this organization presumably allows for the emergence of specialized brain modules. As already noted, in extrastriate visual areas the representations of the upper and lower quadrants are separated from each other by the earlier visual areas (4). This separation could thus allow the local circuitry of the upper and lower parts of extrastriate visual areas to develop different specializations in visual processing (17). From an ecological point of view, specialization in scene segmentation in the lower field may be the result of a more frequent occurrence of occlusion situations there or of a greater survival importance for segmentation in the ground plane (18, 19).

Another possibility is the existence of a localized brain module that takes part in scene segmentation computations for the entire visual field. The behavioral up/down asymmetry we found could then be the result of a greater accessibility of the cortical representations of the lower versus upper visual field to this specialized module, due to anatomical proximity. Neuropsychological studies (20) and recent imaging results (21) provide some support for this hypothesis. The two alternatives discussed above are not unrelated, because a specialized brain module may emerge as a consequence of an initial advantage of one anatomically isolated part of a neural network
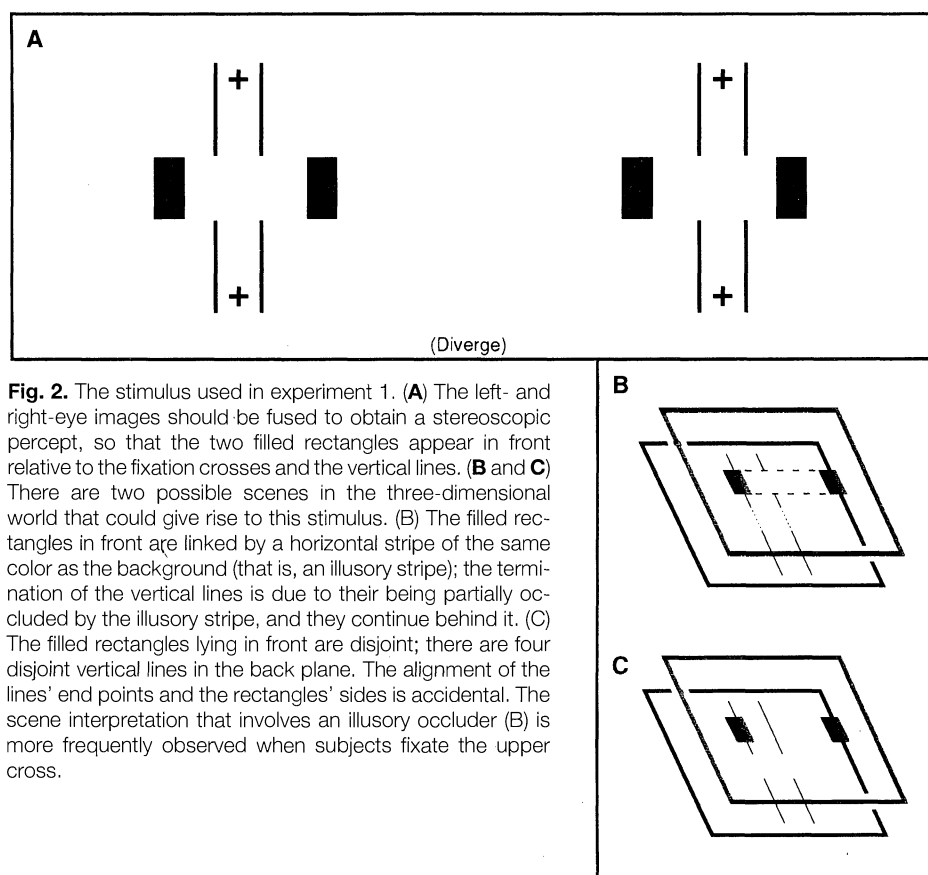

Fig. 2. The stimulus used in experiment 1. (**A**) The left- and right-eye images should be fused to obtain a stereoscopic percept, so that the two filled rectangles appear in front relative to the fixation crosses and the vertical lines. (**B** and **C**) There are two possible scenes in the three-dimensional world that could give rise to this stimulus. (B) The filled rectangles in front are linked by a horizontal stripe of the same color as the background (that is, an illusory stripe); the termination of the vertical lines is due to their being partially occluded by the illusory stripe, and they continue behind it. (C) The filled rectangles lying in front are disjoint; there are four disjoint vertical lines in the back plane. The alignment of the lines' end points and the rectangles' sides is accidental. The scene interpretation that involves an illusory occluder (B) is more frequently observed when subjects fixate the upper cross.
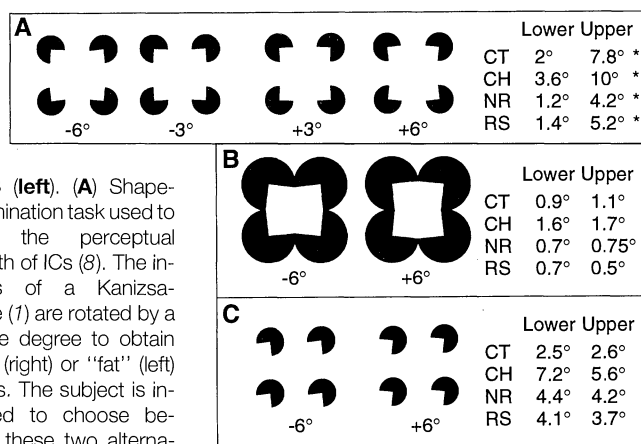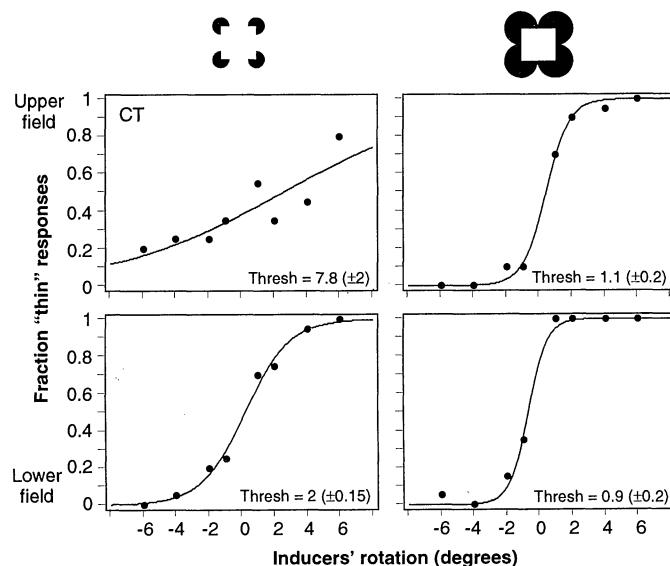

Fig. 3 (**left**). (**A**) Shape-discrimination task used to study the perceptual strength of ICs (8). The inducers of a Kanizsa-square (1) are rotated by a variable degree to obtain "thin" (right) or "fat" (left) shapes. The subject is instructed to choose between these two alternatives. (**B**) Control for shape discrimination in the absence of ICs. The shapes are now bounded by a luminance edge all around. (**C**) Control for visibility differences of the local inducers. The subject is required to decide whether they are oriented slightly above or below the horizon (13). The table next to each stimulus condition in (A) to (C) gives the threshold performances (see text) of four subjects for the lower and upper visual hemifields. Asterisk indicates rows where the difference between the thresholds in the lower and upper hemifields is statistically significant. High thresholds indicate poor performance. **Fig. 4** (**right**). Performance of an individual subject (CT) in experiment 2. The fraction of times (out of 20repetitions per stimulus value) for which the subject judged the stimulus to be "thin" is plotted as a function of the amount of rotation of the inducing elements. The graphs describe four different experimental conditions. The upper (lower) panels correspond to stimulus presentations on the upper (lower) hemifield. (**Left panels**) Performance in the experimental (IC) condition. (**Right panels**) Performance in the shape-discrimination control task.

over another in performing a specific kind of computation (22).

In conclusion, the enhanced performance of IC-related tasks below the horizontal meridian indicates that physiological studies and theoretical models of scene segmentation should take into account early cortical processing inhomogeneities and functional specialization. In addition, testing other visual tasks (for example, perceptual grouping) for up/down asymmetry may help to establish relations between the different components of visual processing.

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4. In extrastriate cortical areas (V2 and higher) of humans and other primates, the upper and lower visual quadrants are represented, respectively, on the lower and upper parts of the cortical sheet within each hemisphere, with visual area V1 physically separating them [D. J. Felleman and D. C. van Essen, *Cereb. Cortex* **1**, 1 (1991); J. C. Horton and W. F. Hoyt, *Arch. Ophthalmol.* **109**, 816 (1991)]. In human neurological patients, this can lead to pronounced quadrantic field defects—a sharp change in visual capacity across the horizontal meridian [G. Holmes, *Proc. R. Soc. London Ser. B.* **132**, 348 (1945); J. C. Horton and W. F. Hoyt, *Brain* **114**, 1703 (1991)].
5. The stereoscopic stimulus was presented with the use of a prism stereo viewer (11 subjects) or as a red/green anaglyph (15 subjects) [B. Julesz, *Foundations of Cyclopean Vision* (Univ. of Chicago Press, Chicago, 1971)].
6. The four remaining subjects could not discern a perceptual difference between the two fixation conditions.
7. In that respect, the stimulus of Fig. 2 is different from most other stereograms involving an illusory occluder [for example, S. Blomfield, *Nature New Biol.* **245**, 256 (1973)], because an (illusory) edge in any orientation other than the horizontal would result in a disparity in the left- and right-eye images for which the only ecologically valid interpretation is one of there being an illusory occluder.
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9. Subjects CT and CH were naïve about the purpose of the experiment. All subjects received extensive practice in performing the shape-discrimination task with the stimulus centered around the fixation point before the collection of the data presented.
10. The stimulus subtended a visual angle of 2.75° and was centered 3.4° above or below the fixation point. The stimulus was presented for 83 ms, followed by a blank screen for 83 ms and then by a mask for 250 ms. The stimulus and the mask were white (12 cd/m²) on a dark background. The subject was restrained with a chin and forehead rest, and the experiment room was dark.
11. A sigmoid curve ({1 + tanh[b(x − a)]}/2) was fit to the data of each psychometric function, with the slope (b) and bias (a) as free parameters; the thresholds were computed from the fitted curves.
12. The differences in thresholds between the upper and lower visual hemifields were statistically significant in the IC condition (Fig. 3A) for all subjects. The differences in the two control conditions were not significant for any of the subjects. The error bars of the slopes (b) were estimated from the variance-covariance matrix [R. Fletcher, *Practical Methods of Optimization* (Wiley, New York, 1980)].
13. For the two presentation conditions (upper and lower hemifields), the stimuli were mirror-reflected about a horizontal line passing through the center, such that in both cases the inducers' arcs were facing the fixation point.
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17. This raises the possibility that the differential specialization in scene segmentation reported here may in turn be related to functional specialization of higher visual areas in the ventral and dorsal streams [L. G. Ungerleider and M. Mishkin, in *Analysis of Visual Behavior*, D. J. Ingle, M. A. Goodale, R. J. W. Mansfield, Eds. (MIT Press, Cambridge, MA, 1982); M. A. Goodale and A. D. Milner, *Trends Neurosci.* **15**, 20 (1992)], because the lower and upper parts of early visual areas project more to ventral and dorsal areas outside the occipital lobe, respectively [J. H. R. Maunsell and W. T. Newsome, *Annu. Rev. Neurosci* **10**, 363 (1987); (19)].
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Use-Dependent Blockers and Exit Rate of the Last Ion from the Multi-Ion Pore of a K+ Channel

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Quaternary ammonium blockers inhibit many voltage-activated potassium (K+) channels from the intracellular side. When applied to *Drosophila* Shaker potassium channels expressed in mammalian cells, these rapidly reversible blockers produced use-dependent inhibition through an unusual mechanism—they promoted an intrinsic conformational change known as C-type inactivation, from which recovery is slow. The blockers did so by cutting off potassium ion flow to a site in the pore, which then emptied at a rate of 10⁵ ions per second. This slow rate probably reflected the departure of the last ion from the multi-ion pore: Permeation of ions (at 10⁷ per second) occurs rapidly because of ion-ion repulsion, but the last ion to leave would experience no such repulsion.

U se dependence is a valuable property for therapeutic inhibitors of ion channels. The ability to block channels during periods of particularly high activity while leaving resting channels relatively unaffected makes use-dependent channel inhibitors valuable as anticonvulsant or antiarrhythmic agents (1). The accepted mechanism of use-dependent inhibition is that an inhibitor binds better when the channel is used and then dissociates slowly (2). In studying open-channel blockers of voltage-activated K+ channels, we found a different mechanism of use dependence. Although the blockers dissociated quickly from the channel, their effect was long lasting because they promot-

ed the intrinsic inactivation gating of the channel, which itself was slow to recover. This influence on inactivation occurred through alteration of the K+ movements in the channel that affect inactivation rather than through an allosteric change in blocker binding to the channel. Analysis of this previously unknown mechanism of use dependence provided information about the kinetics of ion movements in the K+ channel pore.

We used the cloned Shaker-H4 K+ channel from *Drosophila* with a deletion mutation (Δ6–46) that removes the rapid N-type inactivation (3, 4). These channels (ShΔ channels), expressed in mammalian cells by transient transfection, have the gating behavior of delayed rectifier K+ channels: They activate rapidly in response to a depolarizing voltage step and then inactivate rather slowly. This inactivation occurs

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