Reports

Binocular Depth Reversals Despite Familiarity Cues

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Stereoscopic depth can be reversed by interchanging the left- and right-eye views (pseudoscopy) when abstract stereograms are used, but not when stereograms contain natural objects or scenes. This resistance to reversal of depth has traditionally been attributed to familiarity with the shape of objects and the presence of monocular depth cues. However, when texture disparity is neutralized by making the texture perspective of surfaces identical for both eyes, even a highly familiar object, like a monocularly recognizable human face, appears as concave (nose pointing inwards) when viewed pseudoscopically.

IN 1852 WHEATSTONE (*1*) REPORTED that when the disparity of objects is reversed by interchanging the view of the left and right eye ("pseudoscopy" or "pseudoscopic viewing"), apparent depth is also reversed. He also noted, however, that pseudoscopy fails when the shape of an object is familiar or can be monocularly verified. Since Wheatstone's day, it has been generally assumed that cognitive influences counteract the perception of the improbable shapes and depth relations produced by pseudoscopy of natural objects. Well-known instances include photographic stereograms of human faces, which either show essentially normal depth or lack of all depth when they are viewed pseudoscopically. But are monocular depth cues and familiarity considerations indeed responsible for this failure of pseudoscopy?

It is the purpose of this report to show that cognition is not a relevant factor and that only conflicting disparity information stands in the way of binocular depth reversal. Pseudoscopy generally fails in detailed photographic stereograms of natural objects and scenes. Stereograms of this kind have a global depth cue in common that is absent in most abstract stereograms: the perspective of the fine detail of surfaces or texture perspective. Pseudoscopy fails because the disparity of texture perspective cannot be reversed in the same way as the disparity of edges. Interchanging the view of each eye has the effect that edges and other local features of the image are shifted to the correct retinal locations for reversed depth perception. Global image features, however, like the shape and texture perspective of surfaces, remain in the interchanged views characteristic of the original object. For instance, a concave object will as a rule be perceived as concave by both eyes, so interchanging the views does not change the global aspect of concavity.

Figure 1 shows that the difference in texture perspective of an object and its depth-reversed shape can be considerable. Even comparable shapes, such as concave and convex cylindrical surfaces, cannot be correctly reversed in depth unless texture perspective is changed substantially. Therefore, if texture perspective would contribute to binocular depth perception, then stereopsis mechanisms would have to operate on conflicting information in the pseudoscopic viewing situation: the correct disparity of edges and the false disparity of texture perspective.

An indication that texture perspective can function as a binocular depth cue is the marked absence of texture perspective disparity (different texture density gradients of the same surface in the left- and right-eye views) in the only types of stereograms that, as a rule, allow pseudoscopic depth reversals: line and random-dot stereograms. In

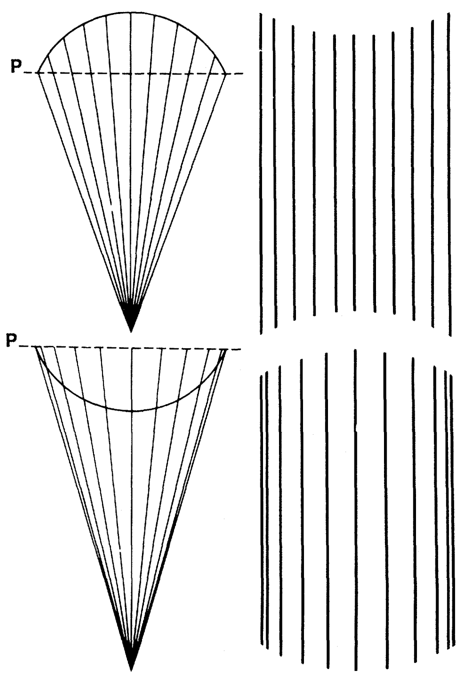

Fig. 1. Texture perspective of a concave (**top**) and a convex (**bottom**) cylindrical surface. Differences in texture perspective are most noticeable near the left and right edges, where the increase in perceived texture density is far more pronounced for convex than for concave cylindrical surfaces.

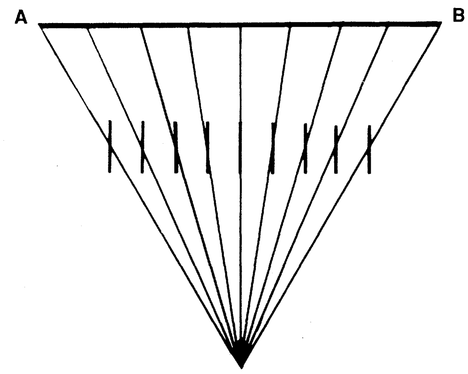

Fig. 2. Texture perspective of a fronto-parallel plane (AB); average viewing distance determines the perceived texture density (symbolized by a bar pattern) and not the length and surface angle of individual lines of sight (as is the case with all other surface orientations). Consequently fronto-parallel planes have an identical or "neutral" texture perspective in the left- and right-eye views.

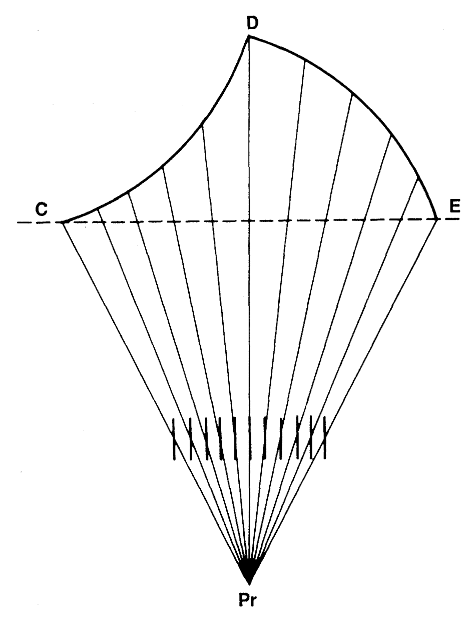

Fig. 3. Texture perspective can be neutralized by projecting a texture with a uniform distribution of elements (symbolized by a bar pattern) onto the surface of an object [the arbitrary concave-convex shape (CDE)] and viewing from the same position as the projection point (Pr). The different distances between the projected points on the surface are under this viewing condition perceived as equal.

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the classical line stereograms of geometrical objects, texture and texture perspective are absent and cannot, therefore, affect the pseudoscopic depth image adversely. Texture is essential to the random-dot stereograms of Julesz (*2*), but note that texture perspective disparity is carefully avoided.

In order to obtain a cyclopean (only binocularly visible) image in depth, texture perspective must be unrelated to the shape and position of the objects in the stereogram, because differences in texture density can make objects monocularly visible. A uniform (random) distribution of texture elements meets this requirement, but this distribution has the additional effect of making the texture perspective of random-dot stereograms "neutral." We use the term "neutral" to mean that texture perspective is unrelated to the shape and position in depth of the object and identical in the view of each eye. In natural viewing situations only fronto-parallel planes have such a neutral texture perspective (Fig. 2).

In this view, neutral texture perspective and not absence of familiarity considerations is the main factor in pseudoscopic depth reversals of random-dot stereograms. If we are correct, then pseudoscopy should be possible regardless of the presence of monocular depth cues and familarity, providing neutral texture perspective is present. A crucial test of this hypothesis would be a stereogram of a monocularly recognizable human face (known as "impossible" to reverse in depth) in which texture perspective is neutral.

We made such a stereogram by the method described by Georgeson (*3*). In this method the original texture of an object is masked by projecting a texture with a uniform distribution of elements onto the object from a position close, or, ideally identical to the viewpoint of the observer (Fig. 3). With cameras near the projection point, stereophotographs can be made that have approximately the same uniform texture density and neutral perspective as the projected texture.

For most readers with good stereoscopic ability [to be tested (*4*) with the line stereogram at the bottom of Figs. 4 to 6], prolonged viewing (10 to 60 s) of the pseudoscopic image of Fig. 5 results in a progressively more detailed reversed shape in depth:

Fig. 4. Stereogram with a neutral texture perspective. The pseudoscopic image has a reversed depth (face is concave; nose pointing inwards). Line stereograms serves as an aid for fusion; a concave or convex pyramid indicating pseudoscopic or stereoscopic fusion respectively.

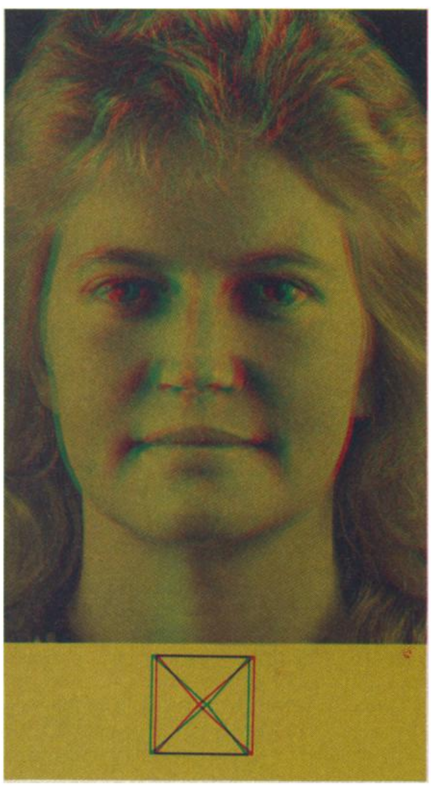

Fig. 5 (left). Anaglyph version of Fig. 4 [to be viewed with red-green spectacles (*5*)]. All perceived depth relations can be reversed by exchanging the filters. With the red filter in front of the left eye and the green filter in front of the right eye normal stereoscopic depth can be seen, for example, the nose points forward. With the filters exchanged, so that the red filter is in front of the right eye, reversed depth becomes apparent and the nose will appear as concave. **Fig. 6 (right).** Anaglyph stereogram of a human face with natural texture perspective (same model as Figs. 4 and 5). In contrast to the solid depth of the stereoscopic image, the pseudoscopic image looks flat and cannot be inverted. The pseudoscopic image is observed by placing the red filter in front of the right eye.

the chin appears deeper than the neck; the convexity of the face becomes concave; nose points inwards. Latency can be reduced by concentrating the gaze on the tip of the nose in the fused image. Masking of the texture of the skin is evident, but most facial features can be recognized without difficulty (Fig. 4). In this stereogram familiarity with the object is clearly a very prominent feature; yet familiarity does not prevent reversal. In contrast, when texture perspective is natural (Fig. 6), the fused image defies any effort to the perceived as inverted.

The creation of a neutral texture perspective has the effect in a monocular view of introducing some flatness into the impression of the face, much as if it had been painted on coarse canvas. Most textures with a sufficiently high density and an approximately uniform distribution of elements proved effective in neutralizing texture perspective. All concave or convex objects (for example, balls, bowls, and boxes) we investigated could be reversed in depth, regardless of familiarity or complexity of shape.

Our stereogram confirms Julesz' emphasis on the role of global factors in binocular depth perception. Neutralizing texture perspective has the binocular effect of eliminating texture perspective disparity. In this way texture perspective is made ineffective as a global binocular depth cue, while the disparity of other global image features, like clusters of texture elements, remains compatible with the disparity of local texture elements. The failure of pseudoscopy when texture perspective disparity is present, shows that a cooperation between local and global disparity information is essential for binocular depth perception.

REFERENCES AND NOTES

1. C. Wheatstone, *Philos. Mag.* **4**, 504 (1852).
2. B. Julesz, *Foundations of Cyclopean Perception* (Univ. of Chicago Press, Chicago, IL, 1971).
3. M. A. Georgeson, *Percept.* **8**, 585 (1979).
4. Readers not being in the possession of a stereoscope or prism can try to fuse the stereogram by crossing their eyes. This can be done by slowly moving a pencil or finger from the stereogram toward the eyes, while concentrating the gaze on the tip. In this way the images should shift until three images are apparent; the middle image will come to depth; the outer images should be disregarded. For a first attempt the reader is advised to fuse the line stereogram: a downward pointing pyramid indicating correct pseudoscopic fusion. Fused images may initially look unsharp, but after a few seconds the eyes will accommodate. We found fusion and accommodation relatively easy with the stereogram held at arm's length.
5. Anaglyphs are constructed by superimposing the left and right views of a stereogram in red and green. To appreciate the depth effect the anaglyphs have to be viewed through a red-green stereo viewer, which separates the original images by filtering, based on the physical wavelengths of light: the eye with the red filter in front can only see the green image and the eye with the green filter in front sees only the red image. The image in depth may not instantly be apparent, since the eyes have to adapt to the filters and to the disparity in the fused image. Good color vision is not necessary, but viewing in good light is essential. Some residual images cannot be avoided, particularly when anaglyphs are reproduced by a regular four-color printing process. For this reason we developed a yellow-green background, which masks most of the red and green residues.
6. We are grateful to R. M. Steinman for critical reading of the manuscript and to J. Brinkman and W. Rÿnders of the Amsterdam School of Graphics for preparing the anaglyphs.

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Crystal Versus Solution Structures of Enzymes: NMR Spectroscopy of a Crystalline Serine Protease

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The hydrogen-bonding status of His^{57} in the catalytic triad (Asp-His-Ser) of serine proteases has important mechanistic implications for this class of enzymes. Recent nitrogen-15 nuclear magnetic resonance (NMR) studies of α-lytic protease find His^{57} and Ser^{195} to be strongly hydrogen-bonded, a result that conflicts with the corresponding crystallographic studies, thereby suggesting that the crystal and solution structures may differ. This discrepancy is addressed and resolved in a nitrogen-15 NMR study of the enzyme in the crystalline state. The results show that the His-Ser and Asp-His interactions are identical in crystals and solutions, but that in crystals His^{57} titrates with a pK_a of 7.9, nearly one pK_a unit higher than in solution. This elevated pK_a accounts for the absence of the His-Ser hydrogen bond in previous x-ray studies.

MOST HIGH-RESOLUTION STRUCTURAL information about proteins comes from x-ray diffraction studies of crystals, whereas functional properties of proteins are usually studied in solution. Thus, the question of whether or not the crystal and solution structures are the same often arises when functional properties are correlated with structure. In the case of enzymes, this question can be especially troublesome, because even small differences in the positions of key functional groups can have important mechanistic implications, and such differences have frequently been noted.

A case in point is the apparent discrepancy concerning the hydrogen-bonding status between His^{57} and Ser^{195} in the active site of serine proteases. Recent solution NMR studies (*1*) of α-lytic protease (α-LP, E.C. 3.4.21.12) have provided evidence for a His-Ser hydrogen bond based on the ^{15}N chemical shifts of the active site His. However, these results conflict with the x-ray crystallographic studies of α-LP (*2–4*) [and of other serine proteases (*5–9*)], which have concluded that Oγ of Ser^{195} and Nε2 of His^{57} are too far apart and not properly aligned to form a hydrogen bond. This discrepancy, though small, nevertheless has important implications for the catalytic mechanism of these enzymes, a mechanism that has been the subject of intense interest and debate (*10–13*). To summarize, the existence of this hydrogen bond would indicate a role for the Asp-His diad in activating the serine hydroxyl group for nucleophilic attack on the substrate. In its absence, such activation would probably not take place, instead the Asp-His diad may be more important in catalyzing the breakdown of the tetrahedral intermediate.

The above discrepancy between the solution and crystalline state studies does not prove that the solution and crystal structures of the enzyme are different. Instead, it raises the question of whether or not either the NMR or x-ray diffraction data could have been misinterpreted or in some other way be in error. (This would be true of any such comparison involving the results of different techniques.) To address this question, we have carried out a ^{15}N NMR study of α-LP in the crystalline state using magic angle spinning (MAS). The results provide a direct comparison with the corresponding solution state study, thereby eliminating the uncertainty described above associated with comparing interpretations of nonequivalent experimental data.

The solution ^{15}N NMR work (*1*), which

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