

The best frequency and the minimum threshold of the MEM reflex are 25 to 40 kHz and 20 db SPL, respectively (3). For comparison, the threshold curve of the acoustic LM reflex was measured with a 40-msec tone burst as the responses of the cricothyroid muscle and the inferior laryngeal nerve (Fig. 1, E and F). The threshold curve was of triangular shape and was narrower than that of the acoustic MEM reflex. The best frequency was between 30 and 40 kHz, similar to that of the acoustic MEM reflex, and the lowest threshold was 50 db SPL, about 30 db higher than that of the acoustic MEM reflex. The Q-10 db values of threshold curves of 68 single cricothyroid muscle fibers ranged from 1.3 to 10 (average, 3.1). For FM sounds similar to orientation sounds of *M. lucifugus*, the threshold of the acoustic LM reflex was about 20 db lower than that for pure tones. The vocal self-stimulation in terms of  $N_1$  (the summated auditory nerve response to an acoustic stimulus) is 80 to 90 db SPL when the bat emits orientation sounds (6), so that the acoustic LM reflex could be evoked by vocal self-stimulation and also intense echoes.

What is the function of the acoustic LM reflex? *M. lucifugus* emits FM orientation sounds 3 to 4 msec in duration at a rate of 10 to 15 sec<sup>-1</sup> during searching or cruising flight. When the bat finds a target and approaches it, the duration of orientation sounds decreases and the rate of sound emission increases. In the terminal phase of echolocation, the duration is often as short as 0.5 msec and the rate as high as 200 sec<sup>-1</sup> (7). If emitted sounds and echoes are both considered, the rate of stimulation of the auditory system goes up to 400 sec<sup>-1</sup>. The acoustic LM reflex may play some role in rapid sound emission. In order to find the possible roles of the reflex, the FM sound comparable to the natural orientation sound was elicited from the bat by electrically stimulating a certain part of the midbrain reticular formation (8), and the effect of an acoustic stimulus on the emission of the FM sound was examined. When a 4-msec tone burst was delivered before the vocalization and the acoustic LM reflex was evoked, the following vocalization was slightly reduced for 150 msec. When the tone burst was delivered after the vocalization, the acoustic LM reflex evoked by the tone burst was augmented for 70 msec. These data suggest that vocalization augments the echo-evoked LM reflex occurring within 70 msec, and the reflex in turn suppresses vocalization following it within 150 msec. In other words, the acoustic LM reflex works as a weak negative feedback for vocalization. A negative feedback in the motor system has been

considered to stabilize the operation of the system. The primary function of the acoustic LM reflex is probably the stabilization of the performance of the vocalization system.

In the above experiment, the electric stimulus that elicited vocalization and the tone burst that evoked the reflex were delivered at a rate of 2 sec<sup>-1</sup>. Since *M. lucifugus* emits orientation sounds at rates higher than 10 sec<sup>-1</sup>, we tried to explore the functional role of the acoustic LM reflex with the bat vocalizing at rates higher than 10 sec<sup>-1</sup>, but we could not obtain data to make any conclusions beyond those given above. It also remains to be determined whether the acoustic LM reflex exists in other mammals or is unique in echolocating bats. As far as we know, this is the first description of the acoustic LM reflex (9).

PHILIP H.-S. JEN\*, NOBUO SUGA

Department of Biology,  
Washington University,  
St. Louis, Missouri 63130

## Perceptual Illusion of Rotation of Three-Dimensional Objects

**Abstract.** *Perspective views of the same three-dimensional object in two orientations, when presented in alternation, produced an illusion of rigid rotation. The minimum cycle duration required for the illusion increased linearly with the angular difference between the orientations and at the same slope for rotations in depth and in the picture plane.*

Shepard and Metzler (1) found that the time required to determine whether two perspective views portray the same three-dimensional object is a linear function of the angular difference between the two orientations portrayed. The decision time is the same for rotations in depth and rotations in the two-dimensional picture plane. They proposed that subjects make the comparisons by carrying out a mental analog of the actual physical rotation of one object into congruence with the other and, further, that the mental representations that are internally transformed in this way are more akin to the three-dimensional objects portrayed than to the two-dimensional retinal projections of those objects.

To say that the internal process is a mental analog of an external process is, in part, to say that the internal process is similar in important respects to the perceptual process that would take place if a subject were actually to watch the corresponding physical rotation (2). We investigated a perceptual illusion of apparent rotational movement in order to further explore the possible role of perceptual mechanisms in mental rotation. By alternately presenting two of the Shepard-Metzler perspective

## References and Notes

1. W. R. Zemlin, *Speech and Hearing Science* (Prentice-Hall, Englewood Cliffs, N.J., 1968).
  2. A. Novick and D. R. Griffin, *J. Exp. Zool.* **148**, 125 (1961).
  3. N. Suga and P. H.-S. Jen, *J. Exp. Biol.* **62**, 277 (1975).
  4. O. W. Henson, Jr., *J. Physiol. London* **180**, 871 (1965); in *Animal Sonar Systems*, R. G. Busnel, Ed. (Laboratory of Auditory Physiology, Jouy-en-Josas, France, 1967), vol. 2, pp. 949-1003.
  5. N. Suga, *J. Physiol. London* **198**, 51 (1968).
  6. \_\_\_\_\_ and P. Schlegel, *J. Acoust. Soc. Am.* **54**, 174 (1973); N. Suga and T. Shimozawa, *Science* **183**, 1211 (1974).
  7. D. R. Griffin, *Listening in the Dark* (Yale Univ. Press, New Haven, Conn., 1958); \_\_\_\_\_, F. A. Webster, C. R. Michael, *Anim. Behav.* **8**, 141 (1960); A. D. Grinnell and D. R. Griffin, *Biol. Bull.* **114**, 10 (1958); N. Suga, *J. Physiol. London* **203**, 707 (1969).
  8. N. Suga, P. Schlegel, T. Shimozawa, J. A. Simmons, *J. Acoust. Soc. Am.* **54**, 793 (1973).
  9. We presented these findings at the 1975 spring meeting of the Acoustical Society of America [P. H.-S. Jen and N. Suga, *J. Acoust. Soc. Am.* **57**, S42 (1975)]. A. Yanovitz, J. Lozar, and C. W. Mitchell then repeated the same experiment with rats and found the acoustic LM reflex. Their preliminary experiments were reported at the 1975 fall meeting of the Acoustical Society of America [*J. Acoust. Soc. Am.* **58**, S123 (1975)]. Thus the acoustic LM reflex may be common in mammals.
  10. Supported by NSF grants GB-40018 and BMS 75-17077.
- \* Present address: Division of Biological Sciences, University of Missouri, Columbia 65201.

15 September 1975; revised 5 November 1975

views of a three-dimensional object, we created the appearance of a single object rotating back and forth either (i) in depth about the vertical axis of the object or (ii) around a circle in the two-dimensional picture plane.

Presumably the rotational trajectory through which the object seemed to move as a result of these alternations is the same path through which subjects imagined one object moving into congruence with the other in the mental rotation task. The distinguishing factor is that, in the present case of apparent movement, the subjective experience is of a much more clearly perceptual nature. Instead of actively having to imagine one object rotated into the other, possibly step-by-step or even piece-by-piece, subjects effortlessly experienced the object rapidly and smoothly rocking back and forth as a rigid whole. This phenomenon of apparent rotation thus seems to be less readily accounted for in terms of theories—currently popular in cognitive psychology and artificial intelligence—that emphasize processes of sequential search, recoding, and discrete manipulation of symbolic or propositional structures.

In classical studies of apparent movement, a simple stimulus (for example, a lu-

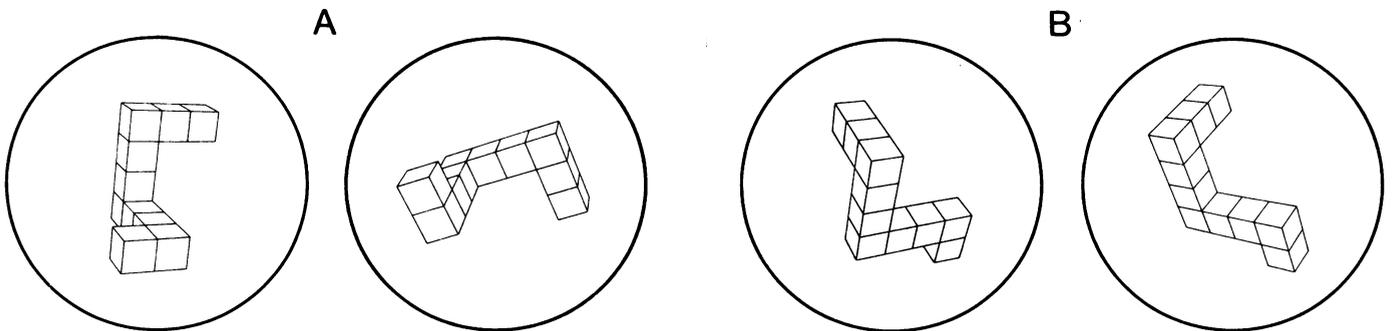


Fig. 1. Pairs of perspective views of the three-dimensional objects, illustrating an angular difference of 60° in the picture plane (A) and in depth (B).

minous spot) alternately presented in each of two locations appeared to move back and forth without discontinuity. Moreover, as the spatial separation between the two presentations was increased, the temporal delay between the onsets of those presentations had to be increased in order to maintain optimum apparent movement (3). In our rotational extension of this perceptual illusion, the two alternating stimuli were presented in the same spatial location, and the difference between them was one of orientation. In a manner analogous to that of the classical studies, we determined, for each of several angular differences, the shortest delay between onsets for which the subject was still able to experience coherent rotational movement.

The delay times were all much shorter than the corresponding decision times measured in the earlier, more intellectually effortful task of mental rotation (1). Apart from this difference in absolute level, however, the pattern of the time data was similar. The minimum field duration at which rotation was rated as coherent and rigid increased linearly with the angular difference between the two presented orientations and at virtually the same slope for rotations in depth and in the picture plane. Such a similarity in pattern suggests that the same mechanism may underlie subjects' performance in these two different tasks and, further, that holistic perceptual imagery, rather than discrete feature analysis and symbol manipulation, plays the principal role.

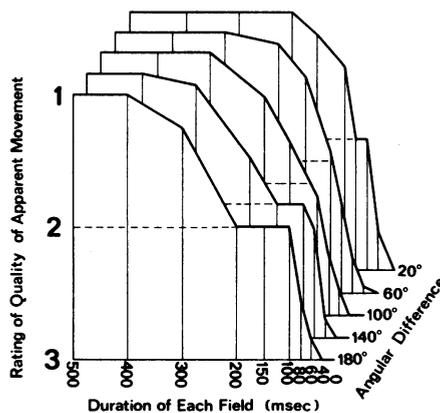
Examples of the pairs of perspective views for the depth and picture-plane conditions are shown in Fig. 1. The views were a subset of the computer-generated perspective projections of ten-cube objects originally used by Shepard and Metzler (1). We chose two objects (one for each condition) which produced rotational illusions that were viewed from an easily interpretable perspective and moved with a minimum of ambiguity. The perspective views were combined to construct pairs that differed in orientation by 20°, 60°, 100°, 140°, or 180°.

At each of these angular differences, each of ten subjects was presented with one picture-plane pair and two depth pairs. We used two different depth pairs in order to reduce the possibility that any one pair would contain perspective views that would be particularly difficult to interpret. In both conditions, the end cube nearest the top of the object (when in standard upright position) was colored yellow, which essentially eliminated the ambiguity in the mode of apparent movement that otherwise occurred even at slow rates of alternation of some pairs for which the perspective projections appeared especially symmetrical.

The two views comprising each pair were presented in continuous alternation in two fields of an Iconix tachistoscope. The termination of one field coincided with the onset of the other. The duration of the presentation of each field, always the same for both, ranged from 500 msec to 40 msec (Fig. 2A).

At the beginning of the experiment each subject was instructed and trained to rate the quality of the apparent rotation on a scale from 1 to 3, including ratings by tenths between the points. The three points on the scale were chosen to correspond to what seemed to be three distinct stages through which the phenomenal appearance passed as the rate of alternation increased. In the first stage, indicated by a rating of "1," the experience is strikingly similar to seeing an actual three-dimensional object rocking back and forth; the object seems to rotate as a rigid whole throughout its entire trajectory. In the second stage, rated as "2," there is also apparent movement, but of a nonrigid or noncoherent sort. For pairs differing by a large angle, different parts of the object appear to move independently or to deform into other non-corresponding parts (often yielding a sort of jumbling motion). For pairs differing only slightly in orientation, the motion takes on the quality of a vibration; motion

A. SUBJECT 1: DEPTH CONDITION



B. GROUP RESULTS: ALL TEN SUBJECTS

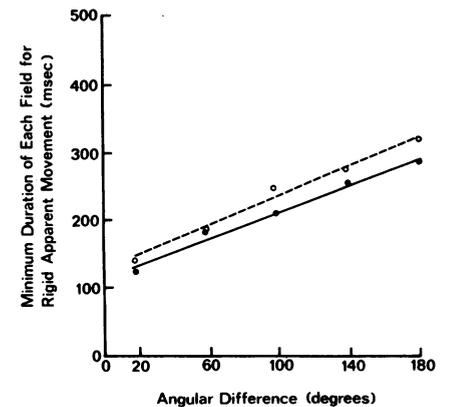


Fig. 2. Results. (A) Profiles illustrating, for a typical subject, how ratings of apparent movement depended upon the duration of each of the two alternately presented views, for each of the five angular differences between the objects. Rating "1" is for rigid motion, "2" is nonrigid motion, and "3" is no motion. (B) Mean field duration at which rigid apparent rotation breaks down, plotted for the group of ten subjects as a function of angular difference between the two views, for pairs of objects differing by a rotation in depth (closed circles and solid line) and in the picture plane (open circles and dashed lines). Straight lines have been fitted by the method of least squares to the plotted points. The slopes and intercepts of the best-fitting lines are 1.10 msec/deg and 121 msec, for the rotations in the picture plane, and 0.97 msec/deg and 112 msec, for rotations in depth. Breakdown of rigid rotation is defined in terms of the point at which a rating profile (A) crosses 1.5.

is perceived but the object moves too rapidly to be followed as a rigid whole throughout its trajectory. In the final stage, rated "3," the two alternating views appear superimposed. There is flickering but no apparent movement.

The subject took as much time as he needed on each trial to rate the quality of the apparent movement for a given pair at a particular rate of alternation. The trials were grouped into three equal blocks by condition, with half of the depth pairs preceding and half following the block of picture-plane pairs. Each subject rated a particular pair at all nine rates of alternation before proceeding to another pair with a new angular difference. The order of the five angular differences was counterbalanced across subjects, and the order of the nine rates of alternation within each angular difference was randomized separately for each subject.

Although the subjects were not informed of either the angular difference or the randomly chosen rate of alternation for each successive trial, each subject gave consistent ratings, which generally changed monotonically with rate of alternation. Out of the 1350 ratings, there were only five violations of monotonicity. According to the subjects, the perceptual experience produced by a given rate of alternation of a given pair of views was quite distinctive and readily classified on the three-point scale.

For sufficiently slow alternations, ratings of "1" are consistently given, but beyond some critical rate, the rigid coherence of the apparent movement is lost and the ratings rather abruptly fall off toward "2" (Fig. 2A). (Some subjects exhibit a short plateau at "2," which indicates that the experience of nonrigidity or non-coherence of the motion can occur over a range of rates.) Typically, as the angular difference is reduced, the drop occurs at shorter field durations; that is, for smaller angles, the appearance of rigid rotation of the object as a whole is maintained into more rapid rates of alternation.

As a quantitative estimate of the field duration at which the appearance of coherent rigid motion breaks down for each pair of views, we took the duration corresponding to the point at which the linear rating profile, starting from the level 1, first reached the level of 1.5, halfway between the ratings for rigid and nonrigid motion. For the rating profiles shown in Fig. 2A, this crossing point occurred at durations (to within 5 msec) of 100, 140, 180, 230, and 270 msec for angles of 20°, 60°, 100°, 140°, and 180°, respectively.

Although the results for individual subjects are more variable for this task than they were in the mental rotation task of

Shepard and Metzler (1), the mean results (Fig. 2B) are parallel. Again we find that estimated time increases linearly with angular difference; the slope is virtually the same for differences in depth and in the picture plane. Statistical analyses indicated no significant departure from linearity in either of the two functions and no significant difference between their slopes. [The fact that the absolute times were again slightly longer, overall, for the picture-plane pairs may be attributable, as in the earlier studies (1, 2), to properties peculiar to the particular objects and views chosen for the depth and picture-plane pairs.]

The total range of times here of only 190 msec (from about 110 msec at 0° to 300 msec at 180°) is much less than the corresponding 3500-msec range (from 1 second at 0° to between 4 and 5 seconds at 180°) in the previous mental rotation task. Whereas the earlier range corresponded to an estimated rate of mental rotation of 50° to 60° per second, the present range corresponds to a vastly greater rate of nearly 1000° per second. The similarity between the patterns of these and the earlier results is consistent with the growing body of findings that corresponding processes of visual imagery generally proceed much more rapidly when (as in more perceptual tasks) they are driven externally than when (as in purely imaginal tasks) they must be generated internally (4).

The finding of near equivalence between

the breakdown times for apparent rotation in depth and in the picture plane adds to earlier evidence (5) that phenomena of apparent movement are governed by relations in an internally constructed representation of something three-dimensional rather than by distances in the purely two-dimensional retinal image.

ROGER N. SHEPARD, SHERRYL A. JUDD  
*Department of Psychology,  
Stanford University,  
Stanford, California 94305*

#### References and Notes

1. R. N. Shepard and J. Metzler, *Science* 171, 701 (1971).
2. For recent work and theoretical discussions concerning mental rotation, see J. Metzler and R. N. Shepard [in *Theories in Cognitive Psychology: The Loyola Symposium*, R. Solso, Ed. (Erlbaum, Potomac, Md., 1974), pp. 147-201], L. A. Cooper and R. N. Shepard [in *Visual Information Processing*, W. G. Chase, Ed. (Academic Press, New York, 1973), pp. 75-76], and L. A. Cooper [in *Cognitive Psychol.* 7, 20 (1975)].
3. This relation is generally known as Korte's third law. Reviews of some of the classical work on apparent movement can be found in E. G. Boring [in *Sensation and Perception in the History of Experimental Psychology* (Appleton-Century-Crofts, New York, 1942)] and in P. A. Kollers [in *Aspects of Motion Perception* (Pergamon, New York, 1972)].
4. See, for example, R. J. Weber and J. Castleman [in *Percept. Psychophys.* 8, 165 (1970)], M. I. Posner [in *Visual Information Processing*, W. G. Chase, Ed. (Academic Press, New York, 1973), pp. 35-73 (especially pp. 54-57)], and S. M. Kosslyn [thesis, Stanford University (1974)].
5. H. H. Corbin, *Arch. Psychol.* No. 273 (1942); F. Attneave and G. Block, *Percept. Psychophys.* 13, 301 (1973).
6. Supported by NSF grant BMS 75-02806 to R.N.S. Under her former name, S. J. Huntsberger, S.A.J. presented this work at the annual meeting of the American Psychological Association in Chicago, 31 August 1975.

29 September 1975

## A Line, Not a Space, Represents Visual Distinctness of Borders Formed by Different Colors

**Abstract.** *When observers are asked to rate the visual distinctness of borders formed by the junction of two photic stimuli, normal trichromatic subjects behave in a manner similar to that of tritanopes in a color mixture experiment. All stimuli that look the same to the tritanope produce the same border distinctness with any other stimulus. Sets of such stimuli, whose members do not form borders with each other, map as single points along a curved line, where the Euclidean distance between pairs of points representing the two stimuli is nearly proportional to the rated distinctness of the border formed between them. In the absence of luminance differences, the perception of contour apparently depends on the stimulation of only two cone types.*

Colors of equal luminance are typically conceived as being arranged in a two-dimensional space. White is at the center, spectral colors form the outer limits, complementary colors are opposite, and non-spectral colors fill the space defined by spectral colors and nonspectral purples. This representation characterizes chromaticity diagrams derived from color mixture data, and also describes purely psychological color diagrams based upon the appearance of colored chips without regard to their physical characteristics (1, 2).

In experiments described here, observers were required to ignore color appearance and judge instead the distinctness of a contour formed between two adjacent fields of light (3). In each case, before the distinctness judgment, the intensity of one field was varied with respect to the other until the border formed between them appeared minimally distinct. By this criterion of judging color pairs, we have obtained the unexpected and surprising result that all colors—spectral and nonspectral alike—can be ordered along a line.