$-1/3$ power) of the body mass, m.

The $-1/3$ power dependence can be explained on the basis of a single, simple hypothesis: Energy cost per unit mass per "step" is a constant. If W is the total energy (work) required for an animal of mass m to traverse distance d, this statement becomes

$$W/m = cN = cdl^{-1} \qquad (1)$$

where N is the number of steps the animal must take to cover distance d, and l is a step length or characteristic length for the animal. The energy cost per unit mass per step, c, has units of calories per gram. The characteristic length or step length is measured in centimeters and is comparable, for running, to a "mean radius" of the animal's body. Since, by definition, $W = mdC$, we may rewrite Eq. 1 in the form

$$C = cl^{-1} \qquad (2)$$

It should now be noted that an animal's mass is proportional to the cube of its characteristic length. That is

$$m = kl^3 \qquad (3)$$

where k is a constant which includes geometric and density information and has the dimensions of a density.

Equations 2 and 3 combined give

$$C = ck^{1/3}\, m^{-1/3} \qquad (4)$$

which is in the form of our original fit of the data.

For a sphere of unit density, $k^{1/3} \approx 1.6$ g$^{1/3}$ cm^{-1}. For a man of mass 7×10^4 g whose step length is 100 cm, $k^{1/3} \approx 0.4$. If we take $k = 1$, in order to make an estimate, then from figure 4 of (*1*) we have

$$c = 3 \times 10^{-4} \text{ cal g}^{-1} \text{ (running)}$$

and similarly

$$c = 10^{-4} \text{ cal g}^{-1} \text{ (flying)}$$

$$c = 4 \times 10^{-5} \text{ cal g}^{-1} \text{ (swimming)}$$

What is the origin of the step rule? Why does a stroke cost less than a flap, which in turn costs less than a step? A plausible answer to both these questions might follow along the lines of that given by Alexander (*4*) in his discussion of the relative jumping ability of various species. His key point is that in a single contraction, muscle can do an amount of work proportional to its mass. Let us now interpret step as the unit of locomotive effort involving a single contraction of the animal's propulsive muscles. Then, insofar as the ratio of propulsive muscle mass to total body mass is a constant, the amount of energy available in a step, flap, or stroke per unit body mass is also a constant and gives the form of Eq. 4 immediately (*5*).

With regard to the relative efficiency of running, flying, and swimming, the ratio of propulsive muscle mass to body mass increases from mammals to birds, with their relatively large pectoral development, and finally to fish, where most of the body structure seems devoted to propulsion.

ALBERT GOLD
Rockefeller University,
New York 10021

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2. I have chosen this somewhat less mixed set of units than calories per gram per kilometer which was used in (*1*).
3. In (*1*) this was called body weight.
4. R. M. Alexander, *Animal Mechanics* (Univ. of Washington Press, Seattle, 1968), p. 28.
5. Another plausible argument rests on an analogy to rolling friction or friction in a bearing, as discussed in standard engineering texts [for example, S. Fairman and C. S. Cutshall, *Engineering Mechanics* (Wiley, New York, ed. 2, 1946), p. 39]. In these cases, a frictional dissipation of energy is proportional to the mass of the moving object. The analogy might be tenable in the case of running or flight, where leg or wing joints must bear the entire weight of the animal. The relevance to swimming is not immediately clear.

27 March 1973

Stereoscopic Vision: Cortical Limitations and a Disparity Scaling Effect

Abstract. *The spatial limitations of stereoscopic vision were studied by using vertical line stimuli containing sinusoidal disparity variations such that different parts of the line appeared at different depths. Stimuli with a finer grain than about 3 cycles per degree did not elicit depth perception, even though the sinusoidal curvature was clearly visible monocularly. At low spatial frequencies of curvature, stereoacuity was limited to the same extent as the monocular sensitivity. The limiting disparity for Panum's fusional region and the upper depth limit are subject to a scaling effect in proportion to stimulus dimensions. The disparity scaling can be characterized by a fixed maximum angular difference between the parts of the stereoscopic half-images.*

One interesting feature of stereoscopic vision is that it arises only from the combination of input from the two eyes. This combination first occurs principally at the level of the striate cortex (*1*). It is therefore possible to use stereoscopic data to study the cortical determinants of stereoscopic depth perception (*2*). The first part of this study is concerned with effects of stimulus patterning on monocular and stereoscopic acuity. Blakemore (*3*) mapped stereoacuity as a function of retinal position and disparity using conventional techniques, but he did not study stimulus configuration. Matsubayashi (*4*) found that stereoacuity was degraded as the lengths of the line stimuli used were reduced, but this was not confirmed in a recent study (*5*). Marked differences in the images to the two eyes reduce stereoacuity (*5*), but these are complex signals in terms of the dimensions of stimulus pattern.

Berry (*6*), using vertical line stimuli, studied the relation between vernier acuity and a modified stereoacuity using a vernier-type stimulus to each eye. He found that when the vertical separation of the lines was increased, vernier acuity was at first superior to stereoacuity, and then considerably degraded relative to stereoacuity, which remained essentially constant for all vertical separations. Berry considered that a "cortical interaction" may explain the results, but a simpler hypothesis is that vernier and stereoscopic processing are carried out by two systems operating relatively independently at the higher (cortical) levels. I tested this hypothesis by using vertical line stimuli containing a sinusoidal curvature or displacement, which produced static sinusoidal variations in retinal disparity when viewed binocularly.

The vertical line stimuli were generated on the face of an oscilloscope laid on its side. An oscillator fed a sinusoidal voltage of variable frequency and amplitude to the horizontal axis. The oscilloscope time base of 1 khz provided the vertical extension of the lines. Images to the two eyes were selected by the conventional arrangement of crossed polarizing filters at the oscilloscope screen and at the subject's eyes. The stimulus configuration consisted of a static sinusoidal line viewed in one eye and a straight line in the other. The lines were 15° high and 10′ thick with a luminance of 10 mlam. The subject perceived this stimulus as a line curved sinusoidally in depth, with the depth curvature oriented toward one eye. The stimulus was the sinusoidal version of Panum's limiting case for stereopsis, containing lateral as well as depth displacement. The reason for using this configuration is that it avoids the problem of vertical registration of images to the two eyes.

For stereoscopic sensitivity the subject was asked to determine by the method of adjustment the threshold amplitude of sinusoidal disparity at which all parts of the display appeared at the same depth as every other part. This instruction avoided confusion between lateral and depth effects. The threshold peak-to-peak amplitude of the monocular sinusoidal input was measured as a function of the spatial frequency of the disparity. For comparison monocular sensitivity to the curvature of the sinusoidal line alone was measured in the same manner. Each curve was the mean of one ascending and descending trial. In Figs. 1 and 2, vertical bars show 1 standard deviation of the settings for each mean, averaged over all means in a particular condition. It was found by inspection that the deviations were proportional to the absolute amplitude of the settings, so that a logarithmic transformation of the data was used before the standard deviation calculation.

The results are shown in Fig. 1 for two subjects. Double logarithmic coordinates are used both because the data extend over a range of several orders of magnitude and also for comparison with other studies involving other dimensions of sinusoidal stimulus variation (*7*). The abscissa indicates the sensitivity of the system in terms of the reciprocal of the peak-to-peak threshold disparity. Disparity is therefore plotted increasing downward on the graph. The point of maximum frequency in each condition was obtained by setting the frequency for a fixed amplitude, rather than the amplitude for a fixed frequency, as was the case with all the other points.

Figure 1 shows that in the high-frequency region above 1 cycle per degree (cycle/deg) monocular sensitivity (filled circles) was markedly greater than stereoscopic sensitivity (rectangles), reaching a maximum at around 3 cycle/deg, whereas the stereoscopic maximum occurred below 1 cycle/deg. Monocular sensitivity extended to about 12 cycle/deg, whereas the greatest spatial frequency to which the depth response could be obtained was only 3 cycle/deg. By contrast, at spatial frequencies below 1 cycle/deg stereoscopic sensitivity coincided with monocular sensitivity within the limits of experimental error. Both were reduced considerably with a reduction in spatial frequency. The results suggest that for continuous line stimuli, no further limitations in sensitivity at low frequencies occur as a result of processing for depth perception. Several hypotheses concerning the factors limiting monocular sensitivity are considered elsewhere (*8*), but the high-frequency limitations imposed by stereoscopic processing must be cortical, as mentioned above.

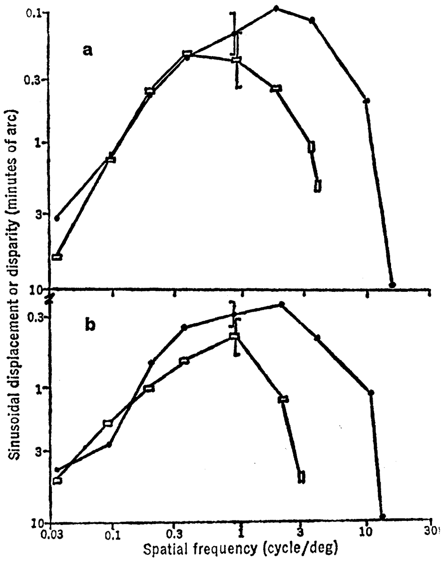

Fig. 1. Monocular sensitivity (filled circles) and stereoscopic depth sensitivity (open rectangles) as a function of spatial frequency of curvature, with a 15° field. (a) Subject C.W.T.; (b) subject J.T.

It is possible that the high-frequency limitations result in some way from the use of the large field of vision (15°) or from the relatively thick (10′) lines. Accordingly, by increasing the viewing distance by a factor of 10 the retinal subtense of the display was reduced to 1.5°, which is strictly foveal, and the line thickness was reduced to 1′, which is close to the limit of optical resolution of the eye. The results for both subjects confirmed those of Fig. 1 and also showed a small increase in the overall sensitivities for both types of response. Thus, the maximum frequency resolvable by the stereoscopic system increased to about 5 cycle/deg, whereas the monocular sensitivity was raised to about 30 cycle/deg. The effect of reducing the visual angle of the display is therefore to increase slightly the discrepancy between monocular and stereoscopic sensitivities.

In contrast to Berry's results (*6*), stereoactivity with the sinusoidal curvature stimulus was never superior to monocular acuity, and each appeared to have its own high-frequency limit. An explanation of both sets of stereoscopic results by cortical interactions beyond the monocular channel is there-

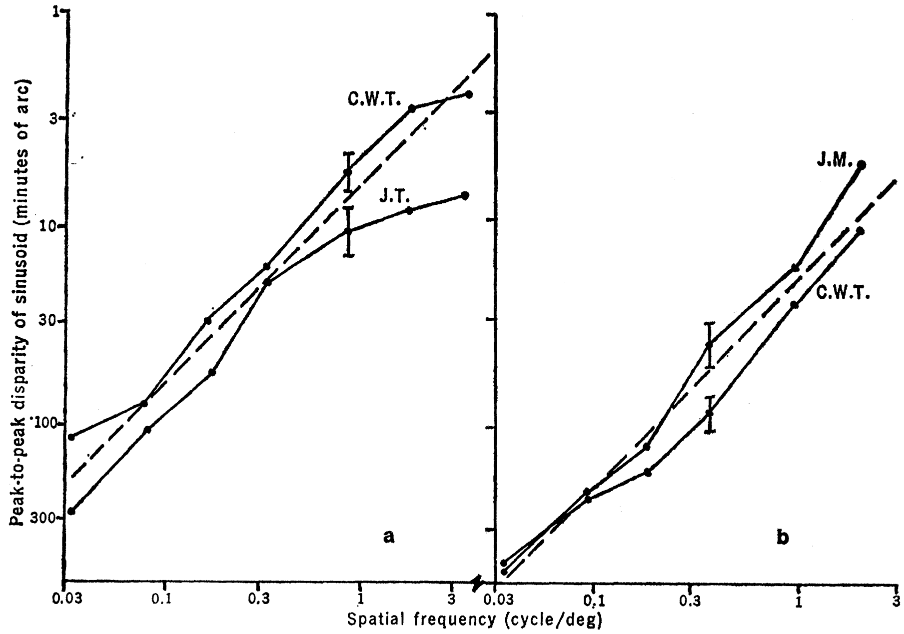

Fig. 2. (a) Panum's fusional limit as a function of spatial frequency of disparity for subjects J.T. and C.W.T. Stimulus is fused in the region above the curves and diplopia occurs below. (b) Maximum disparity limits for depth perception as a function of spatial frequency for subjects C.W.T. and J.M. Depth differences are perceived in the region above the curve but not below. Dashed lines depict inverse proportionality between disparity and spatial frequency.

fore complicated. Instead, the monocular and stereoscopic tasks may involve different discrimination mechanisms operating on the stimulus.

To complement the study of stereoacuity I measured the upper disparity limits for depth perception. Two functions were considered: the upper disparity limit for fusion of the monocular images (Panum's region) and the upper disparity limit for perceived depth. In previous experiments concerning the extent of Panum's area for different stimulus configurations it was found that increasing the spatial extent of the stimulus produced small increases in fusion disparity (*9*). The upper limit for depth impression (or qualitative stereopsis) increases with retinal eccentricity (*10*), and perceived depth decreases with interocular orientation differences (*11*) up to a limit of 60°, but the effects of stimulus configuration on the upper depth limit have not been investigated.

In the experiment reported here, the effects of stimulus configuration were examined by using the sinusoidal depth stimulus already described. The subject set the sinusoidal disparity by the method of adjustment either to the point where the perceived line began to split into two (fusion limit), or to the point where the perceived double image had rotated back into the frontal plane (depth limit). As before, two readings were taken for each condition in ascending and descending series, with two subjects for each condition. Figure 2b shows that within experimental error the upper disparity limit for perception of depth coincides over a range of two log units with the dashed line, which represents strict inverse proportionality between spatial frequency and the limiting disparity. Thus, the larger each cycle of the sinusoid became, the larger was the disparity which could elicit depth perception. The curves through the filled circles in Fig. 2a represent the disparity limit for fusion of the monocular half-images for two subjects. The fusion limit was also inversely proportional to the spatial frequency of the stimulus within the experimental error, over a spatial frequency range of two log units.

It is possible that the reduction in number of cycles visible with spatial frequency reduction was responsible for the increase in the depth limits. The number of cycles visible was therefore held constant at one cycle by decreasing the aperture height of the stimulus as spatial frequency was increased. The results (not shown) were essentially similar to the results with a fixed aperture, so the variation in number of cycles visible with spatial frequency changes is not an important factor.

Experiments involving stimuli restricted to the fovea showed similar results, at least down to a spatial frequency of 0.5 cycle/deg. It is nevertheless conceivable that the variations in Panum's region and the depth limit could be attributed to the inhomogeneity of the retinal area stimulated. Both fusion and depth limits increase progressively with retinal eccentricity, even for foveal stimuli, with fixation between 0° and 1° (*10*). Perhaps the depth limits for high spatial frequencies were set foveally, and those for lower spatial frequencies by more peripheral channels. This possibility was tested by repeating the measurements of Fig. 2, with fixation on a point displaced 7° horizontally from the target. At this distance, the sinusoid extended over a range of 7° to 10° from fixation, a relatively homogeneous retinal area. Although both monocular and depth thresholds were depressed by about one log unit, the forms of both Panum's region and the depth limit were not significantly affected over the range from 0.03 to 1.0 cycle/deg.

The spatial frequency dependence of all three stereoscopic limits can be considered such that the maximum angle between any part of the straight and sinusoidal lines remained constant. For stereoacuity this angular difference was approximately 20′ for subject J.T. and 15′ for subject C.W.T. in the range below 0.3 cycle/deg. Panum's limit occurred at angular differences of about 20° for C.W.T. and 30° for subject J.M., and the upper depth limit fell at about 45° for both subjects tested. Although the fixed orientation limit is a convenient way of describing the data (*11*), it does not necessarily imply that line orientation is the key feature for stereoscopic processing. Experiments designed to test the orientation hypothesis are under way.

The results have the general implication that stereoscopic depth perception is highly dependent on (vertical) stimulus configuration. Although the same is unlikely to occur for other cues to visual space perception, it is worthwhile to know the limitations of stereoscopic processing. It seems that the visual system is not equipped to handle the kind of disparity information present in, for example, dense foliage, a head of hair, or multilayered electronic circuitry. Furthermore, the larger the retinal elements, the greater the disparities that can elicit depth sensations. This relation may be useful in simplifying perception of a visual world in which objects near the observer will tend to have a large retinal size associated with large binocular disparities at average fixation distances.

C. William Tyler

Department of Psychology,
Northeastern University,
Boston, Massachusetts 02115

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1. Although extensive inhibitory binocular interactions have been found in the lateral geniculate nucleus (LGN) in the cat [S. D. Erulkar and M. Fillenz, *J. Physiol. London* **154**, 206 (1960); K. J. Sanderson, I. D. Smith, P. O. Bishop, *Vision Res.* **9**, 1297 (1969)] there is no evidence for cells differentially sensitive to binocular disparity prior to the cortex. In the macaque and man there is highly discrete lamination of the LGN. R. DeValois and A. Jones [in *The Visual System: Neurophysiology and Psychophysics*, R. Jung and H. Kornhuber, Eds. (Springer, Berlin, 1961), p. 179] found that binocular sensitivity of any sort was present in less than 1 percent of LGN cells in the macaque. No cells were found in which a stimulus to one eye modified the response to stimulation in the other eye. An alternative pathway which might serve to mediate stereopsis is the superior colliculus system. However, large cortical lesions in the cat reduce the percentage of binocularly driven cells from 80 percent to 20 to 30 percent [B. Wickelgren and P. Sterling, *J. Neurophysiol.* **32**, 16 (1969); A. C. Rosenquist and L. A. Palmer, *Exp. Neurol.* **33**, 629 (1971)]. It is thus probable that ipsilateral input to the colliculus in the cat is mainly cortical, and that the superior colliculus lies later in the binocular processing pathway than the cortex. In the monkey there have been no reports of disparity-sensitive neurons in the colliculus, while cortical cells in area 18 of the cortex show sharply tuned responses to disparate binocular stimuli [D. Hubel and T. N. Weisel, *Nature* **225**, 41 (1970)]. Further evidence against collicular involvement in stereoscopic processes is provided by studies of eye movement control. D. A. Robinson [*Vision Res.* **11**, 1795 (1972)] and P. Schiller and M. Stryker [*J. Neurophysiol.* **35**, 915 (1972)] report that stimulation of the monkey superior colliculus at all levels evoked only conjugate eye movements which were almost always saccades. In contrast, the eye movements involved in stereoscopic vision are vergent, smooth pursuit movements [C. Rashbass and G. Westheimer, *J. Physiol. London* **159**, 339 (1961)]. These results make it unlikely that the superior colliculus is involved in the mediation of stereoscopic vision. It therefore seems safe to conclude that human stereoscopic processing occurs at or beyond the level of the visual cortex.
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