The expected frequency-of-scores set for a (n,r) maze is therefore:

$$\left[\nu_T{}^{(\alpha)}(r,n) \Big/ \binom{x}{r} \right], \quad \alpha = 0, 1, 2 \ldots n.$$

These and other statistics concerning the distribution of scores may be used to define parameters for the maze which may be related to subjective difficulty.

In this notation m_{ij} equals the number of pathways between dot i and dot j with zero score ($i, j = 0, 1, 2 \ldots r, f$): and if $m_{ij} > 0$, then we may say that dot j is directly accessible from dot i. Developing this concept we may use a binary notation in the form of matrix $M' = (m'_{ij})$ ($i, j = 0, 1, 2 \ldots r, f$) where $m'_{ij} = 1$ if $m_{ij} > 0$ (that is, if j is directly accessible from i) and $= 0$ otherwise. Matrices $V^{(\alpha)\prime}$, $T^{(1)\prime}$, $T^{(2)\prime}$, $T^{(3)\prime}$ may also be derived corresponding to the unprimed matrices given here. The basic difference between the two sets of matrices is that in the first set the number of different pathways with score α between dots i and j is considered, whereas in the second series the number of different sets of α dots lying on pathways between dots i and j is the underlying concept. Thus, for example, $\nu_{of}{}^{(m)\prime}$ gives the number of different solution sets of dots.

Further, the dots (not including o and f) may be divided into n groups corresponding to the n horizontal maze rows, and the vector (d_p) may be defined, where d_p = number of dots on the p^{th} horizontal maze row ($p = 1, 2 \ldots n$).

The matrix M' may now be partitioned into sub-matrices $R_{a\beta}$ where a, β refer to maze rows; here 'maze rows' are taken to include a zero row and an f row and so $\alpha, \beta = 0, 1, 2 \ldots n, f$. $R_{a\beta}$ is a $d_\alpha \times d_\beta$ matrix which gives direct accessibility relationships between dots on the α^{th} row and the β^{th} row. Again, $R_{a\beta} = O$ if $\alpha \geqslant \beta$.

Since one theory describing maze problem-solving activity postulates that individuals differ in the size of the perceptual unit which they use, it seems relevant to illustrate one way in which the present approach could be used to analyse this aspect of the problem. To do this we have defined as a Δ any maze-linked set of dots. A Δ is designated by $\delta(\nu,\gamma)$ where ν is the number of dots in the Δ and γ is the number of gaps, or vacant sites, interspersed between the dots. Now considering M' in the partitioned form $R_{a\beta}$ ($a, \beta = 0, 1, 2 \ldots n, f$) which is an upper triangular matrix with zero sub-matrices $R_{\alpha\alpha}$ in the main diagonal, then it will be seen that the $\delta(\nu,\gamma)$'s are given by the $(\nu - 1 + \gamma)$th parallel of sub-matrices of $M'^{\nu-1}$. If the partitioned matrix $M'_{(\rho)}$ is defined so that $M'_{(\rho)}$ has the same first ρ parallels of sub-matrices as M' but all other parallels consist of zero sub-matrices, then it will be seen that the $\delta(\nu,\gamma)$'s are given by the $(\nu - 1 + \gamma)$th parallel of sub-matrices of $M'^{\nu-1}_{(\gamma+1)}$. In the particular case of the complete solution Δ's, that is, the $\delta(m + 2, n - m)$'s these are given by the $(n + 1)$th parallel of sub-matrices of $M'^{m+1}_{(n-m+1)}$. In other words, $M'_{(n-m+1)}$ and not M' need be considered for the solution. Thus for a maze with $n = 16$, $m = 12$ (that is, $n - m + 1 = 5$), the subject need only consider direct accessibility relationships between dots which are separated by not more than five maze rows.

The foregoing mathematical analysis is one of several which might be equally or more valuable. It is presented in this form because it deals primarily with the target dot relationships and so lends itself to a study of the problem-solving activity involved. It has, we hope, been developed sufficiently to show that a systematic analysis of this test material is both practical and potentially fruitful.

We thank Dr. A. M. Uttley, Mr. C. D. Alway, Mr. E. F. Davis and other members of the Autonomics and Mathematics Divisions of the National Physical Laboratory, and also Mrs. M. Kerr, for advice. Two of us (A. E. and D. N. L.) are receiving support from the Medical Research Council.

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DISTORTION OF VISUAL SPACE AS INAPPROPRIATE CONSTANCY SCALING

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DISTORTIONS of visual space associated with certain simple patterns have been investigated since the beginning of experimental psychology[1], and many theories have been proposed[2], but so far none, in my opinion, has been satisfactory in explaining these so-called 'geometrical' illusions. Figs. 1, 2 and 3 show representative illusions of the kind we are considering.

The traditional theories fall into three classes: (1) That certain shapes produce, or tend to produce, abnormal eye movements. (2) That some kind of central 'confusion' is produced by certain shapes, particularly non-parallel lines and corners. (3) That the figures suggest depth by perspective, and that this 'suggestion' in some way distorts visual space.

The eye movement theories are difficult to support because the illusions occur undiminished when the retinal image is optically stabilized on the retina[3], or when the figures are viewed as after-images following illumination by a bright flash of light. Further, since distortions can occur in opposed directions at the same time (as with the Müller–Lyer figure[4] (Fig. 1*a*) it is difficult to see how either overt or incipient eye movements could be involved. The various 'confusion' theories all suffer from vagueness, and they give us no idea as to why the distortions should occur in the observed directions, or only in certain kinds of figures. The perspective theory[2] is inadequate because it does not suggest why or how perspective should produce distortions in flat figures, but it does imply a generalization which seems to hold true of all the known illusion figures, and this gives a clue vital to understanding the origin of the illusions.

The illusion figures may be thought of as flat projections of typical views of objects lying in three-dimensional space. For example, the outward-going Müller–Lyer arrow figure is a typical projection of, say, the corner of a room—the fins representing the intersections of the walls with the ceiling and floor—while the in-going arrow is a typical projection of an outside corner of a house or a box, the converging lines receding into the distance. The following generalization seems to hold for all the illusion figures thought of in this way: The parts of the figures corresponding to distant objects are expanded and the parts corresponding to nearer objects are reduced. Thus in the Müller–Lyer figure the vertical line would be further away in the diverging case, and is expanded in the illusion, and vice versa, while in the Ponzo figure the upper horizontal line would be farther away and it also is expanded in the flat illusion figure.

Given that this generalization holds for all the illusions, why should these distortions occur ?

Do we know of any other perceptual phenomena involving systematic perceptual modification of the retinal image ? There is a well-known set of phenomena which certainly does involve perceptual modification of retinal images—size constancy[5,6]. This is the tendency for objects to appear much the same size over a wide range of distance

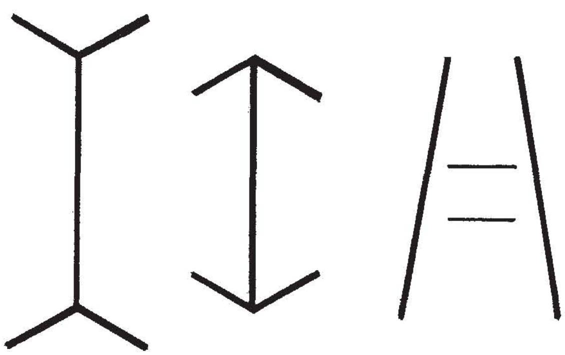

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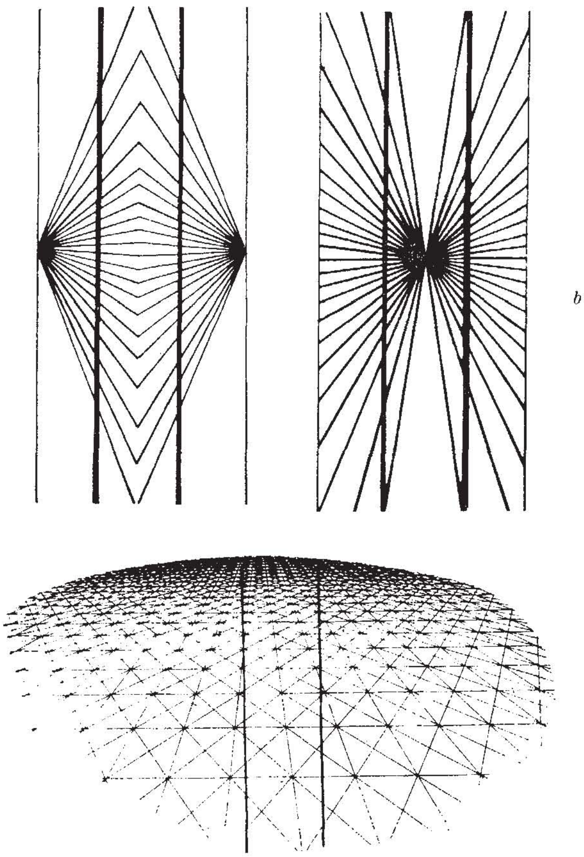
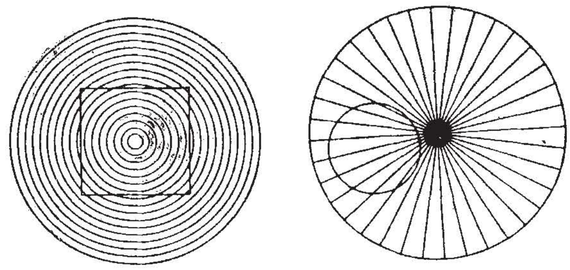
Fig. 1. (*a*) The Müller-Lyer; (*b*) the Ponzo illusion



a b

c

Fig. 2. (*a*) and (*b*) Alternative forms of the Hering illusion. The vertical lines are bowed inwards and outwards, respectively. (*c*) An illusion showing how parallel lines indicating distance seem to diverge when presented on a texture gradient. (The texture taken from Gibson, *The Perception of the Visual World*, 1951)



a b

Fig. 3. Further distortions to be expected on the distance hypothesis; the concentric circles and spokes set the constancy scaling by indicating depth. (Figures, though not interpretation, from Orbison, *Amer. J. Psychol.*, **52**, 39; 1939)

in spite of the changes of the retinal images associated with distance of the object. We may refer to the processes involved as constancy scaling. Now in constancy scaling we find known processes which not only could but also must produce distortion of visual space if the scaling were set inappropriately to the distance of an observed object. It is strange that apparently only one writer, Tausch, has considered constancy in connexion with the geometrical illusions[7].

We can see our own scaling system at work in the following demonstration of Emmert's law[8]. The after-image of a bright light is 'projected' on to a series of screens lying at various distances, or a single screen moved away or towards the observer. Although the effective retinal image is constant, the after-image perceived as lying on a screen looks larger the farther the screen is from the observer. Complete constancy would give a doubling in size for each doubling of distance, and the amount of scaling can be quantified under various conditions for stationary or moving screens[9,10].

Clearly inappropriate constancy scaling would produce distortion of visual space, but why should this occur with the illusion figures which are in fact flat and are generally seen to be flat ? It is generally assumed that constancy scaling depends simply on apparent distance (as Emmert's law might suggest); but if we are to suppose that constancy scaling can operate for figures clearly lying on a flat surface we must challenge this assumption, and suggest that visual features associated with distance can modify constancy scaling even when no depth is seen. If we are to suppose that the illusions are due to misplaced constancy scaling, we must suppose that the scaling can be set directly by depth features of flat figures, and that the scaling is not set simply as a function of apparent distance as is generally thought to be the case.

Perspective drawings and photographs are seen to depict objects as if they lay in three dimensions, and yet at the same time they appear flat, lying on the plane of the paper, and so they are perceptually paradoxical. The surface texture of the paper evidently prevents the perspective from making the objects appear truly three dimensional, for if we remove all texture and view with one eye, then perspective drawings can look as impressively in depth as the real world viewed with one eye.

We have presented the well-known illusion figures with no background texture—by making wire models coated in luminous paint so that they glow in the dark, or using back illuminated transparencies—and we find that, viewed with one eye, they look three dimensional, provided the angles are not marked exaggerations of perspective. The Müller–Lyer arrows, for example, look like corners and not like flat projections when presented as luminous figures in the dark, and those parts which appear most distant are the parts which are expanded in the illusions as normally presented on textured paper. What happens to the distortions when we remove the background texture is complex, and will be discussed more fully elsewhere; but, in general, distortions are reduced or disappear.

Emmert's law may suggest that constancy scaling arises directly from apparent distance; but there is retinal information indicating the distance of each position of the screen, and possibly this might serve directly to set the scaling. However, the following demonstration shows conclusively that scaling can occur simply as a function of apparent depth and independently of retinal or other sensory information.

Fig. 4*a* shows the well-known Necker cube figure—a skeleton cube which reverses spontaneously in depth so that sometimes one face, sometimes another, appears the nearer. As shown on textured paper, it is paradoxical in the manner described here—it looks as if it were in depth and yet it is seen to be flat on the paper. By making a luminous model of this figure, and viewing it in the dark, we find that it still reverses but now it looks like a true three-dimensional figure, and it undergoes size changes—the apparently farther face looking somewhat larger than the nearer, showing that constancy scaling is now operating. Since the retinal image remains unchanged it follows that the scaling is set under these conditions as a simple function of apparent distance. This is shown most dramatically with a three-dimensional luminous cube. This looks like a true cube when seen correctly, but when perceptually reversed in depth it looks like a truncated pyramid, the apparently front face being the smaller[11].

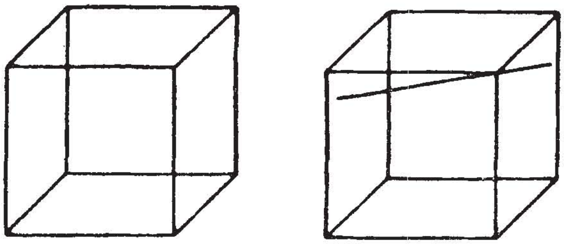


Fig. 4. (*a*) The Necker cube. This reverses in depth. When viewed as a self-luminous figure, the apparent front looks smaller, the back larger. (*b*) Humphrey's figure. The oblique line is seen as slightly bent; the direction of bending being determined by the angle against which it is placed, and not by the way the cube appears to lie in depth

It thus appears that there are two ways in which constancy scaling can be set. We may name these:

(1) *Primary constancy scaling*. This is set by perspective or other features normally associated with distance. These features can be at variance with apparent distance in special cases, such as the illusion figures. (We call it 'primary' because it seems to be primitive, and to be mediated by neural systems situated early in the perceptual system.)

(2) *Secondary constancy scaling* is set simply by apparent distance, and this may be a function of previous knowledge and is not necessarily tied directly to visual information. Its existence is suggested but not proved by Emmert's law; but it is conclusively demonstrated with the ambiguous self-luminous objects which change their shape systematically according to which faces appear nearer or farther though there is no change in the retinal image. Errors in apparent distance should produce distortion of visual space via this secondary scaling system, and the well-known moon illusion may be an example.

Although the self-luminous figures do clearly demonstrate what we have called the secondary constancy scaling system, what clear evidence have we for the primary system, supposed to be set by typical depth cues even in the absence of depth perception ? For our present purpose it is much more important to demonstrate the existence of primary than secondary scaling. To get evidence for primary scaling entirely independent of the illusions is very difficult, but the following is at least suggestive.

(1) It has been noticed by Humphrey[12] that a straight line drawn across a corner of a Necker cube (Fig. 4*b*) appears bent. Now this is particularly interesting because the direction of bending is the same which ever way the cube appears to lie in depth. It is bent in the direction to be expected if constancy scaling is operating from the typical perspective interpretation of the angle against which the line lies.

(2) In primitive races living in houses without corners the geometrical illusions are reduced[13,14]. If learning is important, this would be expected.

(3) In a case of a man blind from the first few months of life, but gaining his sight after operation fifty years later, we have found that the illusions were largely absent, and his constancy appeared abnormal or absent although he could at that time, some weeks after the corneal graft operation, recognize common objects[15]. This has been noted in other cases. (In fact, it was this observation which suggested to me this kind of theory of the illusions.)

We should expect the different scaling systems to have somewhat different time-constants, and we are attempting to measure these to establish their separate existence quite apart from considerations of distortions of visual space.

It further may be suggested that figural after-effects—distortions similar to the geometrical illusions, but produced as a result of prolonged viewing of a suitable stimulus pattern and transferring to a second test pattern—may be due to the primary scaling being set by depth features present in the stimulus pattern, this scaling taking some time after lengthy fixation to become appropriate to the second test pattern, so the second pattern is distorted by scaling carried over from the earlier pattern. Preliminary experiments are providing strong evidence that figural after-effects can be thought of in this way, and such a theory would have advantages over present theories of the figural after-effects which are *ad hoc*, involve dubious physiological speculation and fail to make useful predictions[16,17].

In attempting to give a general account of all illusions involving systematic distortions of visual space, either while viewing a figure or following on prolonged viewing, and relating the distortions to a known perceptual phenomenon—size constancy—we have not attempted to specify the neural processes involved, and we believe this to be impossible at this time. Recent work on recording from the visual regions of the cat's brain while presenting the eyes with moving or fixed patterns[18] gives promise that the underlying neural mechanisms may soon be revealed.

This work was supported by the U.S. Air Force under grant No. *AF-EOAR* 63–93 and monitored by the European Office, Office of Aerospace Research and also by the Medical Research Council.

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the items after 24 h. The differences between the recall scores of Groups I–IV thus appear to be primarily due to proactive interference.

The correlation between speed of learning and recall of *T* was negative but low. However, there were indications in the results of a positive correlation between the number of reinforced repetitions and the probability of recall of individual items, supporting Warr's findings.

The results yield clear-cut evidence for the assumption that proactive inhibition is a factor determining retention, although the effects were smaller than might be expected from Underwood's curve. At the same time the results are consistent with the argument that part of the differences in retention interpreted by Underwood in terms of proactive inhibition may simply reflect differences in degree of learning of the items.

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Illusory Perception as a Constancy Phenomenon

GREGORY[1] offers a general account of visual illusions, relating the apparent distortions in them to the perceptual process of size constancy. He observes that Tausch is the only previous writer to have considered constancy in relation to illusions. However, Gibson[2] has incorporated illusory perceptions within the context of size constancy, and suggests that perception of size is a by-product of a constant scale, which Gregory calls 'constancy scaling', at different distances. Arguing that illusory figures are "flat projections of typical views of objects lying in three-dimensional space", Gregory notes that "the parts of the figure corresponding to distant objects are expanded and the parts corresponding to nearer objects reduced". He states the same principle more simply when he writes: "Those parts of the figures which would normally be further away in 3-D space appear too large in the illusion figures"[3]. These principles are applied to a series of illusions, including those of Müller-Lyer, Ponzo and Hering. Gregory therefore postulates a common process modifying retinal images in constancy scaling and in the perception of illusory figures.

If this general principle operates, it is difficult to understand why the distorting process does not occur under all the conditions in which distance is perceived in two-dimensional figures. In Ponzo's figure the same one of the two central lines appears longer, no matter whether it is seen as nearer or farther after rotating the figure through 180°. Similarly when only the top or bottom half of either forms of Hering's illusion is inspected, the parallel lines appear to be distorted, no matter which way the perceived depth or distance appears to be in the background field. Further, Gregory's contention that "the scaling can be set directly by depth features of flat figures"[4] does not seem to be supported experimentally in all illusions. Green and Hoyle[5], for example, found that the Poggendorff illusion did not give rise to 3-D perception under reduced cue conditions. Their finding also is substantiated by Gibson[6], who reports that when the texture of a pattern becomes indeterminate the observer no longer sees the dimensions of a surface but a depthless shape perceived in the frontal plane.

Gregory's predictions, when applied to different orientations of visual illusions, are therefore not supported. In fact the illusions are more stable than Gregory's predictions would suggest, since changing the constancy relationships does not necessarily change the illusory effects. However, if the constancy interpretation of illusions is to be accepted it must be applicable to all conditions of inspection, and not only to a single orientation of the figure.

Although we do not have an alternative general explanation of the cause of visual illusions, we would offer some suggestions concerning specific factors operating in the illusory patterns being discussed. First, the relative position of the two horizontal lines in Ponzo's figure seems more important than the distance at which they appear to be located. Then, the distortion in Hering's illusion, or in Gibson's texture gradient, occurs as a function of the density of background lines: that is, the closer together these lines are, the more distorted the illusory lines appear, irrespective of which part of the pattern looks nearer or farther away. Further, predictions can only be made about which sections of the illusory lines will be more distorted, and not about the direction of distortion, that is whether the illusory lines will appear closer together or farther apart, as Gregory's account would require. Finally, some of the illusions considered by Gregory (that is, Hering's, Gibson's texture gradient, Orbison's field of concentric circles and the Necker cube) disappear entirely when the viewing slant is altered or when they are viewed from a distance, although the cues for depth, which set the constancy scaling, still operate[7]. We conclude, therefore, that constancy scaling operates only under a set of very limited conditions of inspection of illusory figures.

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THERE are several hints in the literature of perception of a possible tie-up between constancy and the illusions, but Tausch[1] seems to have produced the first reasonably solid treatment, described clearly by Teuber[2], though he has not developed a fully consistent theory. Brown and Houssiadas's reference to J. J. Gibson's *The Perception of the Visual World*[3] in this connexion is surprising, for Gibson holds a view of constancy which precludes this kind of theory. Gibson starts off (p. 163) somewhat disconcertingly: "The aim of this chapter is ultimately to show that the question of why things retain their sizes and shapes under different circumstances is a false question". (The rest of the chapter is, however, devoted to this question.) He develops a theory of depth perception which he attributes to Koffka[4]—the size-at-a-distance theory—which is that all three spatial dimensions are equally available to the perceptual system. But in denying that depth has to be specially computed, Gibson rejects the notion of constancy scaling essential to this theory of the illusions. When Gibson uses the word 'scale' he is evidently not referring to a process of size adjustment normally giving constancy, for several times he explicitly denies such processes in depth perception.

Gibson says of an illusion figure (p. 181): "All three cylinders are the same size on the page; it is not an illusion at all but a demonstration that apparent size depends on apparent distance". But the fact is that illusion figures are not seen as lying in depth when presented on normal textured paper: hence the problem. It was for this reason I removed background texture by using luminous illusion figures for experimental purposes.

I think Brown and Houssiadas are incorrect in attributing this kind of theory to Gibson, while his account of the illusions seems the least satisfactory part of his treatment of perception.

The main question raised by Brown and Houssiadas is whether the distortions occur under all conditions in which distance is perceived in a two-dimensional figure.

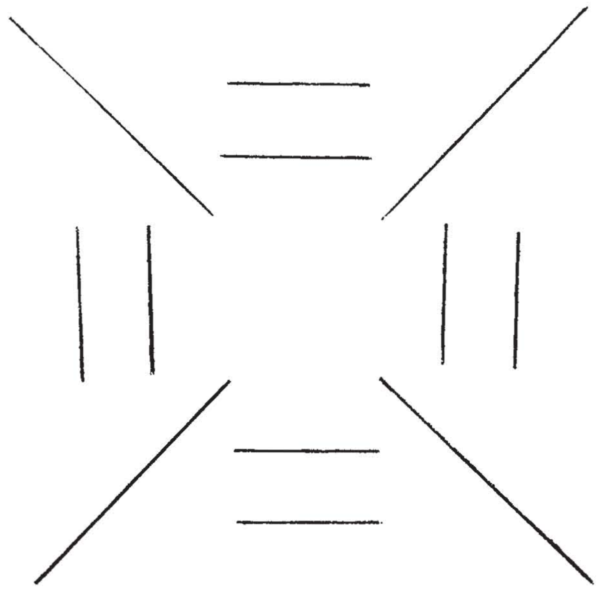

Fig. 1. This shows four differently orientated Ponzo figures. Brown and Houssiadas argue that the illusion should change with the orientation: but the perspective is unchanged, and so this is incorrect

(Actually, as I point out[5], it need not be perceived; for we must suppose that constancy scaling can be set directly by perspective and other depth cues, even when these are countermanded by other features such as the texture of the background. Perspective depth is 'paradoxical'—suggested but not seen as in the real world of objects lying in space.) Now, they are mistaken in regarding their test cases as exceptions; for when a perspective figure is rotated, the perspective does not change. What changes is the effective viewing position, and this is a very different matter. This should be clear from the example given of four differently orientated Ponzo figures—their perspective is the same and so is the illusion. They lie respectively on the 'ground', to the sides and in the 'sky'. The same consideration holds for the case of the partly obscured Hering figure, and the rest.

Brown and Houssiadas give insufficient data on their final point for a useful comment, but it should be pointed out that there is only one distance from which a given perspective is strictly correct. Their findings might be very important in this connexion.

So far no valid objections seem to have been raised to my form of the theory[5]; but the evidence for it is rather indirect. I have, therefore, devised a technique for obtaining objective measures of apparent depth. This makes it possible to relate directly apparent depth with illusory distortions. An established relation between apparent depth in the luminous illusion figures, where depth is not countermanded by texture, and the extent of the illusion in the same figures but viewed on a normal texture background, would be very strong evidence for the theory. Working with Miss Linda Townes at the Massachusetts Institute of Technology, and in a preliminary experiment with Mr. I. Morrell at Cambridge, England, I have found just such a relation.

How to measure apparent depth. The basic scheme is to use binocular depth vision (either the range-finder effect of convergence, or disparity between the retinal images) as a standard against which to measure depth given by perspective. This is done, using convergence, by keeping both eyes open but allowing only one to see the (generally luminous) display figure, by cross-polarizing the light from the display to one eye. A small dim reference light is introduced into the display by means of a half-silvered mirror, this light being seen by both eyes. Its distance is adjusted until it appears the same distance as any selected part of the display figure, viewed with a single eye. Since the reference light is seen by binocular vision, we thus obtain a measure of depth as determined by perspective features of the figure. The positions of the reference light are automatically recorded on graph paper, and so we obtain a complete plot of visual space.

So far I have used this technique on the Müller-Lyer illusion, and on ambiguous figures such as the Necker cube. I am now working on the Poggendorff illusion, and find fluctuating depth with related changes in the illusion. The results on the Müller-Lyer are remarkable: there is a correlation of about 0·9 between the extent of the illusion (as determined by the fin angle; measuring the illusion by setting an adjustable comparison line to equality) with the same figures but luminous, their depth being measured with this technique.

My suggestion[5] that figural after-effects are due to constancy scaling being upset by lengthy fixation of depth clues can now be tested.

A further fact, which seems to hold for all the illusions where background produces a distortion, is that the illusion evidently disappears when the affected lines are displaced in depth from the disturbing background, by introducing disparity with a stereoscope.

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Alpha-frequency of Electroencephalogram and a Stabilized Retinal Image

It is known that the alpha rhythm is suppressed in most subjects when patterned targets are viewed in normal vision[1]. It is now also well known[2–4] that when a pattern is viewed as a stabilized retinal image, perception of it in whole or in part may be lost intermittently. It is evidently of interest to discover what modification, if any, of the alpha component of the human electroencephalogram occurs when a stabilized pattern has actually disappeared.

Until quite recently, methods of achieving a stabilized image have involved the wearing of contact lenses. Despite the fact that compensation for eye movements by this particular method is sufficiently good to promote fragmentation and occasional total disappearance of the image, some mechanical destabilization due to minute translations of the lens relative to the scleral surface must occur[5]. Though this cannot account for all reappearance of the image[6], it undoubtedly induces periodic regenerations of the order of three or four seconds, and since alpha develops relatively slowly in normal situations[7], a clear-cut correlation with such brief events might be hard to achieve. (Since this communication was written, we have heard that comprehensive investigations of the relationship of alpha to image disappearance using the contact lens method of stabilization have been performed by Fender *et al.* at the California Institute of Technology, with results in general agreement with those reported here.)

The after-image method of investigating stabilized patterns[8] removes destabilization as an interfering variable, and, since in any sequence of viewing a prolonged after-image, total disappearances of the pattern tend to become increasingly more common with the passage of

Table 1. GENETIC RECOMBINATION BETWEEN A *waxy* TESTER AND *wx* SITES INDUCED WITH ETHYL-METHANE SULPHONATE IN MAIZE

	Seed treatment conditions			Recombination data	
Mutant	Molarity of EMS	Days at 3° C	24-h post-treatment (° C)	Est. No. microspores ($\times 10^3$)	$\bar{X}$ No. $Wx \times 10^{-5} \times 2$
BNL–85	0·05	2	27	85	25·6
BNL–87	0·025	3	3	376	44·2
BNL–86	0·025	3	3	409	76·2
BNL–88	0·025	3	18	603	86·0

treatment was to ensure thorough penetration without chemical disintegration of the mutagen. This was followed by post-incubation in water at different temperatures (Table 1).

The plants grown from treated seeds were crossed to a tester stock that was recessive at the *waxy* locus. The occurrence of *waxy* kernels in the F_1 indicated a mutation. The presence of *Wx* pollen in the F_1 plants, in excess of back-mutation frequency, was evidence of recombination between the tester and mutant *wx* site.

Recombination results on the four sites are shown in Table 1. These were selected for reporting in this preliminary article because closely comparable results were obtained by two observers (R. B. and E. A.), working completely independently of each other. The figures shown in Table 1 are averages computed from the two sources of data. The number of *Wx* grains has been multiplied by two to be comparable with other recombination maps. The mutant sites are arranged in Table 1 in order of increasing amount of recombination with the tester.

In so far as the *Wx* pollen in F_1 plants heteroallelic for tester and mutant *wx* sites arises from genetic recombination, this result, in itself, is an indication that the mutant sites are positioned differently from the tester site in the *wx* locus. The results in Table 1 have not been corrected for the spontaneous back-mutation rate. Evidence from other research[4] with standard *waxy* sites shows that back-mutation rates range from 0·60 to 2·42 $\times 10^{-5}$, which is about equivalent to a map distance of 0·0012–0·0048. The range of recombination of the mutants reported was from 0·0256 to 0·086. Therefore, the recombination figures shown in Table 1 are considerably in excess of a back-mutation rate from other work. Furthermore, the results presented here indicate a back-mutation frequency of zero for the homoallelic tester used in this research.

Mapping by the described procedures gives the relative recombination distances from one site. However, if a map is constructed by this method it may not give the true spatial relationships since at present all mutants are mapped to one side of the tester site.

Future mapping will be done by first obtaining stocks which are homoallelic for the induced site. These will then be intercrossed in all possible combinations so that the actual recombination distances among induced sites can be determined, rather than only the distance from the tester site. This conventional mapping method should show whether induced sites are distal or proximal to the tester site and, hence, their true spatial relationships. Furthermore, by following such a procedure insight should be gained on whether EMS-induced sites are 'point' mutations or minor deletions. The *ad hoc* mapping procedure used here is not capable of distinguishing small deletions from 'point' mutations since recombination would be expected in both. However, by the conventional mapping procedure, minor deletions should be distinguishable by non-additivity of recombination distances when all the combinations of a diallel system of crosses are tested. In the course of the analysis evidence for major chromosomal damage should also be detectable.

In summary, the evidence for intracistron recombination reported here indicates that EMS induces independent mutations at sites within the *waxy* locus in maize. The occurrence of recombination between mutant and tester *wx* sites is further indication that 'point' mutations, or at least minor deletions, have been induced by this mutagen.

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PSYCHOLOGY

Inappropriate Constancy Explanation of Spatial Distortions

THE perception of two- and three-dimensional space has for long been one of the central issues in the experimental study of sensory and perceptual processes. An aspect of this problem is the apparent distortions of shape, size and direction which occur when the elements of a stimulus pattern (lines, angles, forms, etc.) are juxtaposed in certain spatial relationships. Such spatial illusions, which can be defined as discrepancies between the judged and true physical properties of the stimulus, have not yet been explained satisfactorily. It is clear, however, that their explanation would constitute a considerable advance in our understanding of the perceptual processes involved in space perception.

Interest in illusory patterns has been revived recently by a further attempt at their explanation by Gregory[1–3], who has extended and tested a theory originally proposed by Tausch[4]. Although this theory has the virtue of simplicity in addition to that of interpreting illusory phenomena in the context of the established principle of perceptual constancy, it can be seriously questioned on several grounds. Some criticism has already been raised by Brown and Houssiadas[5].

Gregory argues that the classical spatial illusions are two-dimensional projections of three-dimensional objects such that those elements normally further away in three-dimensional space appear larger. The principle of 'misapplied'[6] or 'inappropriate'[1] constancy can be illustrated in Hering's illusion shown in Fig. 1. The two vertical lines in this pattern are parallel. The radiating lines give a perspective effect; the centre of the pattern represents a point more distant than points around the margin. Since the distance between the two vertical lines is constant throughout, the visual sub-tense is also constant. But the central region of the pattern contains information for greater distance than the margin. In order to subtend the same visual angle, therefore, the separation between the parallels in the centre must be perceived as greater than at the ends, hence the outward bowing effect of the parallels. The principle of inappropriate constancy is also illustrated in the variants of Ponzo's illusion from Teuber[6] also shown in Fig. 1. In summary, information or cues for greater or less distance contained in the background pattern will determine the apparent size of elements in a two-dimensional display.

The principle involved is precisely that invoked by Ptolemy to explain the Moon illusion, that is, the greater apparent size of the Moon at the horizon as compared with its size at zenith. In each location the Moon subtends much the same visual angle, but the horizon is judged further than the vertical distance. Thus the Moon must be judged larger at the horizon. This apparent distance theory of the Moon illusion has been strongly supported by data from a series of recent experiments[7].

A first point of criticism which has already been raised[6] concerns the occurrence of spatial illusions in the tactile modality. It has for long been known that spatial illusions similar to those in vision occur when the same line patterns are impressed on the skin. A number of early investigators and, more recently, Revesz[8] and Rudel and Teuber[9] have demonstrated the occurrence of numerous spatial illusions for both active and passive touch. Further, Revesz has ruled out a dependence of these tactile illusions on vision by observing their occurrence among subjects blind from birth.

Since the touch receptors of the skin constitute a 'contact' sense which is not adapted for three-dimensional spatial discrimination, it is difficult to argue that distance information in the surrounding pattern determines the illusory effect through inappropriate constancy. Both the visual and tactile sense organs are constituted of a spatially extended receptor mosaic and the occurrence of similar illusory effects for each modality strongly suggests similar processes. A parsimonious theory would be expected to account for each. This criticism is reinforced by the recent finding that the receptor mosaics of both the skin and retina contain mechanisms which enhance borders and edges to give the Mach effect[10].

A second point involves numerous variants of the Zöllner illusion. In Fig. 2*A* are shown the Zöllner, Wundt and Orbison illusions, all of which derive from and are complex versions of the intersection of one line with another as shown in Fig. 2*B*. If the line to be judged is vertical its apparent slant in the opposite direction to the slant of the intersecting line is a function of the angle of intersect as shown in Fig. 2*C*. The illusory effect is minimal at angles of approximately 22° and 67°. Thus, if line patterns are of variable angle and direction, as in the three patterns in Fig. 2*A*, the illusory effect will vary

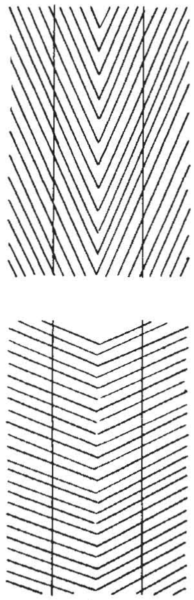

Fig. 3. Illusion of slant as a function of angles of intersection of 22·5° (upper) and 67·5° (lower)

according to the particular locus of the verticals on the background. Although the multilined backgrounds of the patterns in Fig. 2*A* contain perspective information for distance, the same can scarcely be said of the simpler and more basic pattern of Fig. 2*B*. That is, the well-known illusions of Zöllner, Wundt and Orbison are each complex versions of the relatively simple case shown in Fig. 2*B* in which it is extremely difficult to conceive of an apparent distance determinant.

A further point arises out of this variation in the magnitude of 'directional' illusions as a function of intersect angle as shown in Fig. 2*C*. At intersect angles of about 22° the two parallels appear closer in the lower part of the pattern and at angles of about 67° farther apart. But the distance information from the background perspective is the same in each case. This difficulty for the constancy interpretation is illustrated in Fig. 3. It can be noted also that a number of directional and size illusions change, often exhibiting the reverse effect, when the background pattern is systematically varied with respect to certain properties.

The Müller-Lyer illusion is an example of an illusion which can be seen in a variety of patterns. The 'dumbbell' illusion[11] shown in Fig. 4 is one such variant. The attached circles have the effect of lengthening or shortening the horizontal lines. Now, although the angles attached to the lines in the classical Müller-Lyer figure can be thought of as containing perspective information for distance, the same can scarcely be said of the circles in Fig. 4, all of which are the same diameter and vary only in the distance apart of their centres. To attribute distance information to equal circles would seem to be stretching the misapplied constancy hypothesis to breaking point, especially as the two circles suggesting greater distance (those closer together) produce an illusion of being shorter.

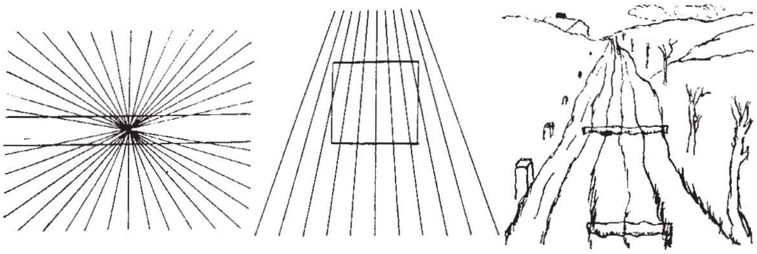

Fig. 1. The Hering illusion (left) and two versions of the Ponzo illusion (right) demonstrating the misapplied constancy principle

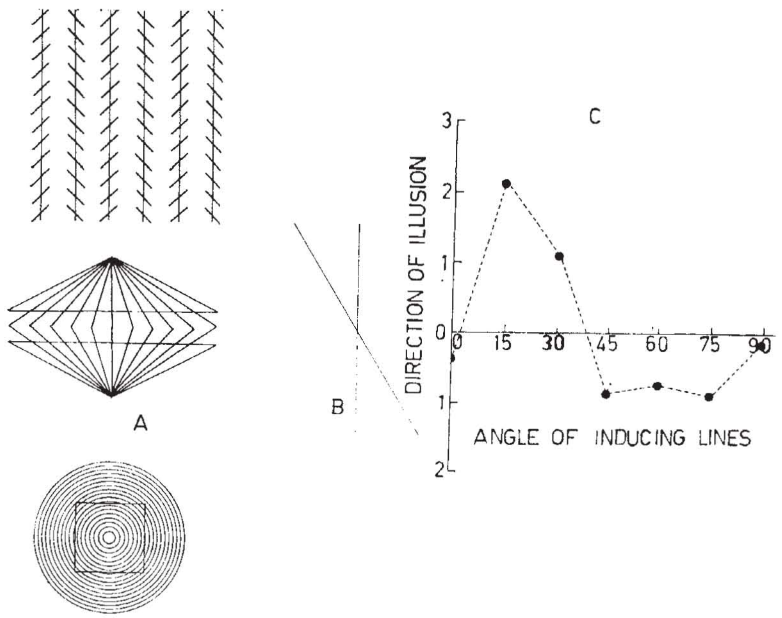

Fig. 2. *A*, Illusions deriving from the intersection of two lines; *B*, the simple case; *C*, variation in the direction of an illusion of slant as a function of the angle of intersection

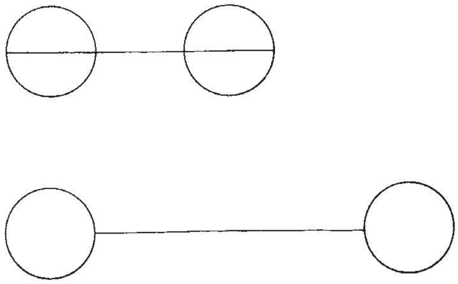

Fig. 4. The 'dumb-bell' illusion. The horizontal lines are equal in length

Gregory has also attempted to explain spatial after-effects in terms of inappropriate constancy. These effects occur in judgments of visual patterns following prolonged stimulation by another. To attribute these effects to the same processes as those responsible for spatial illusions fails to take into account that in using the same patterns to generate an illusion and an after-effect the directions of distortion are frequently opposite. This opposition between illusion and spatial after-effect is illustrated in Fig. 5. The surrounded dotted circle appears larger than the objectively equal but non-surrounded circle. If, however, the surrounding circle is fixated for a minute and then the dotted circle compared, the circle falling within the hitherto stimulated region appears smaller. In any event, it has now been shown that there is no necessary relation between spatial illusions and spatial after-effects[13].

Fig. 5. Figures for showing the opposition between illusion and after-effect

There now seems to be little doubt that certain illusory phenomena derive from an apparent distance-apparent size invariance. The Moon illusion is one such case[7] and is probably a special case of Emmert's law as demonstrated by King and Gruber[13]. The argument that the classical spatial illusions and spatial after-effects derive from an essentially similar size-distance invariance is, to say the least, questionable in view of the contrary evidence presented here. In point of fact there is evidence which strongly suggests that the apparent distortions of illusory figures derive from neural interactions between the processes induced by the judged and background elements of the pattern[14]. If this explanation can be sustained then apparent distance would be a consequence, not a cause, of spatial distortions.

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PROF. DAY omits the major feature of my theory. The omission is evident in his reference to the Moon illusion. What is interesting about the Moon illusion is that its apparent size is not a simple function of its apparent distance. On the horizon it appears large and near. Ptolemy was not correct in attributing its apparent size simply to its apparent distance, and the effect is not a straightforward example of Emmert's law. For this and other reasons I suggested that there is more to constancy than apparent distance: that constancy can be set directly by depth cues which are not always appropriate. Prof. Day disregards what I have called "primary constancy scaling[1]" without which I believe we cannot hope to develop a consistent theory of these distortions in terms of depth perception.

The reported illusions in the tactile modality are certainly interesting, but should not be regarded as a straightforward "criticism", or objection, to a theory of the visual illusions in terms of depth. It seems much more to the point to discover more about these tactile illusions—to discover how they are related to the visual ones. The fact is we know very little about them. Further, it is not at all clear why this "criticism" is reinforced by the fact that borders and edges are neurally enhanced in both touch and vision. Why should the Mach effect be relevant to distortion illusions ?

The discussion of the Zölner, Wundt and Orbison illusions is not aimed at my theory, because the essential point of primary scaling is omitted. In each case the depth features of these figures can be related, by isolating the features and measuring the perceived depth of each, with the technique described briefly in my reply to Brown and Houssiadas[2].

Regarding figural after-effects: the notion that they may be due to constancy scaling taking some time to recover after prolonged fixation was put forward as a suggestion which seems worth following up. It is probably consistent with the known facts; but again it must be discussed in terms of 'primary' scaling. This is set by local depth features which may be opposed by other features or countermanded by the texture of the background. It is not synonymous with apparent distance except in the simplest cases, but in all cases it is possible to isolate the depth features and measure the primary constancy. This can then be directly related to the distortion of visual space in the X- and Y-co-ordinates.

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SOIL SCIENCE

Tracer Technique used in Examination of Activity of Roots of Grass Swards

THE interpretation of measurements of the uptake by plants of tracer isotopes from the soil is complicated by at least three factors. First, exchange takes place between the added labelled ions and the isotope ions present in the soil; the rate of this exchange has been shown to be affected by many factors[1,2]. Secondly, continuous exchange occurs between the nutrient ions in the roots and those in the soil[3-6]. The factors controlling this exchange are unknown. Thirdly, there is the possibility of damage to plant tissues, resulting from accumulation of the tracer. Although a number of experiments have shown no appreciable effects of radiation in terms of yield of dry matter[9-12] and uptake[9,12], the question of radiation damage to plant tissues in long-term uptake experiments remains unsettled. Critical studies[13,14] have shown that even very low doses of radiation may produce some physiological changes in plant cells.

The problems of isotopic exchange make it impossible to compare quantitatively the amounts of tracer found in plants, at different sampling dates, in experiments in of this type of change. From this hypothesis it is predictable that mammalian chromosomes other than the X, that is autosomes, Y and another X, should have numerous minute loci characterized by these (three) features and their distribution on the chromosomes should correspond specifically to the state of the major differentiation of the cell.

This pattern of distribution of the inactivated DNA in autosomes in resting mammalian cells must be very difficult to observe directly because these inactivated portions are so small in these chromosomes and furthermore their identification is complicated by the whirling and intercalation of many long and thin resting chromosomes packed in a small space inside a nucleus. However, distribution of late-replicating loci in the mammalian chromosomes has already been detected by ^{3}H-thymidine autoradiography by many investigators[35-38]. These findings strongly favour our hypothesis that the pattern of gene inactivation is actually distributed also in the whole set of the mammalian chromosomes.

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Change in Sex Ratio in an African Butterfly

IN butterflies, the sex ratio is 1 : 1, or nearly so. Random collections often show a slight excess of males over females, because males are the more active and hence are more often seen and collected.

Acraea encedon L. (Acraeidae) is a common butterfly throughout tropical Africa, inhabiting grassy places and forest edge. It is a slow-flying species and individuals of both sexes are easily caught on the wing. In 1909–12, C. A. Wiggins, at the suggestion of E. B. Poulton, of Oxford University, collected random samples of *A. encedon* from the area between Entebbe and Kampala, Uganda. Poulton was at the time interested in finding the relative frequencies of model and mimetic butterflies, and *A. encedon* is a polymorphic Müllerian mimic. The collection made by Wiggins is preserved in the Hope Department, Oxford, and comprises 96 males and 54 females, suggesting a normal sex ratio. In 1963–64, in order to see if the relative frequency of the polymorphic forms had changed, a random collection of 546 specimens was obtained from the same area. Only nine were males. This change in sex ratio from 64·0 per cent male in 1909–12 to 1·6 per cent male in 1963–64 is highly significant ($P < 0·001$). *A. encedon* occurs in all months and there are two or three generations in the year, so that this drastic reduction in the frequency of males must have occurred in 100–150 generations.

No other large random collections are available for comparison, but in the extensive collections from most parts of Africa in the British Museum and in the Hope Department, the sex ratio appears normal. Three of the nine males collected in 1963–64 were found in copulation with females, but usually when a 'pair' was found flying together as if in sexual display they proved to be females. Broods reared from wild-caught females have produced only females. The possibility of parthenogenesis is being investigated, but whatever the explanation of this highly unusual sex ratio, the present situation has evidently been reached in the past fifty years.

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PSYCHOLOGY

Constancy and the Geometric Illusions

GREGORY has proposed[1] and defended[2] an account of the geometric illusions based on the notion of 'misplaced constancy scaling'. Following Tausch, he suggests that all illusion figures have features indicating depth by perspective which bring into play size constancy scaling, leading to expansion of some parts of the figure relative to others. For this theory he makes the claim that "so far no valid objections seem to have been raised"[2]. The theory nevertheless needs challenging.

Gregory's thesis is this: Illusions result from the operation of a "primary constancy scaling mechanism" triggered by the presence in the figure of (learned) distance cues. This scaling occurs despite the fact that the observer is not conscious of depth in the figure and actually sees it as flat; "primary scaling" is thus distinguished from "secondary scaling" which depends on seeing apparent depth. A theory which appeals to the idea of automatic compensation for unconsciously perceived depth is in obvious danger of being irrefutable. If Gregory's claim to have provided an explanation of the illusions is to be credited he must be able to bolster his theory experimentally in either of two ways, namely: (1) by demonstrating the reality of primary scaling independently of the illusions; (2) by showing that the cues supposed to trigger primary scaling are under some conditions actually treated as cues to depth. His failure in both respects is considered below.

(1) The hope of demonstrating primary scaling independently of the illusions is rendered forlorn by the nature of the concepts involved. The term 'illusion' may be taken to embrace all cases of plane figures the perceived configuration of which differs from the real physical configuration. But this inevitably includes any figure that is constructed to demonstrate primary scaling since such a demonstration must make use of plane figures in order to exclude the apparent depth effects which would activate secondary scaling. Thus the concept of primary scaling is tied to the illusions and cannot be adduced as a general phenomenon of which the illusions are only a specific instance.

(2) Gregory's theory would still be valuable if he were able to show that the cues responsible for primary scaling are genuine depth cues. He would then be able to say independently of the illusions which cues should trigger primary scaling and which should not, and the theory would have some predictive power. In this connexion, he quotes the results of experiments made on luminous figures where he has demonstrated that in the absence of background texture the illusions are commonly seen in depth in the way expected. However, his own results show that this is not always the case. For example, with the Muller-Lyer figure he found that "a model having the optimum angle for the fins (about 40°) shows a marked illusion and is not seen in depth but appears, on the whole, flat"[3]. He concludes: "This evidently produces a discrepancy between constancy and apparent depth". Thus he is prepared to uphold the constancy theory even when the evidence indicates directly that the cues supposed to trigger primary scaling are not treated as depth cues. But to admit that primary scaling cues may or may not be depth cues not only seriously weakens the theory but also undermines the support obtained from the luminous figures which are seen in depth by introducing the possibility that these effects are purely fortuitous.

There seems thus to be little likelihood of obtaining external confirmation for the theory. In this case there can remain only its general consistency to recommend it. Even if primary scaling is not independently demonstrable and even if it cannot be shown that depth cues are the operative features of the illusion figures, it might still be that the theory provides an account of the illusions which is valid in so far as similar cues can be seen to produce similar types of distortion in a variety of figures. In fact the theory fails on this score too. Two examples may suffice: (*a*) Gregory explains the fact that the upper line in the Ponzo illusion (Fig. 1) appears longer than the lower by saying that it lies in a part of the figure which the converging lines indicate to be more distant so that primary scaling magnifies its apparent size. As it stands, this explanation predicts the expansion of any line drawn in the upper (more 'distant') part of the figure, no matter what the orientation of this line might be. It follows that the illusion ought to occur when the two lines of the Ponzo illusion are drawn vertically, instead of horizontally. Fig. 2 shows that this is not so. (*b*) Gregory explains the Orbison illusion (Fig. 3) in a similar way to the Ponzo illusion by supposing that the converging lines indicate depth—presumably a receding tunnel—so that the supraimposed circle is distorted by constancy. The distortion ought to occur in such a way that the perceived figure comes to look more like that figure on the tunnel wall which would give rise to a circle as its retinal image. Careful thought, however, shows that in fact the illusion occurs in the wrong direction. To most observers the circle appears as in Fig. 4, whereas Gregory's theory predicts that it should appear as in Fig. 5. This last figure shows the form that would have a circle as its retinal projection, and this figure should be seen if constancy is at work.

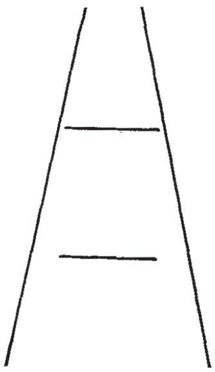

Fig. 1

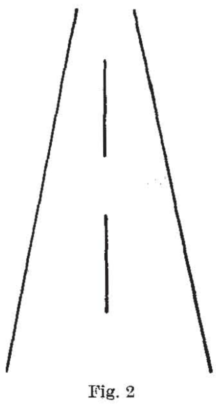

Fig. 2

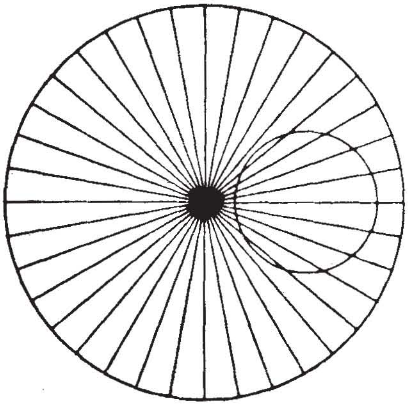

Fig. 3

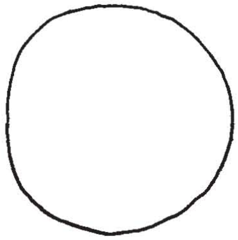

Fig. 4

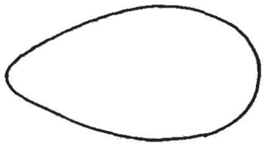

Fig. 5

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PERHAPS it is difficult to demonstrate primary constancy scaling independently of the distortion illusions, but its effects are not limited to plane figures. For example, the apparent size of the Moon is not a simple function of its apparent distance—when low on the horizon it looks both large and near, which contravenes the classical Emmett's Law, and demands some kind of size scaling which is not locked to apparent distance. The worry about lack of perception of depth in luminous plane figures having exaggerated perspective but which give illusory distortions was in fact expressed by myself, in the (unpublished) paper cited by Humphrey and Morgan. If illusions do occur in figures not seen in depth though the countermanding depth-cues are removed, it would have to be supposed that primary constancy can work like a 'super releaser' (as found in ethology), working beyond the normal range at which it is useful. This is quite possible, but if true it would make precise predictions difficult. On present evidence, however, it does not occur: Measuring the apparent depth in luminous Muller–Lyer figures of various fin angles, with the technique briefly described[1], I found that the apparent depth of the illusion figures correlates extremely closely with the measured illusions for each angle tested, over the full range of possible angles of the fins. The distortion and the apparent depth of the figures are both reduced for extreme angles, when normal perspective breaks down. To argue that the relation discovered between apparent depth and the illusions is fortuitous is to fly in the face of a correlation coefficient better than 0·9. There are other and quite different predictions which follow from the theory, and it is compatible with the curious finding that peoples who live in environments largely free of right angular corners and parallel lines, such as the Zulus who live in a 'circular culture' of round huts, do not suffer these illusions to anything like the normal extent[2,3].

The point raised about the Ponzo illusion is interesting. It could be that the vertical line is too far removed from the converging 'perspective' lines or, more interesting, it may indicate an important difference between size and shape constancy for which there is growing evidence.

The Orbison illusions are compatible with Fig. 4*b* (ref. 4). An important feature of primary scaling is that it is set by typical neighbouring depth features, not by the relative depth in the parts of the figure as a whole when this is complex and having conflicting depth features. It is thus entirely different from secondary scaling, which works simply according to apparent distance. Now the Muller–Lyer and the Ponzo figures are simple cases, as there are no other lines in the figures to produce complications; but to understand the Orbison figures it is necessary to isolate the neighbouring disturbing features and measure their apparent depth separately from the rest of the figure. The Orbison Fig. 3*a* (ref. 4) is a useful test case, for here perspective in the figure as a whole may be reversed by changing the spacing of the concentric circles, so that they are spaced either more or less closely from the centre. This reverses the apparent depth in the figure as a whole, but not the illusion when presented on a textured plane. This is again compatible with the interpretation for Fig. 4*b* (*op. cit.*). On the textured plane it is the typical depth information of the neighbouring lines which determines the primary scaling in all cases. These statements are testable by isolating features in any figure, measuring the depth of these isolated features, and comparing the measured depth of the isolated features with the illusion.

Much work remains to be done in relating depth to illusory distortions, but it is now fairly clear how the theory can be tested adequately.

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Occurrence of the Electroencephalographic Alpha Rhythm with Eyes Open

It is well established in electroencephalography that the alpha rhythm occurs much less frequently when the eyes are open in an illuminated environment than when they are closed. Moreover, if the visual enviroment is patterned, then alpha occurrence is even less frequent. Finally, 'paying attention' to the pattern reduces the occurrence of alpha still further[1]. Although these general descriptions are valid, they can be misleading if one wrongly assumes that 'much less frequently' means a very low frequency of occurrence of the alpha rhythm. On the basis of such an assumption one might not attempt certain experiments concerning vision and the alpha rhythm, because the expected amount of alpha rhythm would be too little.

Recently, I have completed a study of the electroencephalographic (EEG) alpha rhythm recorded while nonsense syllables were being read. The apparatus was so arranged that whenever alpha occurred, a nonsense syllable was projected on to a screen for 0·2 sec. If alpha was not present the syllable was not presented. In this closed loop situation the EEG was divided into successive alternations of alpha and non-alpha, activation durations[2]. The increased durations of activation reflected the increased alertness of the subject in response to the nonsense syllable flashed on the screen. A reasonable expectation would be that combining eyes open, increased attention, heightened expectancy, patterned stimuli and illuminated environment, would so decrease the frequency of occurrence of alpha that experimental trials would be excessively long and tedious.

Quite unexpectedly this was found not to be the case. Alpha rhythms, which disappeared when the patterned stimulus was automatically presented, re-appeared soon after the stimulus was automatically removed, permitting the next stimulus to occur. It was, in fact, the atypical subject who could not participate because of insufficient alpha with eyes open[3].

In exploratory investigations now being undertaken here subjects are tested with eyes open in an illuminated room. The experimenters, apparatus, etc., are in view. Using a loop situation similar to that described here, a tone is presented when alpha occurs and is removed when alpha ceases, that is, when cortical activation occurs. We have found that for many subjects, the 'blocking' or inhibition of the alpha rhythm during feedback stimulation is not greatly increased with eyes open when compared with a similar condition with eyes closed. For some subjects, even when instructed to 'pay attention' to the environment, alpha occurs more often than had been expected.

These results are consistent with work described previously where subjects, watching a moving visual stimulus under various conditions of mental set, exhibited alpha about 20 per cent of the time[4].

These observations have convinced me that investigations of electroencephalographic alpha rhythm and attention to patterned stimuli with eyes open would not be critically limited because of an infrequent occurrence of the alpha rhythm.

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