

structure. Another important feature of the metal alkoxides is the relatively low energy (about 10 kcal.) of the intermolecular bonds which hold the polymer together. Clearly the most stable polymer (to thermal dissociation) will be the one containing the maximum number of these weak intermolecular bonds between adjacent units in the polymer. This point can well be illustrated by reference to titanium alkoxides. If all the titanium is octahedrally 6-coordinated there is a choice between the trimer in which the octahedra share faces and each unit is held by three intermolecular bonds, and a higher polymer in which the octahedra share edges and each unit is held by two intermolecular bonds. If the intermolecular bond energy is approximately the same in each case, then 50 per cent more energy is required to detach a unit from the trimer molecule than from the higher polymer. According to these ideas the formation of low polymers need not be limited to the metal alkoxides but could be expected wherever the formation of a polymer is due to covalency expansion of an element and wherein the intermolecular bonds are weak. For example, some of the electron-deficient molecules such as the boron hydrides and metal alkyls support this view. Diborane is formed from  $\text{BH}_3$  because the tricovalent boron increases its covalency to four. This covalency expansion could be achieved in an infinite linear polymer  $(\text{BH}_3)_\infty$  in which each unit of the polymer is held by only one hydrogen bridge as against the two in diborane. However, it must be realized that in some systems of inorganic polymers (for example, borazoles and phosphonitrilic compounds) also involving covalency expansion there are other complicating

factors such as  $\pi$ -bonding and aromaticity which may stabilize particular structures, and it does not follow that the molecule will adopt the lowest possible degree of polymerization.

It is hoped to test the theory discussed above by direct structural measurements on the metal alkoxides. However, it is always possible that in the crystal lattice a metal alkoxide may adopt a degree of polymerization different from that exhibited in solution.

I am indebted to the Chemical Society for permission to reproduce the diagrams in Figs. 1-5, and also to Prof. W. Wardlaw for his guidance and encouragement throughout this work.

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## EYE MOVEMENTS AND THE STABILITY OF THE VISUAL WORLD

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THE visual perception of movement is generally regarded as of primary biological importance, yet far less work has been done on this subject than on topics such as colour vision, visual acuity and the photic sensitivity of the eye. Further, surprisingly little is reliably known about the neurological mechanisms subserving movement perception. There are many unsettled questions, in particular that of the apparent stability of the visual world during voluntary movements of the eye. Some of the problems raised by the visual perception of movement will be discussed in this article.

### Information Channels in the Perception of Movement

The simplest case of movement perception is that given by a moving self-luminous object in a dark room. Perception of its movement may occur under two different sets of conditions: (1) the eyes may follow the object ('tracking'), in which case its image will, ideally, remain stationary upon the retina; and (2) the eyes may remain stationary so that the images travel across the retina. Since movement is experienced under both conditions, there must be at least two information channels subserving movement

perception. The first involves tracking eye movements, and may be called the 'retina/head' system. The second involves shifts of the image across the retina, and may be called the 'image/retina' system. It may be supposed that the two systems are based on essentially different neurological mechanisms.

Movement perceptions may, in special circumstances, be paradoxical. When a fast-flowing river, the view from a moving train, or an endless belt of black-and-white stripes is fixated for several seconds it will be found that if the gaze is transferred to a stationary object it will seem to move in the opposite direction and with corresponding velocities to those of the previously observed real movement. This after-effect of movement is paradoxical, for though movement is clearly observed it may also be seen that nothing is changing in position. Similarly, when a stationary small weak light is observed in total darkness it will seem to move erratically, and yet it may not seem to change its position to any marked extent. Such paradoxical perceptions may be due to incompatible information arriving from the two or more movement channels. Adaptation or random changes in the systems might be the cause.

As is well known, there are two essentially different types of eye movement, first studied systematically by

Dodge<sup>1,2</sup>. When the eye tracks a moving target, once it is 'locked' on to the target it moves smoothly, provided that the target moves in a simple, known manner without excessive changes in direction or velocity. Voluntary movements in the absence of a target take place in small jerks ('saccades') occurring about four times per second, which have been much studied particularly in relation to reading.

It is generally supposed that smooth tracking movements of the eyes occur only in response to retinal cues, that is they form part of what we have called the 'retina/head' system. I have shown that this is not necessarily the case. A small neon lamp is arranged to flash at 25-50 flashes/sec.: the light will appear continuous under conditions of steady fixation, but if, with the eyes remaining still, the lamp is moved steadily across the retina, a regular flicker will be noticed. This is a well-known effect. If now the eye is swept as smoothly as possible by voluntary movement, this regular flicker is not seen. The lamp seems to move in jerks. Evidently the saccadic movements prevent the smooth travel of the image which is necessary for the observation of the regular flicker. On the other hand, when the eyes follow a moving target the flicker may be observed, as when the lamp is moved across the field with the eyes stationary. Using this technique, I have been able to show that it is not necessary for the observer to track a visual object for the smooth eye movements to occur. The regular flicker indicating smooth eye movements may be seen if the observer tries to track his own hand under conditions of complete darkness apart from the light from the neon lamp, his hand being invisible. That is to say, smooth eye movements may be elicited even in the absence of appropriate retinal stimuli. It follows that the retina/head system may involve a proprioceptive component; information from moving members of the body may suffice to actuate the smooth eye movement system. I have also found that the apparent movements of a stationary small weak light viewed in darkness (the 'autokinetic effect') are influenced by slight unbalanced strains imposed on the eye or neck musculature. The effect may normally be due to randomly occurring imbalance of the musculature or proprioceptive systems of the eye and neck.

### Eye Movements and Perceptual Stability

It is a commonplace to state that when the eyes move voluntarily across an extended field (by means of saccadic movements) there is little, if any, change in apparent position of the perceived objects. The visual world does not swing round in the direction opposed to the eye movement. On the other hand, nearly all subjects report that when an object moving across the field is tracked, the stationary background does tend to swing round in the opposed direction. The experience is similar to, though probably less marked than, the movement of the field observed when the eye-ball is moved passively by pressure from the finger. This observation suggests that saccadic eye movements are in some way necessary for the stability of the visual world. It may be that the jerky movements of the eye are themselves important, or that the saccadic mechanism accepts information giving rise to stability which is rejected during smooth tracking movements. Evidence to be given below suggests that the former is the case.

The problem of the stability of the visual world was discussed by Helmholtz<sup>3</sup>, and later by many

other writers, the most recent being Mackay<sup>4</sup>. There have been two main theories. The first, that stabilization is given by proprioceptive information from the extrinsic eye muscles, which has been called the 'inflow' theory, was rejected by Helmholtz, who held that the central command signals (but called by him 'the Will') are monitored by an internal loop which gives appropriate information for providing stability, provided the motor system is functional. This has been called the 'outflow' theory. He pointed out that patients suffering from paralysis of the external recti, and who were therefore unable to execute voluntary eye movements, experience the visual world moving round in the direction in which the eyes should have moved had it been possible to "execute the command". This observation has been confirmed under more controlled conditions<sup>5</sup>.

A useful technique for investigating many of the phenomena of stabilization and movement perception is provided by observations of after-images (preferably produced by fixating a photographic-type electronic flash tube) under various conditions. It is not always realized that after-images observed in complete darkness move, apparently rather precisely, with the eyes during slow voluntary eye movements though they are not affected by passive movements. We should expect some feed-back from the stretch receptors which are now known to exist in the eye muscles<sup>6,7</sup> during passive movements, and this should produce some shift of after-images if the inflow theory were true.

We find that if, in total darkness, the drift of an after-image is observed during (a) slow voluntary eye movements, and (b) during the 'proprioceptive tracking' of the observer's hand described above, the after-image shows small saccadic-like jerks in condition (a), but not in condition (b), when it moves smoothly. If the velocity of the hand movement is changed the after-image may seem to lead or lag, and then to 'lock' on to the proprioceptive locus of the hand. The jerks experienced in condition (a) suggest that the stabilizing system has access to information of saccadic movements.

### The Cancellation Theory

Helmholtz does not clearly state how his outflowing command signals are supposed to produce stability. Since stability depends upon the eyes in fact moving, the shift of the retinal image must be important. The term 'outflow' theory is thus misleading, for it ignores this shift of the retinal image and the information it transmits. Passive eye movements produce marked contrary shifts of the visual world: Helmholtz's theory requires these movement signals in conjunction with his command signals to produce stabilization, and this should be stated explicitly. The 'outflow' theory may, in this form, be called the 'cancellation' theory, where signals from the eye/head system are supposed to be cancelled out by signals from the image/retina system. This is similar to the view put forward by von Holst<sup>8</sup>, but is really a natural extension of Helmholtz's theory.

Mackay<sup>4</sup> has recently made the interesting suggestion that stabilization is not something which is achieved, but rather that things are regarded as stable unless there is sufficient evidence to the contrary. Thus he says: "what requires informational justification is not the maintenance of stability but the perception of change", and also: "the retinal changes resulting from voluntary movement evoke no

perception of world-motion, because they are not an awkward consequence to be compensated, but part of the goal to be achieved". He explains the apparent movement of the perceptual world when the eye movements are paralysed by saying that the 'goal' (which is internal and conceptual) shifts with changing expectations. This may be contrasted with the cancellation of the command signals by retinal movement information.

On the 'cancellation' theory the world moves if the eye movement is thwarted because the command signal is not cancelled by the image/retina system, there being no signal. Similarly, after-images move during voluntary eye movements, because there is no shift of the image across the retina to give an image/retina signal.

On the 'cancellation' theory we may predict that if we could destroy movement information in the image/retina system then the visual world should seem to move with the eye during voluntary eye movements. This may be done simply by illuminating the field with a stroboscope set to 4-5 flashes/sec. Movement is then only seen when the eye follows an object. With the eyes stationary, a moving object is observed to occupy successive positions, but not to move. When it is tracked it does, however, in stroboscopic illumination, appear to move. Voluntary eye movements produce loss of stability; the entire visual field moves in jerks. If now smooth eye movements are produced, by tracking a small self-luminous object held rather close to the eye, the entire visual world may be seen to move with the tracking object, and therefore with the eyes. This is observed best with a faintly glowing filament mounted on a pendulum bob; the visual world then swings with the bob, provided the distance and velocity conditions are appropriate.

This is difficult to reconcile with Mackay's 'null hypothesis' view of the matter, for the expectation of movement can scarcely be supposed to be related to the manner of illumination or to the kind of movement of the eye.

Mackay's observation that a stationary glowing filament moves though the stroboscopically lit field remains relatively stable during passive eye movements would be expected on the 'cancellation' hypothesis, for the image/retina system should give movement information from the self-luminous filament only, and the eye/head system will give no information. The new observation given here, that the visual world moves with the eyes under these conditions when following a target, seems to be positive evidence for the cancellation hypothesis.

It may be suggested that saccadic movements are important in providing large movement signals which may be readily computed to give cancellation.

I wish to thank Prof. O. L. Zangwill for much advice and encouragement, and for most generous help in writing this article. I have benefited by discussions with P. E. K. Donaldson, R. Warren, A. J. Watson, F. Campbell and other colleagues. Miss Jean Wallace gave valuable help testing subjects; the Medical Research Council provided a maintenance grant for Miss Wallace and a grant for apparatus.

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## BETA-PROPIOLACTONE AS A TOXOIDING AGENT

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**T**HE conversion of a bacterial exotoxin into a non-toxic antigen suitable for injection into animals presents special difficulties in the case of an unstable substance such as the  $\beta$ -toxin of *Cl. welchii* Types B and C. This antigen, which is used for vaccinating domestic animals against enterotoxaemia, deteriorates rapidly<sup>1,2</sup>, even at 4° C.

The usual method of toxoiding  $\beta$ -toxin for vaccine preparation involves incubating the culture filtrates with formalin at 37° C. until the material is no longer lethal for mice. Culture filtrates with initial minimum mouse lethal doses of 0.005-0.001 ml. normally require 9-21 days to become non-toxic. More concentrated solutions of  $\beta$ -toxin, prepared by ammonium sulphate precipitation or by freeze-drying of the culture filtrates, take proportionately longer.

The antigenic potency of these vaccines is tested in rabbits as follows: two doses of 2 ml. each of the

inactivated preparations to which alum is added to a final concentration of 1.0 per cent are injected. There is an interval of four weeks between the two injections and the rabbits are bled two weeks later. The antibody contents of sera obtained in this manner from about ninety rabbits used for testing twelve batches of formalin-inactivated culture filtrate averaged 7.58 international  $\beta$ -antitoxin units/ml. Seventeen batches of formalin-inactivated Type B culture were tested by the procedure recommended in the British Veterinary Codex for Lamb Dysentery Vaccine and the antibody contents from the rabbit sera averaged 2.75 international  $\beta$ -antitoxin units/ml. (the minimal response for this vaccine should be 2.5 international  $\beta$ -antitoxin units/ml.).

A concentrated Type C filtrate (minimum mouse lethal dose, 0.0002 ml.) was used for comparing the toxoiding properties of  $\beta$ -propiolactone