in a dose of 2 mu./kg/h intravenously increases the excretion of water and electrolytes in camels, as in sheep<sup>7</sup> so that the low urine flow of camels is as yet unexplained.

When deprived of water in the sun at mean maximum temperatures of 41° C (Table 1) three camels lost weight at rates of only 19-23 g/kg/24 h because of small losses of sweat, urine, respiratory and faceal water<sup>2</sup>, and lowered motabolism. This was half the rate of weight change observed in Merinos at the same temperature. The differential loss of fluids is, however, a point of great interest (Fig. 2). Whereas the average body-weight of camels fell by 20.5 per cent in 9 days, the SCN space was reduced by only 15.6 per cent. Of the weight lost the interstitial fluid yielded 9.3 per cent and the plasma 5.2 per cent. The cells and gut contributed water to the extent of 81.2 per cent of the loss in weight, in contrast with Merino sheep, which provided only 46.2 per cont of the weight lost as water from these sources, in similar environmental circumstances<sup>4</sup>. Measurements on sheep<sup>4</sup> indicate that differential losses of water occur between spaces and that at relatively slow rates of water loss (30 ml./kg/24 h) the sheep depletes the interstitial fluid faster than plasma, but during rapid dehydration relatively more water is drawn from the cell and gut space. In camels the slow rate of loss in weight during exposure to high temperature (41° C) allows adjustments of fluid spaces which resemble those of sheep at lower tomperatures (32° C).

	Camels*	sheep *
Days without water mean max. temp. 41° C.	9	5
Weight lost (% body-weight)	$22 \\ 20.3$	23.5
% from SCN space % from cells and gut	$14.5 \\ 81.2$	$50.4 \\ 45.4$
,v 8		

\* Mean of 3 in each case

The question of whether the cells and alimentary fluids share equally in providing water is hard to answer directly because gut water is not readily estimated. It is known, however, that in camels rumen contents may comprise an average of 110 g/kg (ref. 7) and the alimentary tract may hold up to 180 g/kg, of which more than 80 per cent is water. During dehydration the passage of gut fluids was reduced to about 5 per cent of the initial flow in a fistulated camel studied by Stepankina and Tashenov<sup>8</sup>. The abdomen also of a dehydrated camel has a highly concave contour, as though little contents remain in the

These observations suggest that the alimentary gut. tract may provide much of the water lost.

If it be assumed that the camel begins dehydration with 120 g water/kg in the alimentary tract and that at the end of 9 days without water there is approximate osmotic equilibrium between cells and interstitial fluid, it would then be likely that 52.2 per cent of the weight lost was provided by the gut fluids and 29 per cent by cell water, if both extracellular and cellular water spaces fell by 15.6 per cent. In this sense, the alimentary reserve would not be pure water but a more or less isotonic solution. By using the water component of gut fluids for cooling. and by excreting electrolytes in urine and sweat, the circulating volume would be preserved. In man and sheep the extracellular water takes most of the strain of rapid dehydration, and circulation is likely to be correspondingly unstable, so that men in the sun without water at 41° C succumb in 1-2 days, and tropical Merino sheep in 6 days after losing half the extracellular fluid. Camels survive probably more than 15 days in such conditions while sustaining, like sheep, over 30 per cent of loss of body-weight.

No major difference between the electrophoretic and ultracentrifuge pictures of sheep and camel plasmas was found, so that the differential fluid losses from extracellular and alimentary compartments appear to result from peculiarities of permeability of vascular and intestinal membranes, and the rate of dehydration modifies the amount of transfer from the different compartments.

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- <sup>1</sup> Aristoteles Historia animalium, D'A. W. Thomson (Oxf. Univ. Press, Bk. 8 (7), 596, a, 1949).
- <sup>2</sup> Schmidt-Nielsen, B., Schmidt-Nielsen, K., Houpt, T. R., and Jarnum, S. A., Amer. J. Physiol., **185**, 185 (1956).

- <sup>5</sup> S. A., Amer. J. Progetol., 165 (1950).
  <sup>6</sup> Gauthier-Pilters, H., Mammalia, 25, 195 (1961).
  <sup>4</sup> Macfarlane, W. V., Morris, R. J. H., Howard, B., McDonald, J., and Budtz-Olsen, O. E., Austral. J. Agric. Res., 12, 889 (1961).
  <sup>6</sup> Farnworth, A. J., Austral. J. App. Sci., 7, 233 (1956).
  <sup>6</sup> Kinne, R., Macfarlane, W. V., and Budtz-Olsen, O. E., Nature, 192, 1084 (1961).
- <sup>7</sup> Schnidt-Nielsen, K., Schmidt-Nielsen, B., Houpt, T. R., and Jarnum, S. A. Mammalia, 20, 1 (1956).
- Stepankina, M. K., and Tashenov, K. T., Sechenov Physiol. J. U.S.S.R., 44, 942 (1958).

## A DIFFERENCE BETWEEN REAL AND APPARENT VISUAL MOVEMENT

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NUMBER of workers have confirmed the fact that detectability of the first of two briefly presented flashes of light varies inversely with the luminance of the second and the temporal separation between them. The results of many experiments on this topic have recently been summarized<sup>1</sup>. Extending these investigations on asynchronous stationary visual stimuli to the case of a moving masking stimulus has produced complementary data<sup>2</sup>. The results in the latter case were that the detectability of a brief fixed target stimulus flashed in the path of a moving line varied with the luminance and position of the latter. The brighter the moving line and the closer it was to the target, the less detectable was the latter.

These results provide the opportunity to investigate some properties of a related kind of visual perception, that of apparent (beta) movement. This illusion of movement occurs when two neighbouring stimulus objects of proper luminance are alternated in place at an appropriate rate. When two lines such as A and B of Fig. 1 are presented, each for 50 msec and a proper pause intervenes between the offset of each and the onset of the other, the observer sees a single line moving smoothly and continuously between A and B. The perception is referred to as 'optimal movement'<sup>3</sup>. The apparent movement of the line is a compelling illusion; and many investigators have reported that, for given rates of apparent displacement. the perceptions of real and apparent movement are indistinguishable one from the other. Since a number of these authors have been led by the phenomenal identity of the two perceptions to infer that the underlying mechanisms are similarly identical, the question arises whether a line in apparent movement will affect detectability of a target in the way described here for real movement.



Fig. 1. Spatial arrangement of the alternated forms. A and B are the termini of apparent movement; P, the target or probe flashed in the path of movement; FP, the fixation point. The time diagram shows one sequence of presentations

To answer the question, it is necessary to specify the 'position' of the line in apparent movement during its traverse. This was done by fractionating the temporal interval between A and B that yielded optimal movement, and presenting the small line P for 5 msec at various times between the offset of A and the onset of B. One sequence of presentations is shown in the time diagram of Fig. 1. Let  $T_1$  be the time between the offset of A and the onset of P, and  $T_2$  the time between the offset of P and the onset of B. In the experiments, the sum of  $(T_1 + P + T_2)$  was 105 msec, while the particular values of  $T_1$  and  $T_2$  were varied. For example, when  $T_1$  was 5 msec,  $T_2$  was 95 msec; when  $T_1$  was 25 msec,  $T_2$  was 75 msec; and so on. In this way, the 5 msec long P was made to appear when the line seen as moving between Aand B had proceeded through various portions of its path.

The luminance of the lines A and  $\hat{B}$  was 3 foot-Lamberts, while the luminance of P varied from 0.09 to 0.3 foot-Lamberts for each of three subjects. The latter value was established by finding for each subject the luminance of P when it was presented alone that enabled him to detect it with probability of 0.90+. The stimuli appeared in a  $4 \times 5.5^{\circ}$  field of 0.002 foot-Lamberts luminance. Viewing distance was 75 cm and observations were made monocularly with a dark-adapted eye from within a light-tight booth through a 3-mm artificial pupil. A minute red light (< 2 min visual angle) provided a fixation point. Presentations were made at the rate of one every 8.2 sec, and a warning bell sounded 2 sec before the onset of a presentation.

The results were collected by presenting the subject with identical sets of stimulus conditions a large number of times in various mixed random orders and having him signal each time whether or not he had detected P. The relative frequency of detections, that is, the empirical probability of detection, is the measure used on the data. Each plotted point, thus, is the result of 80 or 100 observations for a given pair of  $T_1-T_2$  values.

In addition to these conditions, the precaution was taken of presenting catch-trials: on approximately 16 per cent of all presentations, P was absent. The 'false alarm' rate in these trials was found always to be less than 10 per cent for all subjects, and will not be further considered.

The results are presented in Fig. 2, each curve showing e results for a single subject. The abscissa plots the the results for a single subject. The abscissa plots the time after the offset of A, and the ordinate shows the probability of detecting P. The curves show a generalized inhibitory effect: the probability of detecting P is always less than 0.90, its minimal values in the absence of Aand B. Within that generalized inhibition, p(P) increases slightly with an increase in  $T_1$  and then decreases, for two subjects, while for the third, p(P) decreases only.



Fig. 2. Probability of detecting the target, P, in the path of apparent movement. The 5 msec long target appeared at a variable interval after the offset of A, that interval shown on the abscissa. Subjects  $D(\bigcirc)$ ,  $K(\bigtriangleup)$  and  $P(\square)$ 

As is shown in Fig. 1, P was placed approximately one-third of the distance between A and B, so that  $T_1 = 25$  msec is the position closest to 'overlap' of the apparently moving line and the target. It is at this position, in Fig. 2, that detectability of P is highest for two subjects. Thus, while Fig. 2 shows that detectability of P varies with the 'position' of the apparently moving line, the form of this variation is exactly opposite that found with the line in real movement, cited here<sup>s</sup>. If the apparently moving line had acted on P in the same way as a physically moving line, the curves of Fig. 2 would be U-shaped: P would be maximally detectable when the apparently moving line was at the beginning or at the end of its traverse, and would be least detectable in the region  $T_1 = 25$  msec. The curves clearly are not of this shape.

One major difference characterizes the stimulus conditions required for the perceptions of real and apparent movement: no image moves across the retina in the latter case. Apparently, then, the image of an object on the retina is required if the detectability of a contiguous object is to be affected. It may be inferred then that the phenomenal identity of the two perceptions notwithstanding, real movement and apparent movement partake of different processes, since their effects are different. The illusion of movement seems to be constructed by the observer out of the information provided by the order and timing of the flickered stimuli. The fragility of this construction will be described in another report.

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- Kolers, P. A., Vision Research, 2, 277 (1962).
  Luria, S. M. and Kolers, P. A. Paper presented to the Opt. Soc. Amer., Autumn 1962 meetings.
- Autumn 1902 meetings.
  Wertheimer, M., Z. Psychol., 61, 161 (1912). Koffka, K. in Handbuch der Normalen und Pathologischen Physiologie, edit. by A. Bethe et al., 12, Pt.2 (Berlin, Springer, 1931). Teuber, H.-L., in Handbook of Physiology-Neurophysiology, 3.