SUN NAVIGATION IN HOMING PIGEONS

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INTRODUCTION

In an earlier paper (Matthews, 1951*b*) it was definitely established that homing pigeons could truly *navigate*. That is, when released in an unknown area in a novel direction they showed a strong initial homeward orientation, and a good proportion returned home in times that would admit of little deviation from the line of direct flight. This has been confirmed by Kramer & St Paul (1952) and by Kramer (1953). Similar evidence of navigation has been obtained with the migratory Manx Shearwater (Matthews, 1952*b*, 1953*b*) and, as regards initial orientation, with the Lesser Black Back Gull (Matthews, 1952*a*).

The experimental work with pigeons had eliminated the possibility of navigation by use of the earth's magnetic field or of an acceleration/displacement recording mechanism. But with all three species indications of a breakdown of the orientation with overcast skies had been obtained. The present paper reviews the evidence that has accumulated for the homing pigeon on this effect, and describes experiments aimed at an analysis of the proposed sun-navigation hypothesis.

MATERIAL AND METHODS

The general technique employed was described in detail in the earlier paper (Matthews, 1951*b*). Young pigeons, 3–5 months old, were used. In 1948–50 they were operated from the lofts of several local pigeon experts, in 1951–2 from a loft established at the Ornithological Field Station, Madingley, Cambridge. They were 'trained', starting in July, by releases in small groups at gradually increasing distances in one direction up to 10–12 miles. Then followed releases at 25, 25, 50, 50, 80, 80 and 130 miles on the same 'training-line', with the birds released singly (watched out of sight with 16 × 40 binoculars before the next was released). Critical releases were made in late August and September off the 'training-line'. The experimental releases at 25 miles or more are numbered for reference: 1948, A and B; 1949, 1–9; 1950, 10–21; 1951, 22–28; 1952, 29–36; with the prefix 'T'. They involved a total of 233 birds in 1306 sorties, for which three indices of performance are available:

Vanishing point	Bearing at which bird was lost from sight.
Orientation time	From release to vanishing.
Homing success	Time to reach home.

The interrelation and value of these indices has been discussed earlier. By far the most useful for throwing light on the orientation process has been the first, represented in radial scatter diagrams, e.g. Fig. 1. Their statistical significance can be tested by considering the mean angular deviation from the home direction, regardless of sign—since, in general, a deviation to the right is as good, or as bad, as an equal deviation to the left. The mean deviation ($\bar{x}$) could then be subjected to a 't' test to see whether it differed significantly from a random distribution, which will have a mean deviation ($\bar{x}_r$) of 90°. In practice it is more realistic to make the comparison with a regular radial scatter of approximately the same number (N_r) of observations. This will still have a mean deviation of 90° but, unlike the ideal random scatter, an error introduced by the essential discontinuity. From the resultant value of t_r* the probability (P) of the scatter under test occurring by chance can be estimated. If $P > 0{\cdot}05$ the scatter cannot be differentiated from random.

A check on the regularity of the distribution is given by a χ^2 test. If this should indicate non-randomness, whereas the 't' test indicated randomness, the conflicting result may have two causes. The distribution may be askew, and this can be tested by recalculating t_r about the algebraic mean (i.e. taking sign into account). If this fails to resolve the conflict, a second possibility is that the distribution should really be considered as being, for instance, bimodal, with concentrations about two, particularly opposite, points. The boundaries of the distributions have to be determined by inspection. These refinements are only of importance when the birds have a conflicting choice of orientation lines, as when the home direction differs markedly from that in which they have been trained. For some purposes it is more appropriate to compare the proportion of points falling within a particular sector, and here the χ^2 test is applied.

For comparing orientation times and homing successes, straightforward 't' or χ^2 tests are used as appropriate. An attempt has been made to save the general reader the boredom of constant repetition of the phrases 'this is significant' and 'this is not significant'. As far as possible the appropriate word or words of a comparison are *italicized* when tests have shown them to have statistical significance—thus, *random*, *different*, *higher*, *less*, etc.

OBSERVATIONAL EVIDENCE FOR A FORM OF SUN NAVIGATION

We may consider first the initial orientation patterns that have resulted when pigeons are released: (a) in sunny conditions, with well-broken cloud, 5/10th or less, (b) with complete cloud cover of such a thickness that the sun cannot shine through. When two lots of birds are released at the same unknown point, either

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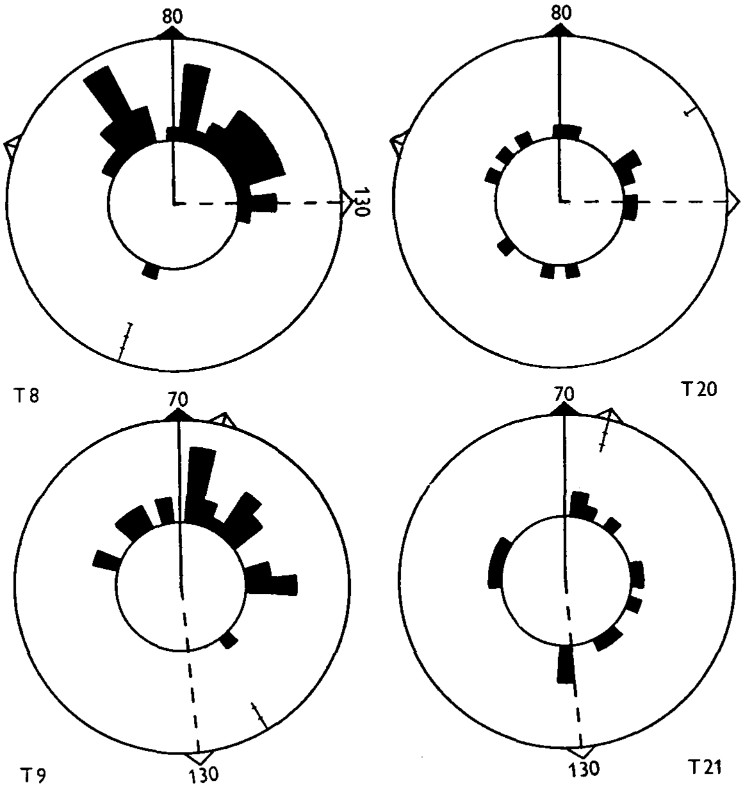
$$* \quad t_r = \frac{(\bar{x} \sim \bar{x}_r)\sqrt{\left[\dfrac{NN_r(N+N_r-2)}{N+N_r}\right]}}{\sqrt{\left[S(x^2) - \dfrac{[S(x)]^2}{N} + S(x_r{}^2) - \dfrac{[S(x_r)]^2}{N_r}\right]}}.$$

80 miles WSW. or 70 SSE. after previous training to 130 miles NNW., we have the result shown in Fig. 1.*

χ^2 tests confirm that the distribution with overcast is *random* in both cases, and *strongly* orientated in the home direction with sun. These are the conditions that would particularly call for accurate bico-ordinate navigation. With releases in the training direction, bico-ordinate navigation may still function, but if it becomes

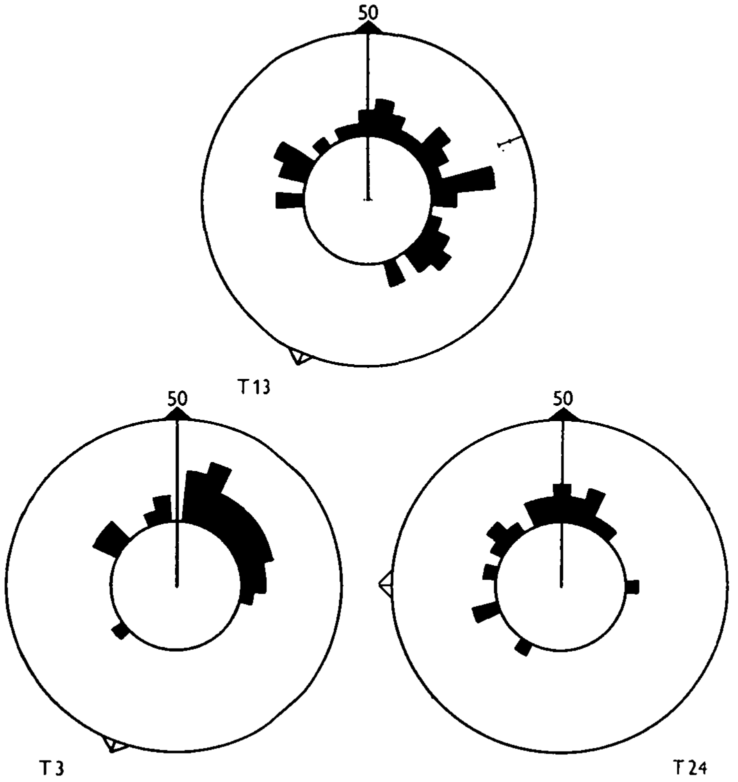


	Sun		Overcast	
	T8	T9	T20	T21
N	47	31	13	16
$\bar{x}$	45°	45°	78°	93°
σ	30°	33°	54°	59°
P	< 0·001	< 0·001	0·6	0·8

Fig. 1. Effect of cloud conditions on initial orientation at right angles (top) and in opposite direction (bottom) to training line.

* Explanation of Fig. 1 and other radial scatter diagrams. In all cases, except Fig. 4, the results shown are those of birds released at the point for the first time. The vanishing points are grouped into 10° sectors. Solid arrow—home direction and distance. Dotted arrow—training direction and distance. Shaftless arrow-head—true north. Thin, centripetal line—wind direction and Beaufort Force, indicated by cross lines. *N*, number of pigeons; $\bar{x}$, mean angular deviation regardless of sign; σ, standard deviation; *P*, probability, based on a '*t*' test, that such a scatter could have arisen by chance.

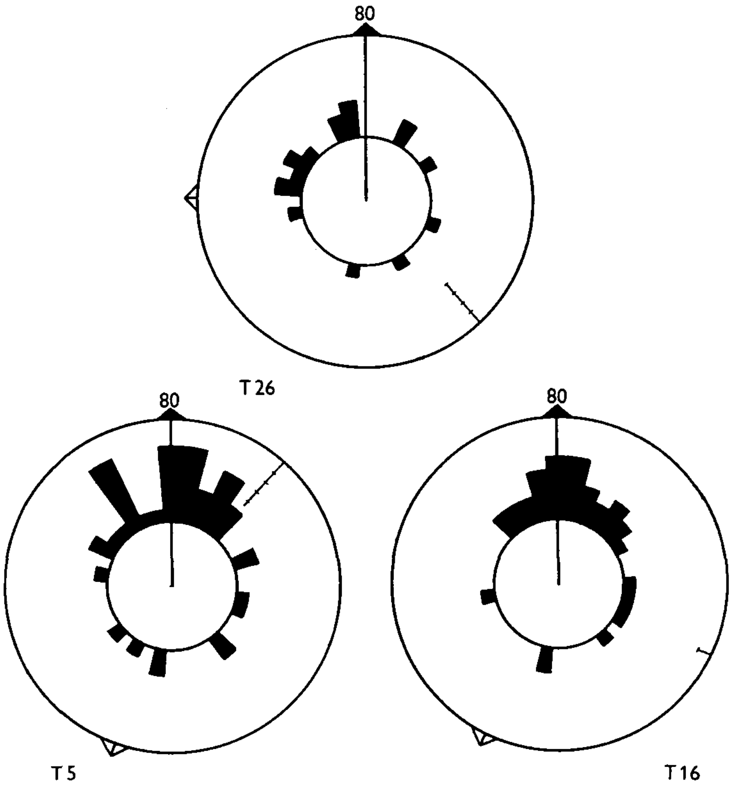
difficult it may be replaced by simpler navigation in one co-ordinate, i.e. if the overcast allowed a very rough estimate of the sun's position this would be sufficient for a homeward tendency to result merely from the birds flying in the training direction. Therefore the effect of overcast would not be expected to be so clear-cut. Nevertheless, at the early stage of 50 miles on the training line, the results in Fig. 2 were obtained. Again there is *good* orientation in sunlight, *random* scatter with overcast (as there is no conflict of directions, the right-handed bias in T13 does not discredit the verdict of the '*t*' test). At the following, 80-mile stage, where the effect of repeatedly flying in the same direction would be expected to be more marked, the same general result is obtained (Fig. 3). The overcast release was again *random*, though closer to the significance level than in the previous cases. Comparison may also be made between the two stages. Where there is overcast in the first and sun in the second (T13 *v.* T16) a *big* improvement in orientation is seen



	Sun	Overcast	Sun
N	37	42	23
$\bar{x}$	46°	78°	41°
σ	30°	45°	41°
P	< 0·001	0·3	0·004

Fig. 2. Effect of cloud conditions on initial orientation on training line at 50 miles.

($P<0{\cdot}001$). Where there is sun on both occasions (T3 *v.* T5) there is a slighter improvement. But when an overcast release follows a sunny one (T24 *v.* T26), the second is worse than the first—the effect of overcast overrides the improvement expected after greater experience and the weeding out of some unsuccessful birds. This is even better shown in cases where a second release at the same place was made with overcast. Fig. 4 illustrates this point. In both cases the primary release was made in sunny conditions. The repeat T6 showed an improvement over the previous T5, while the overcast repeat T4 was worse than the previous T3. It has been shown by laboratory experiments (Matthews, 1952*c*) that the learning of landmarks probably does not play an important part in the orientation and homing of pigeons, the present comparison confirms that this is the case, i.e. that it is much more important that the birds should have a good view of the sun, than that they should have had previous experience of the release point.



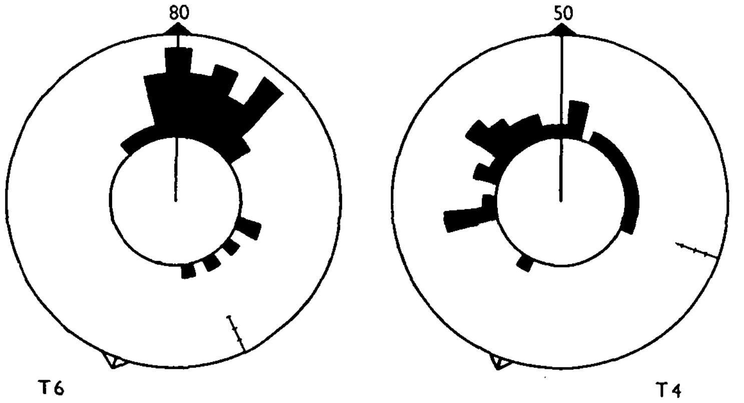
	Sun	Overcast	Sun
N	46	18	39
$\bar{x}$	47°	62°	47°
σ	48°	47°	42°
P	$<0{\cdot}001$	$0{\cdot}1$	$<0{\cdot}001$

Fig. 3. Effect of cloud conditions on initial orientation on training line at 80 miles.

The second index of performance, orientation time, is particularly liable to influence by irrelevant factors, such as birds waiting around for another bird to be released, and by visibility conditions. Nevertheless, comparing the data for sun and overcast releases we have:

Minutes	Off training line				Training line at 50 miles		
	Sun		Overcast		Sun, T3	Overcast, T13	Sun, T24
	T8	T9	T20	T21			
$\bar{x}$	3·3	4·4	7·8	7·5	5·0	4·2	3·7
σ	1·1	2·3	3·1	7·1	3·0	2·0	2·4

Minutes	Training line at 80 miles			Repeat releases	
	Sun, T5	Overcast, T26	Sun, T16	Sun, T6	Overcast, T4
$\bar{x}$	4·7	5·6	2·7	4·7	5·6
σ	1·9	2·5	1·5	2·4	3·2



(cf. T5, Fig. 3)

(cf. T3, Fig. 2)

Sun		Overcast
42	N	34
35°	$\bar{x}$	57°
40°	σ	36°
<0·001	P	0·005

Fig. 4. Effect of cloud conditions on initial orientation for second time at a point.

Thus in six out of seven cases the overcast orientation time was greater than the equivalent sun value. The exception, T3 *v.* T13, would seem to be due to an abnormally high value for the former. The birds concerned in T13 showed a marked drop in orientation time when released at the next stage, T16, in sunny conditions, whereas those in T3 showed only a slight reduction. The differences are *significant* in the two releases off the training line ($P<0·001$ and 0·04), and between T16 and T26 ($P < 0\cdot001$). If we amalgamate the remainder we have:

	Sun	Overcast
N	148	94
$\bar{x}$	4·6	5·0
σ	2·5	2·0

The difference, although small, is *significant* ($P < 0\cdot001$). We can therefore conclude that with overcast there will be considerably more lingering near the release point than in the equivalent sunny conditions. Indeed, since the former produced *random* scatters the relation between orientation time and accuracy of orientation noted before (Matthews, 1951*b*) should not apply. And this is indeed the case. Comparing the proportions falling within the 45° arc centred on the home line we have:

Orientation time (min.)	Sun		Overcast	
	N	Within 45°	N	Within 45°
Less than 3·5	146	41%	38	21%
More than 3·5	119	27%	85	19%

Under sunny conditions birds quickly lost from sight gave a *higher* ($P = 0\cdot02$) proportion of vanishing points close to the home line. With overcast there is no difference between the two categories.

The third index of performance, homing success, is the least likely to show a relation to conditions at release. These are unlikely to be maintained over the whole homeward track. Chances of a badly orientated bird reaching home are quite high at the shorter distances. Speeds of return are considerably affected by the wind force and direction, varying from one test to another, or on the day of release. Detailed examination of individual orientation and homing histories (Matthews, 1952*c*) shows that while there is a general positive relation, marked exceptions are fairly frequent. Bearing these important qualifications in mind, and considering only the proportion of birds back on the day of release and their average speeds, we have:

	Off training line				Training line at 50 miles		
	Sun		Overcast		Sun, T3	Overcast, T13	Sun, T24
	T8	T9	T20	T21			
Back on same day (%)	53	71	38	44	89	81	61
Speed (m.p.h.) $\bar{x}$	23	18	11	12	18	21	11
σ	10	8	3	2	8	7	7

	Training line at 80 miles			Repeat releases	
	Sun, T5	Overcast, T26	Sun, T16	Sun, T6	Overcast, T4
Back on same day (%)	87	22	72	98	87
Speed (m.p.h.) $\bar{x}$	20	15	22	31	17
σ	6	8	9	9	4

At the shorter distance on the training line, conditions at release do not affect homing success. In all the other cases sunny conditions gave more and faster returns on the day than did overcast. The differences are only significant for the proportion returning at the 80-mile training-line point ($P < 0.001$), and for the speed in the repeat releases ($P < 0.001$).

Kramer (1953) has also found, on a small scale, that overcast disorientates pigeons.

To summarize this observational data, we have seen that with sunny conditions good homeward orientation is obtained. With overcast the scatter from the release point is random, and more time is spent near it. The conditions at release also have a discernible effect on homing success. For pigeons, therefore, there can be no doubt that the sun plays an essential part in their navigation. When we add the very similar results obtained with gulls (Matthews, 1952*a*) and shearwaters (Matthews, 1952*b*, 1953*b*) the case for a form of sun navigation is strong indeed.

THE HYPOTHESIS

It is strange that so obvious a means of navigation, and one used by ourselves, should only have recently been considered as applicable to bird orientation. The theories of random/systematic search, of navigation by means of the earth's magnetic field and of displacement/acceleration measurement all had their beginnings around 1870. But it was not until 1945 that Ising, as an adjunct to his Coriolis theory, suggested that birds might determine longitude displacement by time differences in sunrise or sunset. He went further in recognizing that if latitude displacements were large only the noon position of the sun would be suitable for longitude estimation. But he overlooked the fact that latitude could be measured from the sun's altitude at that point. Varian (1948), Davis (1948) and Wilkinson (1949) independently suggested that this could be done, but overlooked the possibility of longitude determination from the sun. Matthews (1951*a*, *b*) put forward a hypothesis for complete sun navigation, deriving both latitude and longitude from the sun's position alone. As the essential part played by the sun has since been more clearly demonstrated, it is appropriate to re-state and re-examine this hypothesis here. The suggestion is:

(1) By observation of the sun's movement over a small part of its arc, and by extrapolation, the highest point of the arc is determined. This gives geographical south and local noon.

(2) Comparison of the remembered noon altitude at home with the observed noon altitude gives the difference in latitude.

(3) Comparison with home position in azimuth at local noon gives the difference in longitude. Alternatively, this might be appreciated as a direct time difference.

(4) All measurements and comparisons are automatic.

Fig. 5 will make these conceptions clearer. Ptolemaic terms are used for simplicity, i.e. the sun moves and not the earth. The formula is the simplest one that will give both latitude and longitude from the sun's position alone. The requirements and assumptions implicit in it may now be considered in detail.

If there were some means of determining the south reference point independently, the first item of the hypothesis could be omitted, and the sun's position as observed compared directly with its position at home *at the same instant*. But any possibilities of such an independent compass have been eliminated. A magnetic one is discredited by the experiments of Gordon (1948), Matthews (1951*b*), Yeagley (1951) and van Riper & Kalmbach (1952). In any case it would still require a correction for local declinations, which would necessitate a knowledge of the very fact required, geographical south. A gyro-compass, requiring a rapidly rotating gyroscope, is a morphological impossibility. A bearing on the Pole star would give the reference point, but to see stars in daylight would require a development of the means used by astronomers to view faint stars—observation in optical blackness through a very small opening—described by Pirenne (1948). Not only is the pigeon's eye structurally unsuited for this, but such a method would make the localization of one star—usually by reference to constellation patterns—almost impossible. It is relevant to note that for conditions in which the magnetic compass is unreliable, near the Poles, a semi-automatic *sun*-compass has been developed for aircraft navigation (Wright, 1950). Kramer (1953) attempted to confuse pigeons by releasing them at the exact instant when the sun at the release point

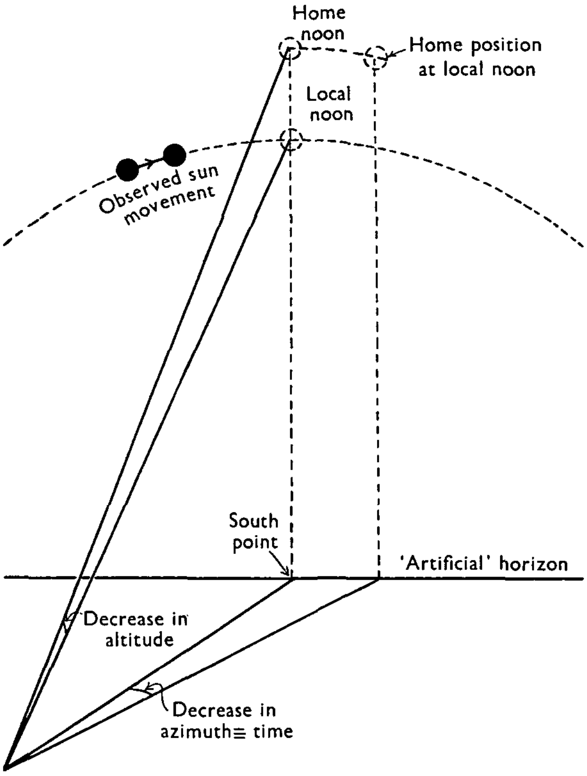


Fig. 5. Diagram illustrating the hypothesis of sun navigation. Release to north and west of home. (Not to scale.)

was at the same height as it was at home. No confusion resulted, as would be expected on the present hypothesis. The avian eye appears well adapted to movement detection, in which the pecten may play an important part (Menner, 1938; Crozier & Wolf, 1943; Griffin, 1952). When we ourselves have some fixed point to observe close to the sun, the latter's movement becomes very obvious, and the blind spots produced by the pecten may function in an analogous way.

Good orientation has been obtained when the horizon was hilly or indistinct through haze. It is therefore necessary to postulate that birds have the equivalent of the bubble sextants (Bennett, 1941) or artificial horizons that enable airmen to measure altitude without reference to the visible horizon. Certainly the band-like *area*, with pigmented borders, found in many birds, though not in pigeons, looks through an ophthalmoscope (Wood, 1917) temptingly like the base-line of an aircraft's artificial horizon. Griffin (1952) has suggested the pecten for this role. Certainly there is good reason to think that the bird's head has the necessary stability in flight to serve as an 'instrument-bed'. Dr R. J. H. Brown has taken a long series of electronic flash cine-photographs of pigeons in fast flight (Brown, 1953), and very kindly permitted me to examine his original prints. The pigeons flew at speeds of from 13 to 26 m.p.h. down a corridor past a squared backcloth. Within the limits of measurement (scale approx. $\frac{1}{10}$th) there is no trace of an up/down movement of the eye's centre in relation to the wing beat cycle. Any changes in the vertical plane were steadily up *or* down, and were very small. For twelve sequences the ratio of horizontal movement to vertical movement averaged 107 : 1 (S.E. 27). The best case was that of a bird flying at 16 m.p.h. through a complete beat cycle (up/down/up) and covering approximately 99 cm. forward with the eye centre moving down less than 0·3 cm.—a ratio of 330 : 1. If such steadiness is achieved at a relatively low speed, in enclosed surroundings, it is not improbable that even better results would be achieved in normal conditions.

The sun's arc rises and falls across the sky with the changing seasons, reaching a maximum altitude on 22 June and a minimum on 22 December—the two solstices. At these dates the daily rate of change in altitude is very small, about 10″ of arc, but it increases to a maximum of about 1400″ of arc at the two equinoxes, 21 March and 23 September. Even if the maximum rate of change (equivalent to 27 miles of latitude) was not allowed for by the bird, no gross error would be introduced in the conditions under which the previous experiments have been made—birds allowed full view of sun and sky on the day before release, taken overnight to points 50–130 miles away and kept covered until release. Nevertheless, this seasonal factor allows an experimental opening which has been exploited (p. 257).

The existence of some form of accurate time mechanism is an essential part of the full hypothesis, though in theory latitude could be obtained without such a chronometer, from the altitude of the highest point of the sun's arc. Until accurate chronometers were available the only method of measuring longitude open to sailors was to start a less accurate clock at local noon (determined by the highest point) and note the time at which some forecast heavenly event occurred. An almanac would give the time after local noon at which the event would occur at, say, Greenwich, and the difference in times would give a rough idea of longitude. This still requires some form of clock, and cannot be used by pigeons, since it is beyond fantasy to provide them with an almanac, and the only suitable events during the day would be the infrequent eclipses of the sun, and the extremely rare transits of Mercury and Venus.

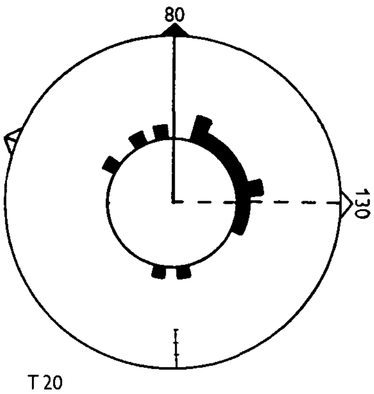
The evidence for some form of general time-keeping mechanism is widespread in animals, as for instance in diurnal rhythms. A more particular time sense has been demonstrated in insects (Beling, 1935, for summary) and in passerine birds (Stein, 1951), in which the animals could be trained to come to food at a particular hour of the day. Stein claims that this time sense was not disturbed by being kept in constant light, by a varying length of fasting before feeding, or by the injection of metabolic drugs. His evidence, particularly of the last two points, is not wholly convincing, and certainly does not permit a decision on whether such a clock would have the necessary accuracy for navigation purposes. The field is clearly wide open for more detailed research. Starlings and pigeons (Kramer 1950; Kramer & Riese, 1952) trained in a particular direction in a laboratory situation can take up the direction with reference to the sun's position in azimuth regardless of the time of day. This confirms work with pigeons in the field by Matthews (1951*b*). So in the present state of evidence, the existence of some form of chronometer is very likely, though almost nothing is known as to its physical basis or its limits of accuracy.

The present hypothesis differs from other 'super' sensitivity theories in two important ways. First, if the displacement is large and swift, say of the order of 500 miles, one could be confident of obtaining a rough fix oneself by the method proposed, without instruments, particularly in latitude. Secondly, when we come down to the order of displacement imposed on the birds, 50–130 miles, the differences to be measured lie within the estimated powers of the organ concerned—the avian eye. Pumphrey (1948) estimates, on the basis of retinal structure, that the limit of resolution would be about 10″ of arc, three times better than the human eye. And the evidence with the latter suggests that the actual maximal acuity is indeed about that forecast on retinal structure. Even with the indirect method of training experiments, Grundlach (1933) found pigeons were resolving down to 23″ of arc at least. We will not be far wrong therefore to accept the structural estimate of a bird's acuity as the threshold. The angular changes it is necessary for the bird to discriminate may be compared with this threshold. Kramer (1953) claims that his birds are orientated within 40 sec. of viewing the sun. This may well be an underestimate, but even so in that short period the sun has moved through an angle 60 times the threshold value. Displacement of 50 miles in latitude results in a change in altitude 260 times the threshold; 50 miles in longitude (at 52° N.) results in a change of azimuth 420 times the threshold. So it is quite possible that the eye could detect the smallest angular changes required of it. We can add that, owing to a lesser contrast between peripheral and foveal vision in birds than in humans, the bird does not have to look directly at an object to follow its movement. Also it suffers no inconvenience from glare. Fifty miles in longitude (at 52° N.) represents a time change of under 5 min., which indicates the limits of accuracy required in the chronometer. We can say nothing positively about this being a likely limit. The human subject is again likely to have a poorer development of a time sense, yet MacLeod & Roff (1936) found that two human subjects kept in a sound-proof room for 86 and 48 hr. could estimate the passage of time so well that their cumulative errors were 0·8 and 0·9%. For a period of 18 hr., which is about the most that pigeons have been kept shut away from the light in the previous experiments, this would represent an error of 8½ min.!

Though the angular differences and probably the time differences required would seem to lie within the limits of the bird's sensory equipment, an objection is that the bird is not required to compare the position of two observed suns. It must compare the position of the observed sun with that of a 'visualized' sun. This would certainly require a very remarkable spatio-temporal memory, for which we have little definite evidence one way or the other. Certainly pigeons have enduring memories for landscape features, *once* these are learnt (Matthews, 1952*c*; Skinner, 1950). Yet the recognition of one skyline from another depends ultimately on a comparison of all the minute angular differences that distinguish them. So perhaps it is only the unfamiliarity of the conception that makes it difficult to credit the memory and 'visualization' of one striking and familiar feature, the sun arc at home.

The interpretation of differences between observed and remembered sun positions would have to be credited, like the measurement itself, to an automatic innate mechanism. The tests have shown, for example, that a previous experience of longitude displacement is not necessary for accurate navigation from the west. Further (Matthews, 1951*b*), increased experience does not bring much improvement in orientation, but only in the speed and success of actual homing. It has since been shown (Matthews, 1953*a*) that completely inexperienced young pigeons give good homeward orientation from a distant point.

It is not considered necessary to extend the possibility of sun-navigation by postulating a sensitivity to the polarization pattern of the sky, especially as Montgomery & Heinemann (1952) have been unable to demonstrate such a sensitivity in pigeons by training experiments. With pigeons the only benefit would be in cloudy conditions. Fig. 6 shows that with 8/10th cloud orientation is worse than in sunny conditions, suggesting that the cloud is a considerable hindrance. However, glimpses of the sun would be obtained fairly frequently, and it is possible that the main effect of clouds is an indirect one in these cases—the cloud movement confusing measurement of the sun's movement. Pigeons rarely fly in twilight, none homed after



T20
(cf. T8 and T20, Fig. 1)
8/10th cloud
N 17
$\bar{x}$ 70°
σ 48°
P 0·06

Fig. 6. Effect of cloud conditions on initial orientation at right angles to training line.

sundown in the present series, and less than 1 % even as late as the hour before. And it is most unlikely that localization of the sun position by this indirect method would be sufficiently accurate for bico-ordinate navigation. At best the bird would get a compass reference for navigation in one co-ordinate (which might be of benefit to night migrants orientating themselves after sundown). This limitation is found in man's own use of the polarization pattern in the Pfund Sky Compass, developed for use in the long polar twilight (Moody, 1950).

We may conclude that although the hypothesis put forward may strain our credulity, it cannot be dismissed out of hand on theoretical grounds. The next step is therefore to examine the accumulated evidence and carry out experiments to see if there is practical support for the proposals.

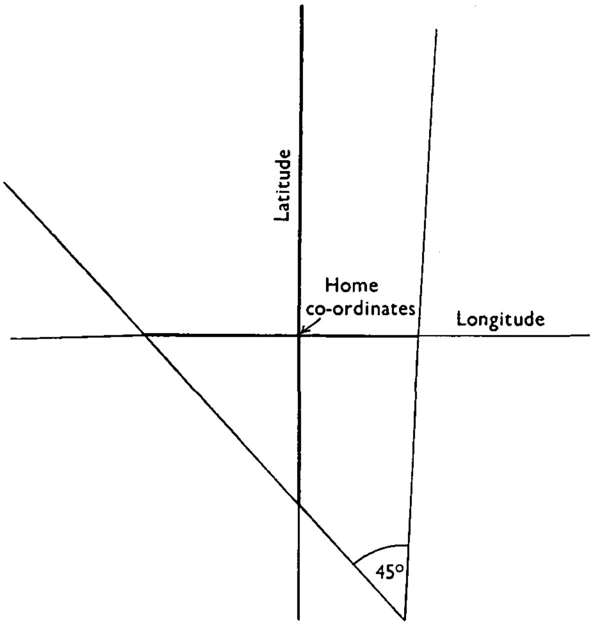


Fig. 7. Diagram illustrating the relative importance of small errors in longitude for a release north or south.

THE ACCURACY OF ORIENTATION VERSUS TIME OF DAY

Consideration of Fig. 5 will show that large errors both in altitude and azimuth would be particularly likely in the early morning (or evening) when the amount of extrapolation is greatest. Conversely, such gross errors are least likely around noon, but here, along the top of the arc, the small errors are more likely to be in azimuth than in altitude. The resultant small errors in longitude are more likely to appear as deviations in the initial orientation when birds are released north or south of the loft. This apparent paradox is resolved by Fig. 7, which shows that in such cases a much smaller margin of error in longitude determination than in latitude determination is permissible if the vanishing point is to fall within the arc of 45° about the home line. The release point is shown as 20° off true north or south, as this was approximately true of all the cases to be considered. It will also be clear that for releases to the west, small errors in longitude determination will have little effect on the observed orientation.

Combining all north and south releases made in sunny conditions, for the first time at the particular release point and with no attempted interference with sun-navigation, we have 231 observations that may be grouped into two-hourly periods:

	G.M.T. plus/minus 1 hr.			
	06.00	08.00	10.00	12.00
Total	34	75	67	55
Gross errors (>90°) (%)	21	13	12	9
Within homeward arc of 45° (%)	44	40	40	22

Both the predictions made on the basis of the hypothesis are fulfilled, the drop in highly accurate (longitude) orientation around noon is *significant* ($P < 0\cdot 03$). Fewer western releases are available for the same conditions, totalling seventy-six observations:

	G.M.T. plus/minus 1 hr.			
	06.00–08.00	10.00	12.00	14.00
Total	29	21	26	17
Gross errors (>90°) (%)	21	14	4	12
Within homeward arc of 45° (%)	38	19	23	24

Again there is a fall in gross errors towards noon, but no drop in highly accurate (latitude) orientation occurs there. While it would be interesting to carry out hundreds of further sorties to check that, with sufficient numbers, the gross error trend would be *significant*, limited research facilities are best employed in direct experimental approach.

THE TIME AVAILABLE FOR OBSERVATION

As the reference point must be determined from the sun, the sun must be observed in movement for a short period. The minimum period necessary is unlikely to be demonstrated in the field, as a bird could always take just so much longer in orientation, and small differences in 'orientation time' will be swamped by other irrelevant factors discussed earlier. But it would be reasonable to expect that birds that had a long time to observe the sun would be better orientated than those released immediately on emergence from covering. Kramer (1953) has carried out such an experiment and permitted me a pre-view of his manuscript. Half the birds were kept for 1 and 2 days exposed on the top of a tower, the others within the tower and unable to see sky or sun. On release (in groups), the second lot being allowed half a minute's prior exposure, Kramer claimed that there was no difference in the accuracy of orientation. But the issue was confused by the inclusion of groups of birds that had already flown from that point the previous year, in sunny conditions on both occasions. We have seen (p. 247) that improvement would be likely to occur in such cases. If we consider only birds released at that point for the first time we can extract the following data for angular deviations from Kramer's diagrams:

	Long exposure	Short exposure
N	5	10
$\bar{x}$	26°	46°
σ	12°	24°

The small number of points available (45 birds were used, but released in groups of 3) makes the application of statistics difficult. The value of '*t*' between the two groups has a $P=0\cdot1$ only, but the difference is so striking, with deviation and scatter twice as great in the short exposure group, that this cannot be cited as evidence against the hypothesis, and can indeed be accepted as tentative evidence for it.

EXPERIMENTAL USE OF THE SEASONAL CHANGE IN ALTITUDE

Under usual conditions of experiment (p. 252) this will have little effect. But *if* pigeons were unable to make a correction for the daily change at an equinox, and were kept out of sight of the sun for several days, the effect on their orientation would be drastic *if* they were indeed measuring latitude by comparing the sun's altitude with that when last seen at home. It is quite likely that pigeons would not be able to make such a correction for it would have little selection value for them. They do not have migrations and a short breeding season governed by day-length, and hence by sun-height. Under normal racing conditions they are not shut off from the sun for long, and the races involving the longest transport take place near the summar solstice. Nor is there much chance of young birds learning that occlusion of the sun for several days is accompanied by a sharp change in altitude. During the summer months April–September inclusive the percentage of completely sunless days at Cambridge was 4, 10, 11 and 4 in the years 1949–52. Sequences of two sunless days occurred once in 1951, of three once in 1949 and twice in 1950.

A test involving such conditions was carried out in 1951, and as insufficient birds were available for statistical purposes, was repeated in 1952.

Between the third week in July and the second week in September the pigeons were trained in the usual fashion up to 80 miles due west of the loft at Madingley. The experimental release was made on 20 September in both years, at the same point, 78 miles S.S.E. Prior to this the birds had been confined to their usual quarters in the loft, for 6 days in 1951 and for 9 in 1952. Blinds prevented the experimental birds from having any view of the sun or sky during this period, and only indirect light reached them. This was sufficient to make the birds aware of dawn and dusk, and was augmented by artificial light from $2\frac{3}{4}$ hr. after sunrise until $2\frac{3}{4}$ hr. before sunset, so that they could feed and exercise freely. Food was provided regularly, 15 min. after lights on and 15 min. before lights off. Other pigeons with free access to the sky were kept in the next compartment, separated only by a thick sacking partition, so that their waking/sleeping movements and other activities could be heard by the experimentals. By these methods it was hoped to prevent any desynchronization of such time-keeping mechanisms as the experimental birds might possess. The control birds were in a similar compartment, fed at the same times, but allowed full view of the sun and sky.

The birds were loaded into a screened van after dark on 19 September and taken through the night to the release point, and kept screened until release. By taking the birds south, an increase in the sun's altitude resulted, partially offsetting the seasonal fall during the incarceration:

	1951	1952
Seasonal fall	2° 19′	3° 28′
Positional rise	1° 04′	1° 04′
Net fall	1° 15′	2° 24′

The longer incarceration in 1952, resulting in a more emphatic net fall, was adopted since no extraneous ill-effects had been noted with the shorter period. With no correction for seasonal fall, a false position of home would be obtained by comparing the position in altitude of the sun when last seen with that on the day of release. The false position would have been correct if the sun had 'stood still' and may be termed the 'solstice' home position. In relation to the release point real and false home positions were:

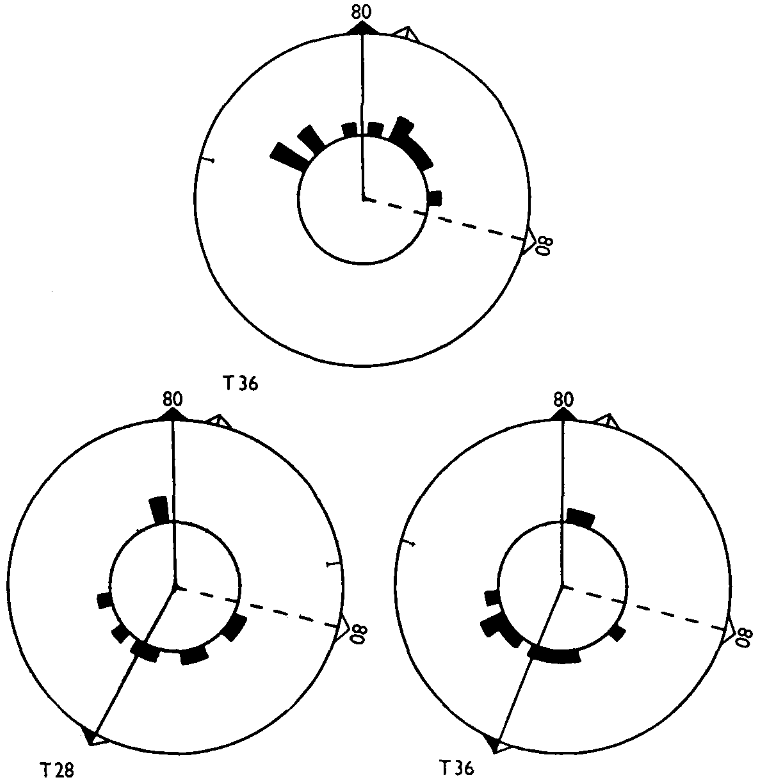
	Latitude (miles)	Longitude (miles)	Bearing
Actual home position	74 N.	21 W.	345°
Solistice home position	86 S.	21 W.	194° in 1951
	166 S.	21 W.	187° in 1952

Only experimental birds were used in 1951, in 1952 experimentals alternated with controls throughout the period of releases. The 1951 releases were with 4/10th stratocumulus, the sun in open sky, those in 1952 with a practically cloudless sky (< 1/10th). The initial orientations are shown in Fig. 8. They may also be compared with earlier releases made at this point with sun, T9, and with overcast, T21, shown in Fig. 1.

The two experimental results are *identical* ($P > 0{\cdot}9$) and each *differs* from the controls, with values of $P < 0{\cdot}001$. There is thus no doubt that experimental technique has resulted in a radically different orientation. But the values of t_r would not indicate that the scatters are *different* from random. If we seek to confirm this by a χ^2 test, comparing the expected and actual numbers falling into quadrats, we find that $\chi^2 = 15{\cdot}0$ which has a $P < 0{\cdot}002$. So by this test the scatter for the experimentals (the two tests combined since there is no doubt that they are from the same population) is strongly *non-random*. This contradiction is not due to any skewness about the home direction, since t_r about the algebraic mean still gives a *random* value. Therefore the alternative, suggested by inspection, that the scatter is not about one point but about two, is statistically acceptable. If we therefore exclude the four birds lost in a radically different direction from the others and consider orientation about the solstice home direction, we have:

N	$\bar{x}$	σ	P
18	36°	26°	< 0·001

These birds were thus very strongly orientated in the false direction, and this is only explicable on the basis of altitude estimation by comparison, without correction for seasonal change. The four (18 %) birds separated from the others appear to have made just as good a start in the true home direction, though the numbers do not allow statistical justification. It would therefore appear that in this stock of pigeons a few are able to make correction for the seasonal changes in sun altitude,



	Experimental	Control	Experimental
N	10	13	12
$\bar{x}$	114°	45°	120°
σ	58°	22°	55°
P	0·4	0·03	0·2

Fig. 8. Effect of prior occlusion of sun and sky on initial orientation off training line. N.B. Half-blocked arrow indicates solstice home direction.

despite the lack of selective value discussed earlier. It is of interest to note that two of these birds were the outstanding birds of their year, having given fast, consistent returns from all previous releases.

The orientation times of the experimentals were slightly higher than for the controls:

	N	$\bar{x}$	σ
Experimental T28	10	5·4	3·6
Control T36	13	3·8	2·3
Experimental T36	12	4·6	2·5

which would be expected as the former were having their first view of the outside world for some time. They were, however, rather lower than in the case of birds released at this point with overcast (T21, $\bar{x}=7{\cdot}5$, $\sigma=7{\cdot}1$), again suggesting that the experimental birds were not dis-orientated, but re-orientated.

It will have been clear from the first section of this paper that the main instrument in the study of pigeon navigation must be the investigation of the initial orientation. So many other factors govern the rapidity and completeness of homing. This is particularly so in the present case, as geographical limitations mean that birds departing in the solstice direction will soon reach the coast and be turned back. There will then be a good chance of such birds finding their way home by prolonged search. Bearing this in mind, we have:

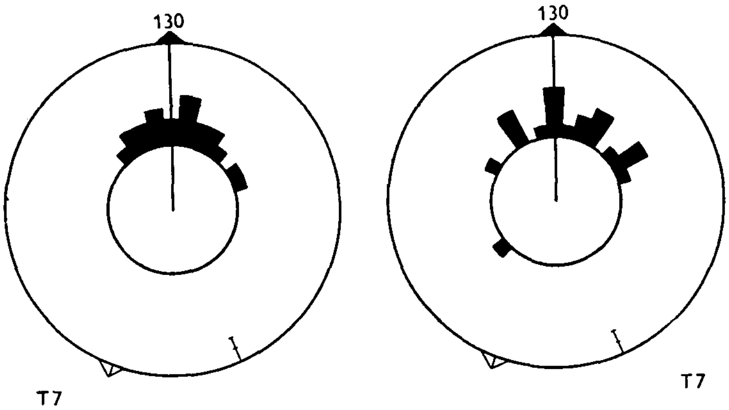
Initial direction	Returned				Lost
	1st day	2nd day	3rd day	Later	
True home ($N=17$)	4	3	2	4	4
Solstice ($N=18$)	0	7	1	6	4

There are thus indications that the re-orientated birds were at a disadvantage over rapid homing, but had not lost the desire to home. The part of the hypothesis dealing with latitude determination can be said to have received very strong support from these experiments. Indeed there seems no other interpretation possible.

EXPERIMENTAL INVESTIGATION OF THE CHRONOMETER FACTOR

There are no convenient seasonal factors in longitude determination from the sun. Thus the sun is always due south at local noon. So any investigation into this part of the hypothesis will have to be aimed at disturbing the working of the inner chronometer, about whose nature we can only guess. Such experiments, at least at first, will have to be of a rather crude nature.

Just as it is probable that over-training in one direction will blunt the ability to navigate in two co-ordinates (Kramer & St Paul, 1951; Matthews, 1951*b*; van Riper & Kalmbach, 1952), it is possible that release at only one time of day might produce an inflexibility in longitude determination. It has been clearly shown (Matthews, 1951*b*, 1952*c*) that there is no question of pigeons using the extremely limited form of orientation given by flying at a fixed angle to the sun, and that changes in the normal time of release can be taken into account. But the birds subjected to such changes did give rather poorer orientations than did the controls, as will be seen from Fig. 9. The birds in this test had been trained up to 80 miles NNW., each individual being released at the same time of day (± *c.* 12 min.) on the last six occasions. They were then released at 130 miles on the same line, the experimentals 6 hr. earlier or later than normal, the controls at the normal time. The difference is noticeable but only has a significance of $P=0\cdot1$. The effect is most marked in the sector close to the home line, in which (see p. 255) small errors in *longitude* determination would have the most effect. Thus the proportions falling within the 45° arc centred on the home line were 62 and 33 %, $P=0\cdot07$.



Control		Experimental
21	N	21
23°	$\bar{x}$	35°
18°	σ	31°
$<0\cdot001$	P	$<0\cdot001$

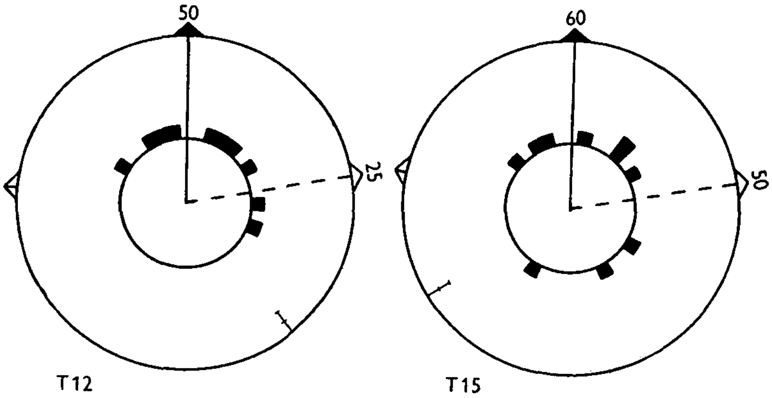
Fig. 9. Effect of radical change in accustomed release time on orientation on training line.

By the same token it would be expected that birds with the most training at a particular time would be the most affected by radical time changes. Fig. 10 illustrates such tests, the birds being released to the west after training to the north at fixed individual times. Those in T 12 had only two such releases, both at 25 miles, those in T 15 had an additional two, at 50 miles. Test releases were 5–7 hr. later than usual at distances of, respectively, 50 and 60 miles. Again the difference is suggestive but not of sufficient significance ($P=0\cdot3$), but is most noticeable in the gross errors, which in a western release are more likely to be affected by longitude determination.

These experiments at least suggested that a time mechanism was concerned in longitude determination, so the next step was to attempt to throw such a mechanism out of order. Whatever the ultimate basis of a biological chronometer (? neural) it seemed probable that it would have to be synchronized in some way. Such work as has been done with birds and insects (cited above) concluded that the 'time sense' had a 24 hr. basis, i.e. animals could be trained to feed once every 24 hr., but not once every 36 hr. Hence likely synchronizing agents are the day/night rhythms of light and darkness and of temperature. Where feeding is very regular this might also be concerned, though this is less 'natural', as foraging in the wild state is spread over many hours.

Birds that had had rather more training to the north than desirable (up to 200 miles) were therefore released to the west after the following treatment:

They were taken from the lofts after dark on 9 September 1952 to the laboratory in a covered van. Half were installed in cages on the roof as controls, being fed regularly at 09.00 and 17.00 G.M.T., having a wide view of the sun and sky to the south and west, and open to temperature changes. The experimental birds were housed in similar cages (allowing *c.* 4½ cu.ft. per bird) in a light-proof room. They were subjected to periods of light and darkness of very unequal length, fed irregularly (total amount of food the same as for controls), and with the temperature fluctuating but little, maxima corresponding to the artificial 'days'. This treatment is shown graphically in Fig. 11, where it is compared with the regularity of the control conditions. The experimental room was not sound-proof, but external sounds were partially muffled and further swamped by the noise of the continuously running electric fan for ventilation. Outside activity was at a minimum during the vacation, and a weekend, with an absence of normal routine, occurred in the middle of the experiment.



Little training		More training
10	*N*	10
47°	$\bar{x}$	67°
31°	σ	51°
0·05	*P*	0·4

Fig. 10. Effect of radical change in accustomed release time in orientation off training line.

The treatment was continued for 6 days, until the night of the 15th, when the birds were loaded on to the screened van after dark and taken to the release point. On arrival the experimental birds were again illuminated, but the controls kept in the dark until after sunrise. when they were also exposed to the internal lighting of the van. Neither could obtain any view of the outside conditions until the moment of release. The orientations achieved by the two sets of birds, released singly and with controls and experimentals alternating, are shown in Fig. 12.

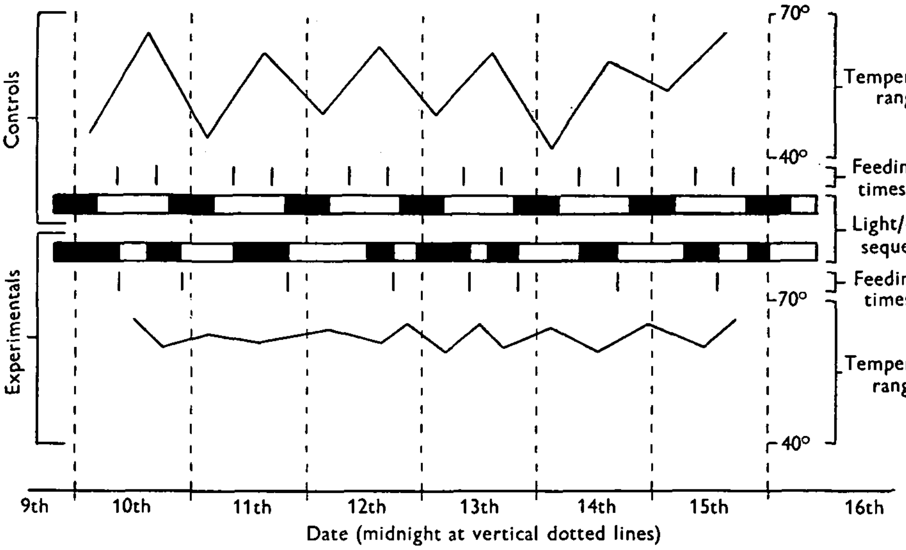
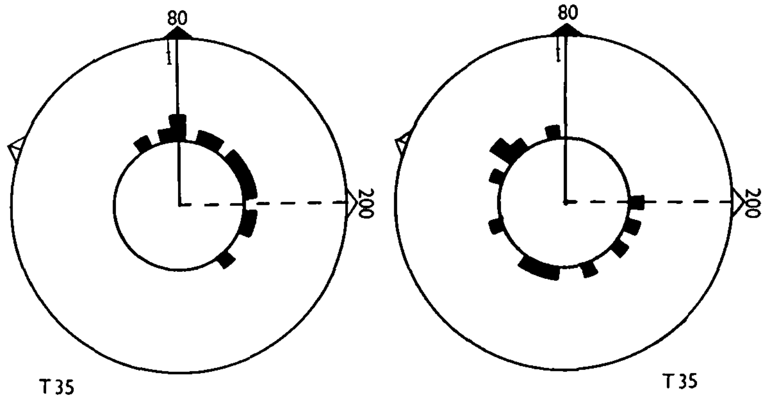


Fig. 11. Diagram of treatment employed in an attempt to desynchronize the chronometers of pigeons.



Control		Experimental
13	N	13
54°	$\bar{x}$	100°
44°	σ	53°
0·09	P	0·6

Fig. 12. Effect of desynchronizing treatment on initial orientation off training line.

Two *different* scatters resulted ($P=0{\cdot}02$). The t_r test does not differentiate the control scatter from a random one, but a χ^2 test shows it to be strongly *non-random* ($P=0{\cdot}004$). Inspection suggests that this conflict is due to the skewness of the distribution, and this is confirmed by recalculating t_r about the algebraic mean, when a value corresponding to $P = 0{\cdot}006$ is obtained. The birds were thus showing a conflict between home and training directions, due to the greater amount of training in the latter. The scatter of the experimental birds is *random* both by the t test and by a χ^2 test ($P = 0{\cdot}2$).

The orientation times were:

	N	$\bar{x}$	σ
Controls	13	3·2	1·1
Experimentals	13	4·0	2·2

As in the altitude comparison experiments the experimental figure is slightly higher, and probably for the same reason. Again we have other releases from the same point, in sunny conditions (T8) and with overcast (T20)—Fig. 1. The latter also gave a scatter which cannot be differentiated from random, but the orientation time ($\bar{x} = 7{\cdot}8$ $\sigma = 3{\cdot}1$) was *higher* ($P = 0{\cdot}003$) than that for the present experimentals. This suggests that the latter were not completely 'lost', but were in fact re-orientated, the individual directions being different because the irregular desynchronizing treatment had affected the individual chronometers to different degrees. The next step will obviously be to introduce a systematic change in the light/dark rhythm, such as bringing the day forward an hour, artificially. This will be done in the coming season.

As with the altitude experiments, the experimental treatment was apparently inimical to swift returns, the difference being rather more marked:

	Returned				Lost
	1st day	2nd day	3rd day	Later	
Controls	3	5	0	2	3
Experimentals	0	3	2	5	3

This might be due to a more lasting disorganization of the navigation mechanism, also to the fact that birds on a wrong course would have much farther to go from this release point before reaching a sea barrier. The fact that the final returns are the same, again shows that the experimental treatment had not extinguished the desire to home.

It will have been noticed that there is no southwards tendency amongst the experimental birds, as might be expected, due to the sun's seasonal drop, reinforced in this case by previous training. This suggests that latitude determination is intimately bound up with the functioning of the chronometer mechanism, and disruption of the latter will throw out the former as well. In other words, the processes (2) and (3) suggested in the hypothesis proceed as one.

We may conclude that the part of the hypothesis dealing with longitude determination has received strong support from the experimental evidence thus far. But more evidence is necessary before a state of certainty is obtained.

CONCLUSIONS

We have seen that pigeons are capable of bico-ordinate navigation only when the sun is available. With complete cloud cover their orientation breaks down, and this has been demonstrated in a number of different situations. The conclusion that the sun is an essential factor in bico-ordinate navigation is inescapable.

When the simplest hypothesis for sun navigation previously suggested is examined in detail, no over-riding theoretical objections to its validity can be raised. It is therefore acceptable as a working basis for further investigation.

The variation of large and small errors with the time of day lends support to the hypothesis, as does the variation of error with the time available for observation.

The sun-occlusion experiments strongly support the suggestion that latitude determination is based on the observation of differences in sun altitude.

The experiments aimed at upsetting the internal chronometer have produced results supporting the suggestion that longitude determination is based on time differences.

If it is possible in the coming season to obtain a definite re-orientation after treatment aimed at producing systematic error in the internal chronometer, the broad outlines will have been definitely established. It is doubtful if the field technique will be sufficiently sensitive to investigate the details of the hypothesis. So far pigeons have proved unco-operative in a simple apparatus of the type used by Kramer, when they are required to indicate the home direction. It would be nearly impossible to reinforce by training since the bird would have to be taken to a different distant point for each test, otherwise it would simply tend to learn a compass direction. One possible, though expensive, solution might be the use of a planetarium in which the complete movement of the sun could be reproduced. The pigeons could then be trained to proceed in different directions to food, corresponding to the changes produced in the 'sun's' co-ordinates. If the apparatus were large enough to allow the birds to fly, the results might be more reliable, for it is always possible that a complicated behaviour pattern, such as sun-navigation, will only be triggered off in the appropriate situation, in the air.

It will be more than doubly conclusive if the more detailed analysis of sun-navigation can be repeated in another species. The excellent Manx shearwater holds out the most possibilities in this direction, though many features of its life may make it more difficult to confuse this bird by experimental treatment.

Lastly, the whole fascinating problem of the accuracy and physical basis of the 'time sense' has barely been touched, and calls for much more detailed research in its own right, as well as in connexion with this particular problem.

SUMMARY

1. The accumulated data of a long series of homing experiments carried out with young pigeons is examined in statistical detail.

2. Bico-ordinate navigation can only be demonstrated in sunny conditions, and with overcast skies the birds scatter at random. This holds for a number of different experimental situations.

3. The hypothesis that pigeons use a form of sun-navigation, deriving latitude and longitude from the sun position alone is re-examined in detail. None of the requirements are outside the theoretical range of the organ concerned, or beyond the bounds of possibility.

4. Examination of the errors made under sunny conditions shows that their nature and variation are as expected on the basis of the hypothesis. So also is the variation in error with the length of time of observation.

5. By excluding sun and sky for a number of days before release a re-orientation away from home was obtained. This could only be explained if the birds were failing to correct for the seasonal variation in the sun's altitude, *and* deriving their latitude from altitude measurements.

6. Radical changes in accustomed release times produced some increase in longitude errors.

7. After treatment aimed at desynchronizing any internal chronometer a disorientation was obtained in the field. It is therefore very probable that longitude determination is on a time basis, as proposed in the hypothesis.

8. Future lines of research in this problem are indicated.

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